
FROM DESCRIBING THE PATTERNS TO
UNDERSTANDING THE PROCESSES -
ADVANCING ECOSYSTEM STUDIES WITH
REMOTE SENSING

HABILITATION THESIS

M U N I
S C I

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“For behind all seen things lies something vaster; everything is but a path, a portal, or a window opening on something other than itself.”

“But you want to remember that below the sea of clouds lies eternity.”

— Antoine de Saint-Exupéry

Acknowledgements

I would like to dedicate this work to my beloved parents that introduced me to the magical world of nature and exciting adventure of science. I hope I passed on some of that excitement to my wonderful children, and to my students. I would like to thank all my colleagues for their enthusiasm, help, great brainstorming and fun that helped me to stay focused and organize my thoughts. I would never make it without them. Especially, I would like to express sincere gratitude to my mentors that guided me on my scientific journey over the years, Petr Pyšek and Karel Prach.

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COMMENTARY TO HABILITATION THESIS

I hereby present my research in the field of ecology, specifically the use of remote sensing to characterize and understand ecosystem state and functioning. As a plant ecologist, throughout my career, I have focused on the application of remote sensing, GIS and modelling in plant ecology and landscape studies. I analyze and interpret remote sensing (RS) data (including satellite, airborne and from unoccupied aerial systems) not only to monitor vegetation state and spatio-temporal changes at both community and landscape levels but also to understand the underlying processes. In my work, I explore human disturbances, plant-environment and plant-human interactions, current and historical disturbances, ecosystem functioning, and ecosystem threats such as invasive species and climate change at both local and regional scales.

The main aims of presented research can be summarized as follows:

- Define concepts and a framework for using a RS approach to study ecosystem complexity and variability across spatial and temporal scales.
- Discuss both the advantages and pitfalls of RS technology in contributing to ecosystem studies.
- Introduce various approaches to mapping and monitoring biodiversity patterns across space and time using RS, either directly, or indirectly via mapping habitats, functional diversity, or spectral diversity.
- Provide examples of how RS can enhance our understanding of ecological processes at local to regional scales, serving as a basis for management and nature conservation in a rapidly changing world.

In presented research, I touch various topics, including plant invasions, ecosystem services and role of human disturbances and climate change on high mountain ecosystems and forest ecosystem health. I hope my research adds bits and pieces to the puzzle of how to conserve the beauty of nature for future generations.

Below are selected peer-reviewed papers included in the Thesis. These are seven original research articles (Paper 6, 8-13), three reviews (Papers 1, 2, 4), one opinion paper (Paper 5), and two book chapters (Paper 3, 7). I served as the first and/or corresponding author on eight of those (Paper 1 – 4, 6 – 7, 9 and 13), with the majority published in Q1 journals. See my contribution to each paper in below. The papers are attached as correspondingly numbered Appendices and are marked in the main text.

[1] Müllerová, J., Gago, X., Bučas, M., Company, J., Estrany, J., Fortesa, J., Manfreda, S., Michez, A., Mokroš, M., Paulus, G., Tiškus, E., Tsiafouli, M., Kent, R. (2021). Characterizing vegetation complexity with unmanned aerial systems (UAS) – A framework and synthesis. *Ecological Indicators* 131, 108156. <https://doi.org/10.1016/j.ecolind.2021.108156>

(JIF 2024: 7.4, ENVIRONMENTAL SCIENCES - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
0	90	50	70

[2] Müllerová, J., Brundu, G., Große-Stoltenberg, A., Kattenborn T., Richardson, D.M. (2023a). Pattern to process, research to practice: Remote sensing of plant invasions. *Biological Invasions* 25, 3651–3676. <https://doi.org/10.1007/s10530-023-03150-z>

(JIF 2024 - 2.6, ECOLOGY - Q2)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
0	80	60	60

[3] Müllerová, J., Bartaloš, T., Gago, X., Kent, R., Michez, A., Mücher, S., Paulus, G., Mokroš, M. (2023b). Vegetation mapping and monitoring by unmanned aerial systems (UAS)—current state and perspectives. In Manfreda & Ben Dor, *Unmanned Aerial Systems for Monitoring Soil, Vegetation, and Riverine Environments*, p. 93-124, Elsevier. ISBN 9780323852838. <https://doi.org/10.1016/B978-0-323-85283-8.00008-4>

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
10	80	60	60

[4] Müllerová, J., Kent, R., Brůna, J., Bučas, M., Estrany, J., Gago, X., Michez, A., Mokroš, M., Tsiafouli, M., Manfreda, S. (2025). Understanding spatio-temporal complexity of vegetation using drones, what could we improve? *Journal of Environmental Management* 373, 123656. <https://doi.org/10.1016/j.jenvman.2024.123656>

(JIF 2024: 8.4, ENVIRONMENTAL SCIENCES - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)

0	70	70	60
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[5] Fassnacht, F. E, **Müllerová, J.**, Conti, L., Malavasi, M. & Schmidtlein, S. (2022) About the link between biodiversity and spectral variation. Applied Vegetation Science 25, e12643.

<https://doi.org/10.1111/avsc.12643>

(JIF 2024: 2.6, ECOLOGY – Q2)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
0	20	25	20

[6] **Müllerová J.**, Pergl J. & Pyšek P. (2013). Remote sensing as a tool for monitoring plant invasions: testing the effects of data resolution and image classification approach on the detection of a model plant species *Heracleum mantegazzianum* (giant hogweed). International Journal of Applied Earth Observation and Geoinformation 25, 55–65. <https://doi.org/10.1016/j.jag.2013.03.004>

(JIF 2024: 8.6, REMOTE SENSING - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
100	40	90	60

[7] **Müllerová, J. (2019).** UAS for Nature Conservation–Monitoring Invasive Species. In: J. B. Sharma (ed), Applications of Small Unmanned Aircraft Systems: Best Practices and Case Studies, CRC Press, pp. 157-178, ISBN 9780367199241. <https://doi.org/10.1201/9780429244117>

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
100	100	100	100

[8] Kupková, L., Červená, L., Potůčková, M., Lysák, J., Roubalová, M., Hrázský, Z., Březina, S. & **Müllerová, J. (2023).** Towards reliable monitoring of grass species in nature conservation practice: evaluation of the potential of UAV and PlanetScope multi-temporal data in the Central European tundra. Remote Sensing of Environment 294, 113645. <https://doi.org/10.1016/j.rse.2023.113645>

(JIF 2024: 11.4, ENVIRONMENTAL SCIENCES - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
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30	40	40	50
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[9] Müllerová J., Vítková, M., Vítek, O. (2011). The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient poor environment. Science of the Total Environment 19, 3839-3849. <https://doi.org/10.1016/j.scitotenv.2011.06.056>

(JIF 2024: 8, ENVIRONMENTAL SCIENCES - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
40	40	50	50

[10] Potůčková, M., Kupková, L., Červená, L., Lysák, J., Krause, D., Hrázský, Z., Březina, S. & Müllerová, J. (2021). Towards resolving conservation issues through historical aerial imagery: vegetation cover changes in the Central European tundra. Biodiversity and Conservation 30(12), 3433-3455. <https://doi.org/10.1007/s10531-021-02255-y>

(JIF 2024: 3.1, BIODIVERSITY CONSERVATION - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
30	50	25	40

[11] Pergl P., Müllerová J., Perglová I., Herben T. & Pyšek P. (2011). The role of long-distance seed dispersal in the local population dynamics of an invasive plant species. Diversity and Distributions 17, 725-738. <https://doi.org/10.1111/j.1472-4642.2011.00771.x>

(JIF 2024: 4.2, ECOLOGY - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
20	0	20	20

[12] Dostál P., Müllerová J., Pyšek P., Pergl J., Klinerová T. (2013). The impact of an invasive plant changes over time. Ecology Letters 16, 1277–1284. <https://doi.org/10.1111/ele.12166>

(JIF 2024: 7.9, ECOLOGY - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
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20	20	20	20
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[13] Müllerová, J., Šiffel, E. (2025). Cooling the Land Surface: Ecosystem Health and Water Availability Drive the Landscape Capacity to Mitigate Climate Change. *Ecological Indicators* 172, 113265. <https://doi.org/10.1016/j.ecolind.2025.113265>

(JIF 2024: 7.4, ENVIRONMENTAL SCIENCES - Q1)

Experimental work (%)	Supervision (%)	Manuscript (%)	Research direction (%)
20	100	80	100

Abstract

This thesis summarizes my work leveraging remote sensing technology to describe and analyze ecosystem state and functioning. Rather than merely monitoring vegetation patterns, this work integrates the analysis of spatio-temporal changes at community and landscape levels to better understand underlying ecological processes. Specifically, the research establishes a conceptual framework for studying ecosystem complexity and variability across spatial and temporal scales, while critically evaluating the advantages and limitations of RS technologies. By introducing diverse mapping approaches—from direct biodiversity monitoring to indirect mapping of habitats and assessments of functional and spectral diversity—it demonstrates how RS enhances our understanding of ecological processes. Ultimately, these applications provide a basis for management and conservation under rapid environmental change, addressing themes such as plant invasions, ecosystem services, and the impacts of climate change on forest health and high-mountain ecosystems.

1. Structure and aims of the thesis

In my theses, I would like to guide you through my research over the years. Being raised as a plant ecologist and having worked in the remote sensing (RS) field for years, I have summarized some of the related concepts, and demonstrate how powerful RS tools can be for understanding ecosystems. Beyond describing patterns, RS can also help to explain ecological processes, and, last but not least, contribute to nature conservation practice - provided we are able to transfer and implement it effectively. This is one of the many challenges related to RS applications that I address here.

My theses consists of eleven papers published in scientific journals and two book chapters that I choose from my publication list as the most relevant to the topic.

2. Introduction

Understanding and managing natural ecosystems is challenging due to their inherent complexity and variability. Ecological patterns and processes operate and are often simultaneously driven by processes running at multiple spatial and temporal scales, demanding that their observations be designed accordingly (Marvin et al., 2016; Begstad et al., 2018; Bradshaw et Fortin, 2000). Detailed characterization of vegetation at different scales is thus essential but difficult and labor-intensive using traditional field methods. Remote sensing offers a powerful alternative, providing the necessary spatio-temporal data to observe, map and monitor ecological patterns and processes at the level of ecosystem, landscape, community and individual, offering deep insights into their dynamics, and in some cases enabling retrospective analysis (Müllerová et al., 2021 – PAPER 1; Reddy et al., 2021; Müllerová et al., 2023 – PAPER 2). Applications in vegetation studies are very broad, such as biodiversity mapping and monitoring, exploring the vegetation patterns, assessing ecosystem structure and species traits, modelling the plant growth, evaluating effects of disturbances and plant stress, and studying the ecosystem functions, mechanisms and impacts as well as environmental factors that drive these processes at the landscape scale (Senf et al., 2017; Camaretta et al., 2020; Cavender-Bares et al., 2020; Müllerová, 2023a – PAPER 2).

Technological advancements have greatly enhanced RS capabilities, offering improved resolution, data accessibility and processing (Corcoran et al., 2021, Müllerová et al., 2023b – PAPER 3). They not only made the analysis more precise but also allowed for assessment of ecosystem features, processes and changes over time that were not possible before. A significant change in this field is connected to the deployment of Unmanned Aerial Systems (UASs), so called drones, in ecological applications. Drones effectively bridge the gap between field surveys and satellite remote sensing by providing ultra-high

spatial resolution and flexible data acquisition (Alvarez-Vanhard et al., 2020). This is particularly valuable for biodiversity monitoring and habitat mapping, assisting predictive modeling and supporting management, capturing dynamic ecosystem processes, and understanding their mechanisms by providing continuous environmental information at scales fine enough to reveal underlying ecological processes (Bulusu et al, 2023).

RS, especially with the capabilities offered by drones, long-term satellite missions, new sensors, and powerful algorithms, is ultimately transforming our ability to gather ecological information (Anderson and Gaston, 2013; Gonzalez et al., 2016; Bergamo et al., 2023). It serves as a critical link between scientific understanding and practical land management needs.

In the following chapters, I will briefly summarize my research employing RS techniques in various fields of ecosystem studies, introducing the concept and possible framework, addressing different components of ecosystem complexity (patterns - state of vegetation/ecosystem, or processes - function and dynamics), and discussing the challenges and limitations that hamper the transfer of RS research to practice.

3. Concept and framework

Natural ecosystems are fundamentally complex and exhibit significant variability across spatial and temporal scales. Still, the question remains on how to actually measure the ecosystem complexity. It can be broadly understood through plant composition (biodiversity), vegetation structure (e.g., biomass), status (e.g., phenology, stress), and dynamics (e.g., disturbances) (Müllerová et al., 2021 - PAPER 1.). These components cover both static and dynamic processes. Following the concept of Essential Biodiversity Variables (EBV), these components can be translated into compositional, structural, and functional diversity. Measuring this complexity in the field is challenging and labor-intensive, making RS a great alternative, in case we are able to relate ecosystem complexity to remotely sensed signal. This could be done e. g. via assessing spectral heterogeneity, spatial arrangements, or plant height and size (Fig. 1).

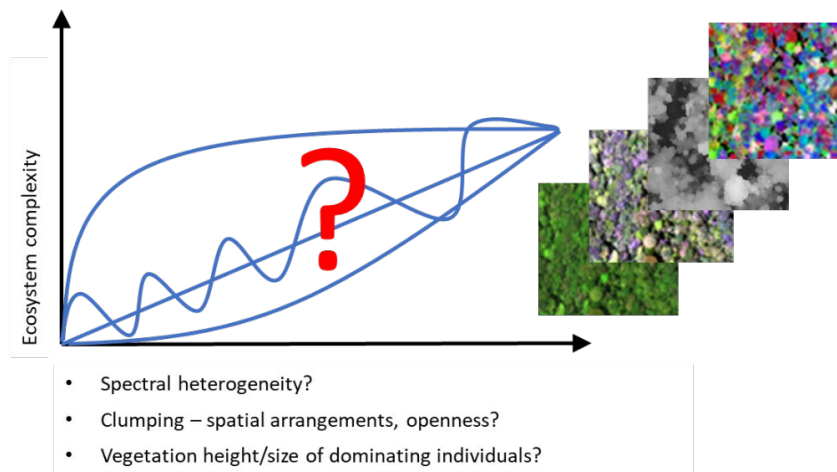


Figure 1. Concept on possible quantification of vegetation heterogeneity (Y axes) using remote sensing (X axes)

Thus, to understand ecological processes, moving across space and time seems indispensable and RS observations are a perfect tool for that. According to a concept referred to as 'rocking' (Müllerová et al., 2023a - PAPER 2), combining RS data with different spectral, spatial, and temporal resolutions (utilizing growing archives of data like Landsat and Sentinel and historical aerial datasets), allows for adjusting the focus on various spatio-temporal aspects to achieve a more complete picture. Such 'rocking' across space and time can, for instance, help capture key phenological phases across heterogeneous landscapes, unravel ecological impacts of invasive species on ecosystem functioning, reconstruct the course of invasion or a disturbance, and develop hypotheses about dispersal mechanisms and drivers (Fig. 2). The ability to map vegetation properties as a continuum in space and time provides novel insights into ecological patterns and processes.

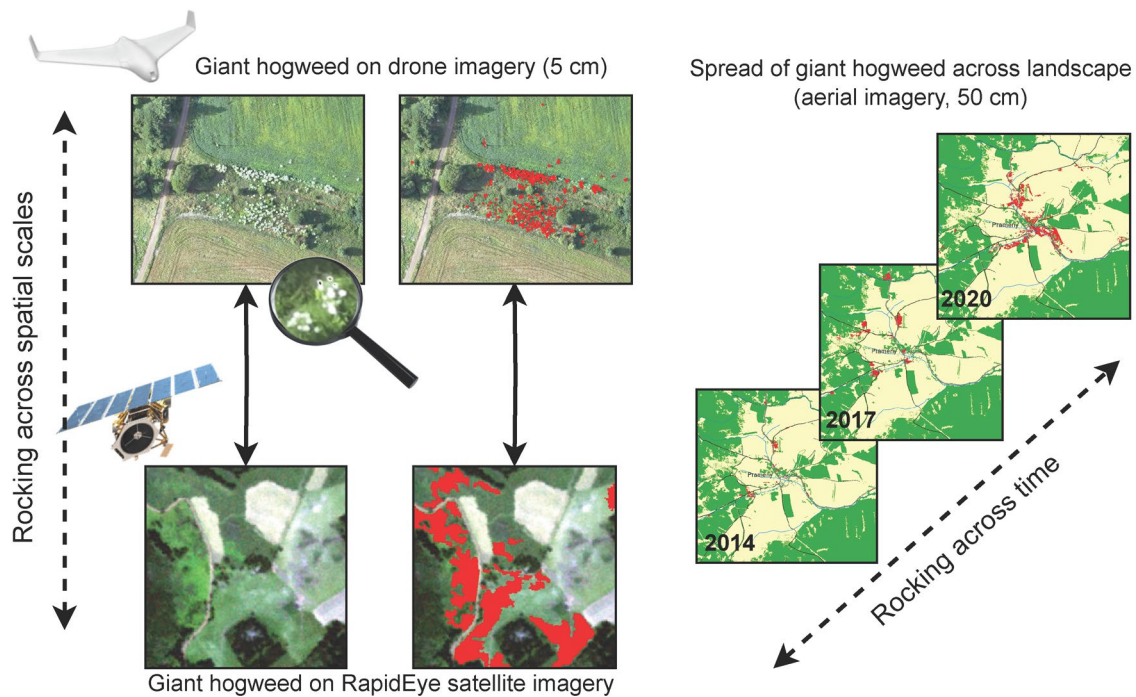


Figure 2. The concept of 'rocking' across space and time, illustrating on the example from an invasion of giant hogweed (*Heracleum mantegazzianum*) how the 'rocking' can help to better understand invasion dynamics. Rocking enabled to reconstruct the course of invasion at the landscape scale, and served to analyze invasion patterns, processes and impacts (adapted from Müllerová et al., 2023a - PAPER 2, and based on works of Müllerová et al., 2005, 2013 - PAPER 6, 2017b; Nehrbass et al., 2007; Pyšek et al., 2008; Pergl et al., 2011 - PAPER 11; Dostál et al., 2013 - PAPER 12). For more details see Müllerová et al., 2023a - PAPER 2.

The spatial resolution of RS data significantly impacts the ability to capture ecosystem complexity. While high resolution reveals fine details, it can also introduce noise, making it difficult to differentiate real ecological heterogeneity from measurement errors. Conversely, too coarse a resolution can obscure important patterns. Identifying the optimal spatial resolution is crucial and depends on the ecosystem's specific characteristics. Similarly, spectral resolution influences the data's intricacy and the power to distinguish different vegetation properties. Temporal complexity requires careful consideration of the timing and frequency of data acquisition to capture vegetation dynamics accurately and avoid artificial variability (Müllerová et al., 2021 - PAPER 1).

Historically, a scale gap between field and RS data hampered the study of ecological processes at relevant scales, a gap that drones, with their fine spatial and flexible temporal capabilities, are helping to bridge. In recent years, drones have become indispensable for characterizing vegetation patterns and processes. For natural vegetation, this high resolution is particularly beneficial for tasks such as

biodiversity monitoring, habitat mapping, and measures against ecosystem degradation, including that caused by invasive species. The high frequency of data acquisition proves valuable for studying dynamic ecosystem functions. They provide rich spectral and structural information, often presenting a more cost-effective alternative to expensive active sensors (laser scanning, LIDAR), and their increasing availability at lower costs is spurring new applications in both vegetation research and practical management. Drones are well-suited for deriving remote sensing-enabled essential biodiversity variables (EBVs) related to species composition, ecosystem structure, traits, and functions, and help to upscale point-based field measurements to the landscape level, overcoming limitations of traditional *in situ* methods. With their ultrahigh spatial resolution and flexibility, they offer a way to replace or complement labor-intensive field work (Müllerová et al., 2023b – PAPER 3). They are ideal for both research experiments and targeted operational use, such as in nature protection (Müllerová et al., 2017a; Müllerová, 2019 - PAPER 7; Kupková et al., 2023 - PAPER 8).

The actual utility of RS in managing biodiversity is closely tied to the specific characteristics of the plant and phenomenon to be studied, and thus requires careful optimization of survey design, ensuring that the spatial, spectral, and temporal scales align with the specific characteristics of the ecosystem and the research objectives (Müllerová et al., 2025 - PAPER 4). A general framework, prepared by Müllerová et al. (2021 - PAPER 1) for drone-based vegetation studies (Fig. 3), suggests steps including becoming familiar with the phenomenon to be studied, choosing suitable temporal, spatial, and spectral resolution, selecting appropriate processing and classification algorithms, and carefully interpreting results while considering the limitations of the methods. Among the main benefits of using drones for vegetation assessment are high spatial resolution and flexibility, along with efficiency, low costs, and the ability to derive structural information as well. Key challenges involved technical issues (like distinguishing data errors from real heterogeneity), conceptual challenges related to measuring complexity and the intricacy of processing. This emphasizes the crucial role of standardization of protocols and metadata, particularly at finer spatial scales, to separate data errors from informative heterogeneity (Müllerová et al., 2025 - PAPER 4).

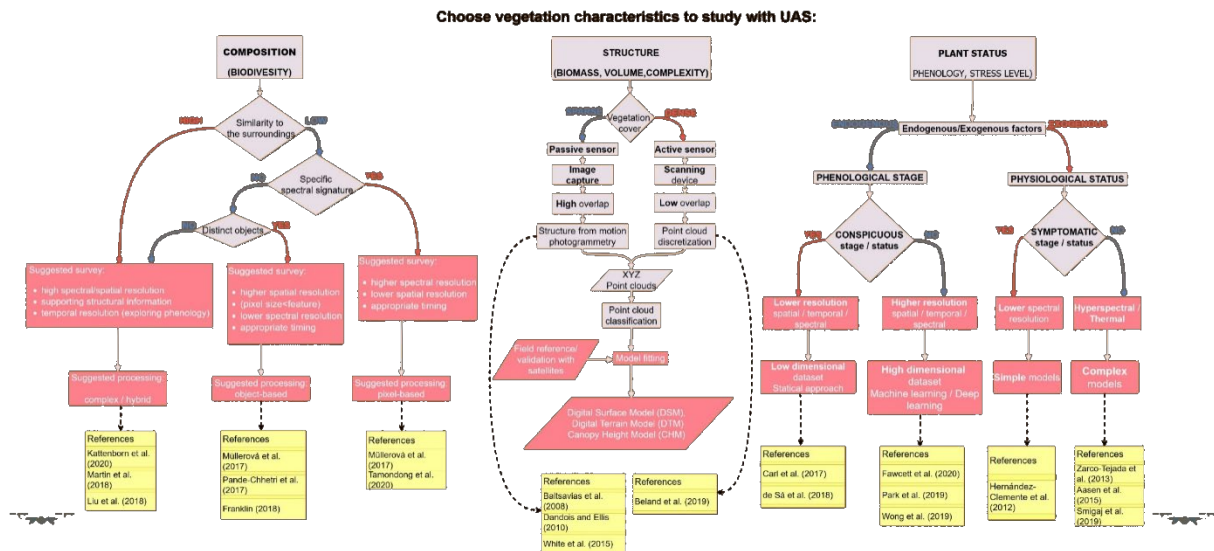


Figure 3. A framework for designing a drone-based study of vegetation (adapted from Müllerová et al., 2021 - PAPER 1)

Key technological innovations such as enhanced spatial and temporal resolution, broader coverage, and accessibility of RS data, platforms, sensors, software, and computational power are opening up new possibilities. They allow for the precise detection of even inconspicuous species and phenomenon (Müllerová et al., 2021 – PAPER 1). Furthermore, they enable the mapping of the dynamics over time using multi-temporal data, assist in assessing and quantifying impacts, support risk assessment and predictive modeling, and deepen our understanding of mechanisms by providing continuous, detailed environmental information at scales fine enough to reveal underlying ecological processes (Müllerová et al., 2023a – PAPER 2). New methods facilitate the assessment of vegetation properties directly applicable to biodiversity research, including mapping plant traits, functional types, and plant communities with their spatio-temporal variability (Rocchini et al., 2022).

The practical applications of RS to study vegetation involve a variety of methods both two-dimensional and three-dimensional, using diverse sensor types, including standard optical cameras, multispectral, hyperspectral, and LIDAR. Processing techniques are crucial for handling the unprecedented detail of very high-resolution data. Object-Based Image Analysis (OBIA) is particularly effective for fine-resolution imagery, analyzing segments rather than individual pixels and incorporating textural and pattern information akin to human visual interpretation. Advanced Machine Learning and Deep Learning algorithms are increasingly employed for classification and identification tasks, learning complex patterns from large datasets, though Deep Learning often requires extensive training data. Combining 2D spectral data with 3D structural information (data fusion), for instance, integrating LIDAR point clouds with hyperspectral imagery, has proven to enhance mapping accuracy by leveraging

the strengths of different data types. Furthermore, integrating drone data with other sources like terrestrial or satellite data extends the scope and allows for the adaptation of existing monitoring schemes. The increasing availability of free and open-source software (FOSS) for tasks like flight planning, orthomosaic generation, classification, and OBIA is also facilitating the adoption of drone-based workflows, making advanced vegetation monitoring more accessible despite some current limitations in readily available complex workflows (Müllerová et al., 2023b – PAPER 3).

Remote sensing contributes to ecosystem studies in various ways. Most applications focus on describing the patterns, such as mapping and monitoring, that can be relatively easy depending on the level of conspicuousness of the species/phenomena and the quality of the available RS data (Müllerová et al., 2021 – PAPER 1). On the other hand, the potential of RS is not fully exploited for assessment of ecosystem dynamics, functions and services (Fig. 4; Müllerová et al., 2025 – PAPER 4).

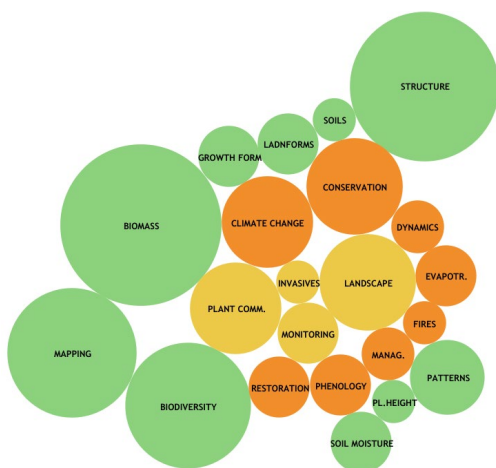


Figure 4. Bubble plot of keywords from research studies employing drones to characterize natural and semi-natural vegetation. The keywords were manually assigned as objectives, and divided into the following groups: patterns (ecosystem state and structure) in green, and processes (ecosystem status and dynamics) in orange. Keywords that apply for both mentioned categories are in yellow. The size of the bubbles is relative to the number of keywords mentioned (Müllerová et al., 2025 – PAPER 4).

For example, in case of plant invasions, RS research is primarily focused on spatio-temporal patterns of invasion, while topics like early monitoring, revealing invasion mechanisms, and assessing impacts have received less attention (Fig. 5). There is a need to move beyond simple description of the state towards understanding of the processes. RS-derived information on spatio-temporal patterns can be used not only to assess the dynamics but also to understand the underlying mechanisms and ecological

processes, and provide input data for models simulating current and future distribution under different management and climatic scenarios (Müllerová et al., 2023a – PAPER 2).

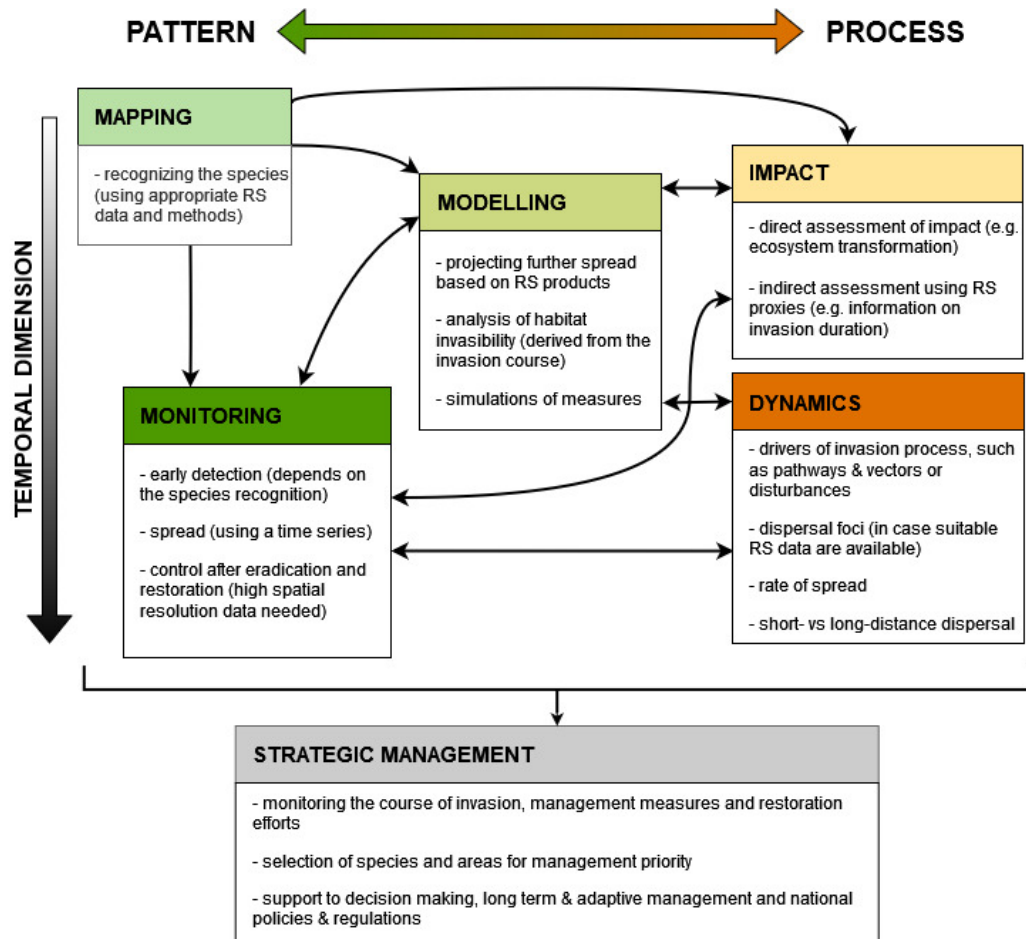


Figure 5. A conceptualization of the contribution of remote sensing to the knowledge of plant invasions (Müllerová et al., 2023a – PAPER 2)

4. Patterns (State)

RS technology is considered crucial for addressing the challenges of mapping and monitoring biodiversity patterns across space. Several approaches on how to employ RS in mapping biodiversity exist, based on (i) direct species mapping, (ii) habitat mapping, (iii) mapping functional diversity, and (iv) spectral diversity (Wang and Gamon, 2019; Fassnacht et al., 2022 – PAPER 5).

In case of direct mapping of specific species or plant communities, detection success depends strongly on the target species' characteristics, the data source, and classification approach (Müllerová, 2019 – PAPER 7, Fig. 6). Ultra-high spatial resolution from drones allows detecting very small species or fine-

grain vegetation mosaics, however, increasing spectral information is connected to growing processing complexity (Müllerová et al., 2023b – PAPER 3). On the other hand, different components of resolution (spatial, spectral and temporal) can, to certain extent, compensate for each other (Müllerová et al., 2013 – PAPER 6). Sophisticated processing approaches are expected to improve results, such as object-based (OBIA) classification, especially for detailed drone imagery by incorporating spatial structure and context, and particularly for detecting targets with specific shapes, or machine and deep learning algorithms that enable mapping even less distinct species. Still, the choice of the best classification method is case-specific, varying according the target plant and imagery characteristics, with a certain trade-off between the necessary accuracy and large-scale applicability needed for practical applications (Müllerová et al., 2013 – PAPER 6; Müllerová, 2019 – PAPER 7).

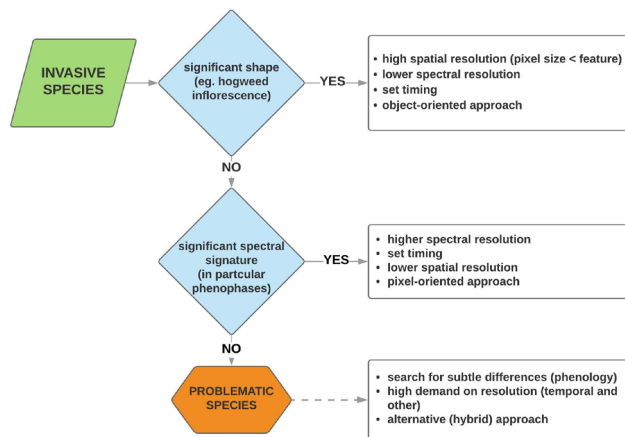


Figure 6. Decision tree for choosing optimal data and classification approach depending on the target invasive species (adapted from Müllerová, 2019 – PAPER 7).

Timing of the data acquisition is extremely important, being strongly dependent on the phenological phase of the target species. The flexibility of drone data acquisition timing is particularly suitable for studying the role of phenology for detection. Some species show distinct flowering or senescenting phase due to the change in color; see examples of giant hogweed (Müllerová et al., 2013 – PAPER 6), invasive knotweeds (Müllerová 2019 – PAPER 7, Müllerová et al., 2017b), deciduous trees (Müllerová et al., 2023b – PAPER 3), and sub-alpine grasslands (Kupková et al., 2023 – PAPER 8) (Fig. 7). However, the time window of favourable phenological phase can be short or with weather constraints, for practical applications, other options, possibly supported by more complex workflow might be necessary (Müllerová et al., 2017a; Martin et al., 2018).

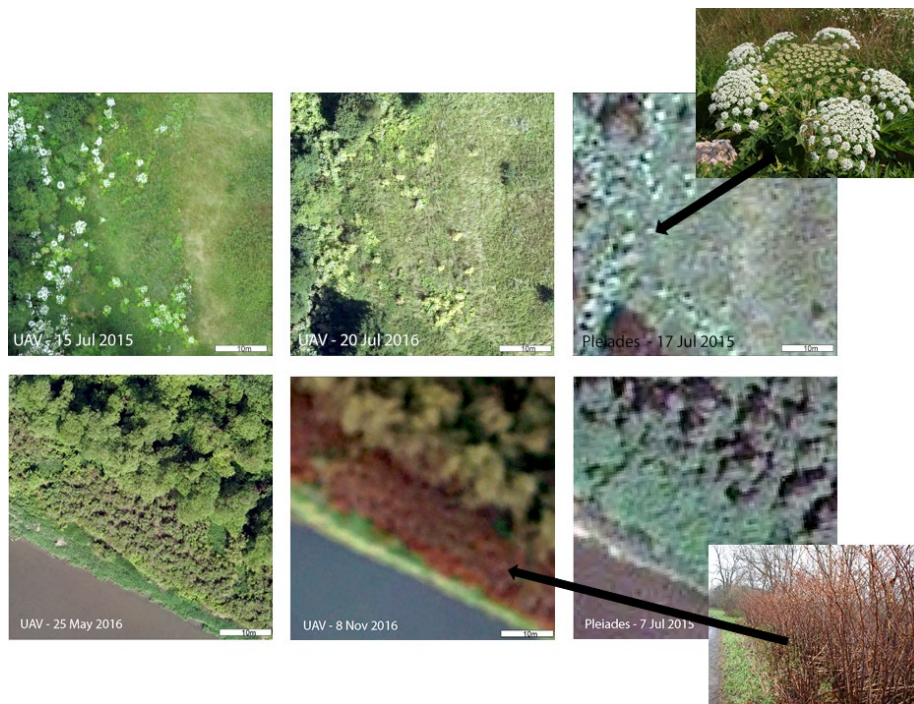


Figure 7. Effect of timing and scale of the RS data acquisition on conspicuousness of two invasive species (upper row – giant hogweed, lower row – invasive knotweeds). Adapted from Müllerová et al. (2017b)

The distinctness of a target plant does not only depend on its own properties but also on its surroundings. Additional variables beyond spectral features, such as texture, canopy height models derived from photogrammetry, and multitemporal band ratios, can be used to improve detection. For example, changes in canopy height have shown potential for detecting fast growing invasive plants with rapid increase of biomass (Martin et al., 2018). For trees, photogrammetry-based surface roughness (Müllerová et al., 2017b) or LIDAR point cloud collected from different platforms can be used for reliable individual tree species classification using deep learning models, regardless of the data source (Puliti et al., 2025).

Even though the recent advancement related to the sophisticated deep learning algorithms and increasing availability of spatially and temporally rich datasets, ability to directly map species is limited in space, restricted for the least distinct species, and is often site- and species-specific with limited transferability (Müllerová et al., 2023a – PAPER 2). It is also mostly reserved for larger and/or dominant species, whereas small and low-frequency species, often rare species of high nature conservation interest might be overlooked (Kupková et al., 2023 – PAPER 8). Ultra-high spatial resolution from drones can aid such tasks, like identification of non-flowering individuals, small species or patches, that can be important also in mapping biodiversity threats such as early invasion stages (Müllerová, 2019 – PAPER 7).

Another RS-based approach in biodiversity assessment is via habitat mapping, where species distribution or counts are inferred from maps of habitats or vegetation types, assuming their relationship with the (number of) species. This essentially involves creating detailed land-cover maps using RS. This approach is based on categorical types, making it difficult to capture gradients of species richness within a habitat (Fassnacht et al., 2022 – PAPER 5).

Mapping functional diversity via plant functional traits is another approach to bypass limitations in discriminating large numbers of plant species. RS can capture the range and variation of biochemical and structural traits, allowing mapping of trait diversity patterns (Kattenborn et al., 2019). Because areas with higher trait diversity tend to harbor more species, measure of functional diversity can serve as a proxy for species diversity. On top of that, since the trait diversity is also related to ecosystem services and functioning, it plays an important role in maintaining biodiversity (Fassnacht et al., 2022 – PAPER 5). The species can also be mapped indirectly via their effect, such as in case of invasive species (Müllerová et al., 2023a – PAPER 2)

The last-mentioned option is based on relationship between spectral and species diversity, supported by Spectral Variation Hypothesis (SVH, Palmer et al., 2000, 2002). The 'spectral species' concept involves partitioning the spectral space into groups of pixels with similar spectral signatures (optical types) that can serve as proxies for ecologically relevant groups (Fig. 8). This concept is consistent with the SVH and can facilitate the identification of rare species that occupy few pixels (Rocchini et al., 2022).

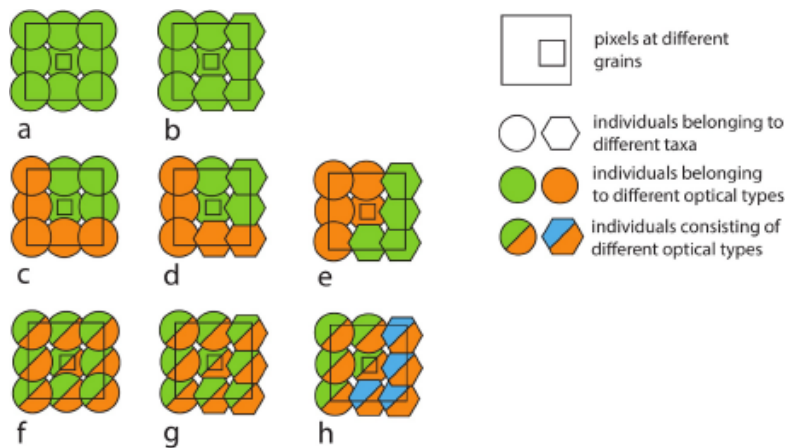


Figure 8. Some potential scenarios that can happen in optical remote sensing of vegetation canopies (Rocchini et al, 2022, for more explanation, see the source).

Empirical studies often report correlations between spectral variation and biodiversity variables, such as plant species counts, but the strength of these correlations varies (Fassnacht et al, 2022 – PAPER 5). A notable challenge lies in the direct linkage between spectral signatures and taxonomic species identity. The spectral species concept proposes clustering pixels with similar spectral signals, yet a single spectral signature may not uniquely correspond to a single species but a group of species sharing similar biochemical properties, reflecting rather the functional traits than the taxonomy or reflect the same species in different developmental stages or under varying environmental conditions (Fig. 9). Therefore, accurately identifying a taxonomically defined species with a unique spectral signature remains complex and often requires supplementary empirical evidence from field data collections, experimental studies, or modeling (Rocchini et al., 2022, Perrone et al., 2023).

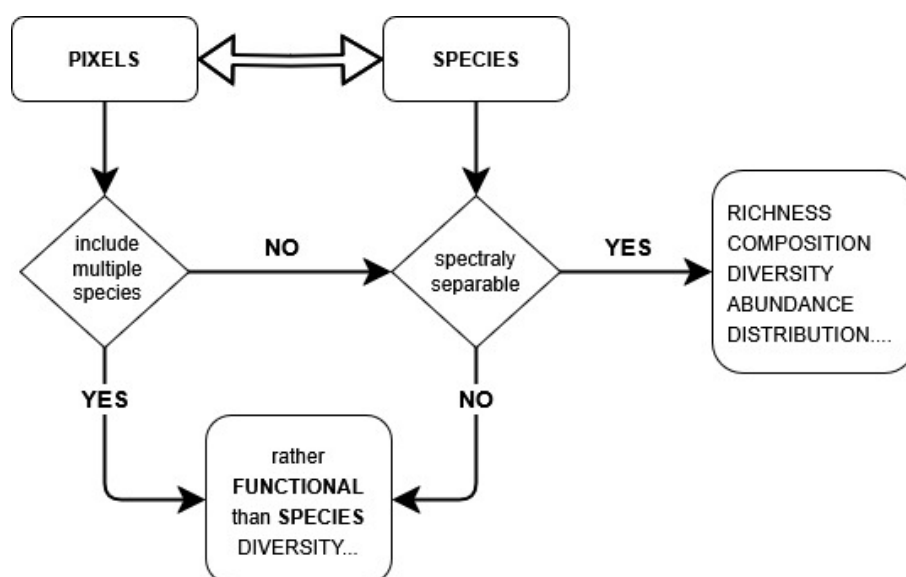


Figure 9. Relationship between spectral, functional and species diversity.

The applicability and accuracy of mapping biodiversity based on spectral diversity are context-dependent, influenced by factors like habitat type, scale (spatial extent and grain), temporal effects (phenology), and the specific spectral metrics used. The spectral variation caused by species or functional traits can be subtle in comparison to other factors like seasonality and physiological status. Minor shifts in plant development (phenotypic variability) may also result in a single species having multiple spectral signatures corresponding to different growth stages. Challenges exist in complex landscapes or when dealing with varying spatial grain (Tab. 1, Fassnacht et al., 2022 – PAPER 5; Rocchini et al., 2022 ; Perrone et al., 2023).

Table 1. Factors that can affect the spectral-species diversity relationship. Based on Fassnacht et al. (2022 – PAPER 5)

Factor	Effect on Spectral Diversity ~ Biodiversity relationship
a) Scale	- Optimal spatial grain depends on the size of the basic entity which constitutes the level of biological organization under investigation - Number of entities (e.g. species-area relationship) and SD increases with extent - SD increases with finer spatial grain while number of entities remains the same (at a fixed extent) ⇒ important to identify optimal scales and understanding how the scale depends on the size of the entity
b) Phenology	- Both SD and biodiversity vary over the year ⇒ important to identify optimal timing
c) Applied metrics	- Distance-based metrics (absolute reflectance values vs. normalized values of bands) and shape-based metrics (shape of spectra) may differ in their correlation strength with biodiversity ⇒ important to identify stable metrics
d) Type of ecosystem	- The vertical structure may hamper the optical detection of some of the ecosystem strata

The spectral species concept is expected to make a major contribution in mapping biodiversity from hyperspectral imagery. Even if spectral species concept does not precisely identify taxonomic species numbers, it can provide an exploratory tool to detect areas of low to high diversity Rocchini et al., 2022).

There is an urgent need for operational biodiversity monitoring systems. Effective monitoring requires analysis across multiple spatial and temporal scales ('rocking') to account for the natural dynamics of ecosystems, since temporal factors like seasonality and phenology can influence the relationships (Fassnacht et al., 2022 – PAPER 5). Using multi-temporal composites can help to smooth out inter-annual variability and capture optimal vegetation cover (Perrone et al., 2023). While field surveys can provide higher quality direct mapping of biodiversity, RS can aid in detecting biodiversity patterns, including threats from invasive species, through analysis of spectral, structural and temporal properties, using various approaches from habitat mapping to functional diversity and spectral species mapping, albeit with context-dependent accuracy and challenges related to scale and phenology. RS can also assist in improving sampling design for field surveys by pre-stratifying the study area, and is particularly suitable for monitoring changes in landscapes over time, and hence potential changes in biodiversity and ecosystem functioning. Understanding the complex and context-dependent links

between remotely sensed data and ground-based biodiversity remains an ongoing area of research, highlighting the need for systematic testing and integration with field data and ecological knowledge.

5. Processes (Function, Dynamics)

By providing spatio-temporal data difficult to obtain through traditional field studies, RS supports the analysis of ecological processes across scales, from local dynamics to regional vegetation change, and provides a foundation for adaptive management and conservation strategies under climate change.

RS can be used to reconstruct the vegetation patterns including plant invasion by combining archival RS data with other historical information, and the results support subsequent analysis of the drivers of change and its impact on the ecosystems. It can assist in study of the drivers of species distribution change, being either native or invasive species. For example, RS enabled to study the threats to sensitive mountain ecosystems, such as sub-alpine tundra of Krkonoše Mts., being a subject of multiple pressure running simultaneously - increasing human impact, global warming and increasing nitrogen deposition under the climate change, and cessation of traditional management. Retrospective analysis of available archival high-resolution data supported analysis of processes such as shrub encroachment and its impact, expansion of competitive native grasses or human induced alteration of plant composition along tourist trails and chalets (Müllerová, 2005; Müllerová et al., 2011 – PAPER 9; Collins et al., 2020; Potůčková et al., 2021 – PAPER 10).

In case of invasive alien species, RS applications are broad (Müllerová et al., 2023a – PAPER 2; Sankaran et al., 2023). Using the same approach of retrospective analysis, course of invasion can be reconstructed, serving as an input for, among others, deriving details on dispersal foci and the rate of spread, revealing mechanisms of spread, modeling habitat invasibility, and analyzing landscape drivers of invasion, such as landscape history, disturbances, landuse and land abandonment, landscape fragmentation, connectivity and availability of suitable habitats (Pyšek et al., 2008; Pergl et al., 2011 – PAPER 11). Derived information on invasion duration at the landscape scale can then be used to assess the impact of invader on biodiversity and soil properties, such as the plant soil feedback (Dostál et al., 2013 – PAPER 12; Jandová et al., 2014). RS can also indirectly support invasion science and management by providing data for models that simulate current and future distribution, management measures and risk assessment (Nehrbass et al., 2006; Müllerová et al., 2023a – PAPER 2).

Information derived from satellite or other RS data can serve as a proxy for underlying ecological processes, including disturbances. In recent years, forest ecosystems are under increasing stress from climate change, manifested by decreasing forest ecosystem health and elevated tree mortality. Field

observations on forest health are rather sparse and often not comparable among the regions. RS data provide a valuable source of information, especially if coupled with powerful deep learning algorithms (Mosig et al., 2026). Earth observation data, such as satellite optical and aerial lidar data can provide insights into the effects of forest disturbances, specifically bark beetle infestation and subsequent forest die-off, on invertebrate and plant species and functional diversity (Holcová et al., 2025). Thermal information provided by satellites, such as Landsat and MODIS, enable to study not only the impact of climate change on ecosystem processes, but also the role of ecosystem state and landscape settings on shaping and ameliorating the land surface temperature. Study of Müllerová et Šiffel (2025 – PAPER 13) explored the role of water availability and ecosystem health in alleviating temperature extremes. It showed that predicted high spatial and temporal resolution of land surface temperature helps to disentangle local temperature patterns and environmental drivers in complex landscapes. Besides directly derived information on land surface temperature, RS can also provide a proxy for microclimatic condition within the stand. The forest microclimate can be modeled using spatially continuous and rather detailed information on forest structure. Especially drones can provide information on canopy cover and structure, key predictors of air and soil temperature and moisture, at a very fine spatial scales relevant to organisms living in the forest understory (Kašpar et al., 2021). On top of that, studies such as Müllerová et Šiffel (2025 – PAPER 13) show rather high correlation between the temperature of forest canopy inferred from the satellites and in-situ measured temperature inside the forest (15 cm above the forest floor). Such research is very promising since the forest microclimate is an essential variable shaping especially the plant and invertebrate biodiversity of forests, and availability of spatially explicit, continuous and repeated data would tremendously increase our understanding of forest biodiversity patterns.

Certain processes and impacts, like the transformation of grassland to shrubland or productivity-related impacts, are relatively easy to identify using RS. However, more sophisticated sensors (hyperspectral or LIDAR) or interpreting RS data as a proxy might be necessary for detecting more subtle impacts, or to disentangle coupled or more complex processes.

6. Transfer to practice

Despite the significant potential and technological advances in RS and many case studies, large discrepancies remain between possibilities and actual implications in research and practical management. Applications of RS often remain experimental, with limited evidence of effective implementation in management and policy (Müllerová et al., 2025 – PAPER 4). Current input of the technology does not reflect its potential (Fig. 10). For example, in case of plant invasions, level of RS

contribution varies across the introduction-naturalization-invasion continuum, from single-dimension to multi-scaled approaches (Fig. 11, Müllerová et al., 2023a – PAPER 2).

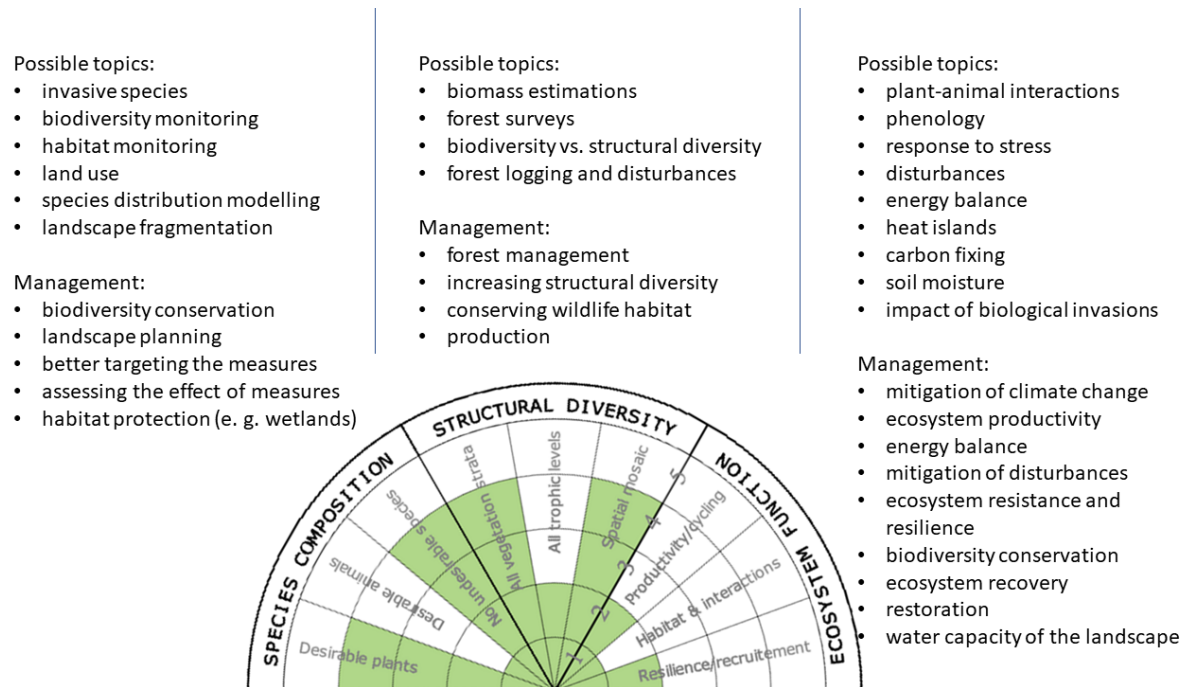


Figure 10. Potential of remote sensing surveys for practice in relation to the ecosystem complexity. Green fields indicate the current input of the drone technology. Müllerová et al. (2025 - PAPER 4), based on Recovery wheel (McDonald et al., 2016).

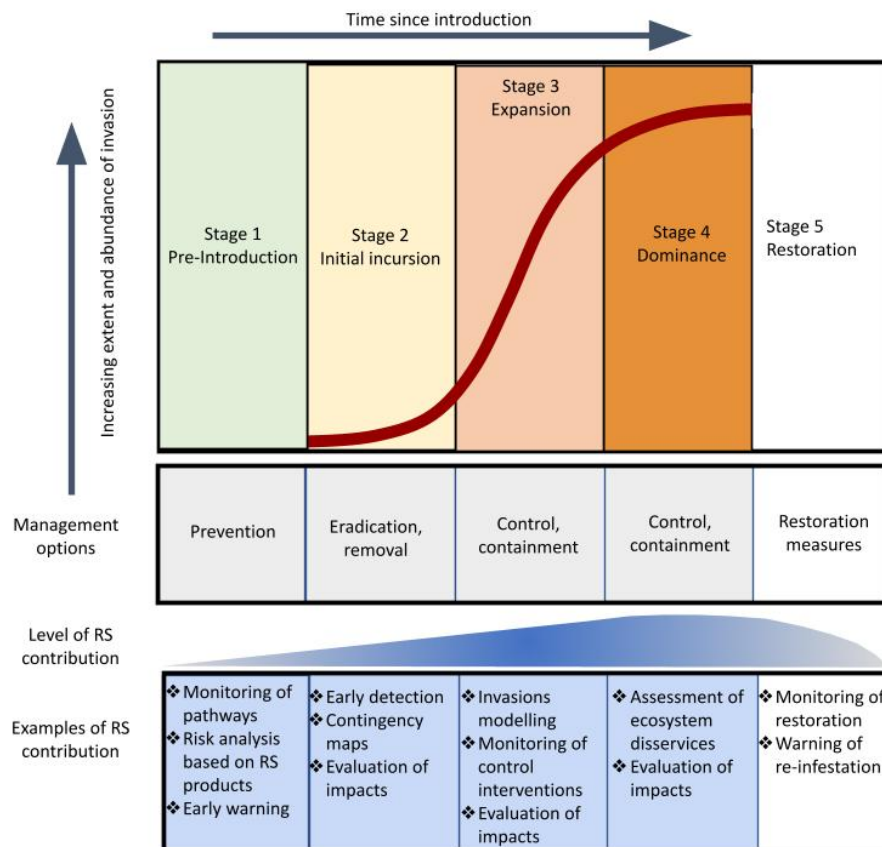


Figure 11. Potential contribution of remote sensing to different management options during the course of plant invasion. The red line in the top section indicates the extent and abundance of invasion. Müllerová et al. (2023a – PAPER 2), the background diagram (invasion curve) was inspired by van Wilgen et al. (2014).

Barriers to operationalization include complexity of tools, methods, and data, low transferability of workflows, uncertainty and imprecision, technical issues, costs, and delays in delivering products. Increased availability of high-resolution data and employment of artificial intelligence (deep learning algorithms) significantly advance the opportunities for using high-resolution spatial data, however, maintaining long time-series of high spatial resolution data and acquisition of reference data, critical for model development and validation, especially in case of deep learning, remains challenging. Possible solutions involve leveraging the ability to move across spatial and temporal scales ('rocking'), simplifying and standardizing the workflows, establishing real-time monitoring, deploying high-resolution data, utilizing cloud solutions, and promoting open data and Free and Open Source Software (FOSS). Ultimately, while technological advances are expected to overcome many limitations, a combination of profound ecological background and robust knowledge of the limits of RS technology is indispensable to avoid misinterpretations. Effective communication and engagement between field

ecologists, managers, and RS specialists are crucial for bridging the gap between research and practice. Popularizing RS among land managers and invasion ecologists, providing transparent assessments, engaging end-users from the beginning and shaping the workflow according to their needs is essential for effective transfer of the technology from research to management (Müllerová et al., 2023a – PAPER 2; Müllerová et al., 2025 – PAPER 4).

7. Conclusions

RS represents a powerful mean that allows the assessment and monitoring of ecosystems and their change over time, contributing to monitoring EBVs, particularly those describing community composition and ecosystem structure, and understanding ecosystem processes and functions in space and time, at both coarse and fine scales. Although not capable to provide such a detail as the in-situ measurements, the continuous nature of RS data can add a landscape context. Thus, it is not meant to substitute but rather augment the field-collected data, and provide a new perspective, revealing some phenomenon not obvious or difficult to assess by traditional ground-based methods. Recent technological advances and new missions open new perspectives for monitoring changes in biodiversity over large geographic areas as well as at very detailed microscale. This primarily involves mapping, monitoring and assessment of changes in vegetation cover, distribution, and functioning, and can be linked to drivers of change like biological invasions, disturbances and other underlying processes. Time-series studies of RS data and moving across space and time allow us to understand better changes and dynamics of vegetation, and possibly to separate natural variations from the change induced by local and global human impact. Increasing availability of open/accessible datasets (drones, new satellite missions) and powerful recognition and modeling tools enable studying dynamic ecosystem processes at unprecedented temporal and spatial detail, and potentially bridge the gap between detailed but scattered in-situ and continuous but coarse distant measurements. Still, the holy grail is in communication between field ecologists and remote sensing specialists. Standing in between the two communities I hope my work contributes to the dialog.

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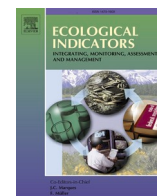
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9. Appendices

Appendix 1.

PAPER 1. **Müllerová**, J., Gago, X., Bučas, M., Company, J., Estrany, J., Fortesa, J., Manfreda, S., Michez, A., Mokroš, M., Paulus, G., Tiškus, E., Tsiadouli, M., Kent, R. (2021). Characterizing vegetation complexity with unmanned aerial systems (UAS) – A framework and synthesis. *Ecological Indicators* 131: 108156. <https://doi.org/10.1016/j.ecolind.2021.108156>



Review

Characterizing vegetation complexity with unmanned aerial systems (UAS) – A framework and synthesis

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ABSTRACT

Ecosystem complexity is among the important drivers of biodiversity and ecosystem functioning, and unmanned aerial systems (UASs) are becoming an important tool for characterizing vegetation patterns and processes. The variety of UASs applications is immense, and so are the procedures to process UASs data described in the literature. Optimizing the workflow is still a matter of discussion. Here, we present a comprehensive synthesis aiming to identify common rules that shape workflows applied in UAS-based studies facing complexity in ecosystems. Analysing the studies, we found similarities irrespective of the ecosystem, according to the character of the property addressed, such as species composition (biodiversity), ecosystem structure (stand volume/complexity), plant status (phenology and stress levels), and dynamics (disturbances and regeneration). We propose a general framework allowing to design UAS-based vegetation surveys according to its purpose and the component of ecosystem complexity addressed. We support the framework by detailed schemes as well as examples of best practices of UAS studies covering each of the vegetation properties (i.e. composition, structure, status and dynamics) and related applications. For an efficient UAS survey, the following points are crucial: knowledge of the phenomenon, choice of platform, sensor, resolution (temporal, spatial and spectral), model and classification algorithm according to the phenomenon, as well as careful interpretation of the results. The simpler the procedure, the more robust, repeatable, applicable and cost effective it is. Therefore, the proper design can minimize the efforts while maximizing the quality of the results.

1. Introduction

There are considerable gaps between field-based and remote sensing-based approaches as the field variables differ from those assessed by remote sensing techniques. Thanks to a very fine resolution, unmanned

aerial systems (UASs), also called unmanned aerial vehicles (UAVs), remotely piloted aerial systems (RPASs) and informally drones, can help to upscale the point or plot field measurements into the landscape scale, and potentially to larger areas bridging the gap between field surveys and satellite data (Alvarez-Vanhard et al., 2020). UASs are increasingly

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used in the last decade, becoming an important tool for characterizing different aspects/components of vegetation in many ecosystems worldwide. The tool is ideal for both research experiments and targeted operational use; e.g., in nature protection (Gonzalez et al., 2016; Jiménez López and Mulero-Pázmány, 2019; Müllerová et al., 2017a). A wide choice of aircraft types (different types of copters or fixed-wings), sensors (multispectral, hyperspectral, Light Detection and Ranging - LiDAR), procedures and algorithms are available for the acquisition as well as the processing and interpretation of data (Colomina and Molina, 2014; Fig. 1). UAS surveys can thus be customized and designed for a variety of applications (Yao et al., 2019). In order to maximize the benefits of UAS, it is crucial to choose appropriate system settings, design of the field campaign, preprocessing of the data and the algorithms (Tmušić et al., 2020). Considering the research purpose and characteristics of the studied ecosystem shows to be likewise important.

Within vegetation studies, UAS tool is being used for a large variety of purposes, including mapping current vegetation state, studying processes at the level of ecosystem, community and individual, assessing and modelling the plant growth, monitoring and evaluating effects of human disturbances and natural disasters such as wildfires, torrential floods and insect outbreaks (Anderson and Gaston, 2013; Bailón-Ruiz et al., 2018; Calsamiglia et al., 2020; Estrany et al., 2019; Holman et al., 2016; Michez et al., 2016; Müllerová, 2019; Näsi et al., 2018). Considering the increasing use of the tool, and the important impact the design of the study has on results, many scientists and practitioners emphasize the need for standardization to assure harmonizing the UAS data acquisition and subsequent processing with the research goal (Manfreda et al., 2018). For such standardization, a great variety of UAS-based research in the field of vegetation science needs to be synthesized into an integrated framework, including the common grounds and challenges.

Here, we present a comprehensive synthesis aiming to categorize research and identify common rules that shape workflows applied in UAS-based studies facing complexity in ecosystems. Ecosystem complexity is regarded as an important driver of biodiversity and ecosystem functioning across taxa, biomes and spatial scales (Stein et al., 2014). The variety of UAS applications in the vegetation heterogeneity assessment is immense, and so are the procedures described in the literature. Irrespective of the ecosystem, similarities can be found

according to the research aims (the ecosystem / community / individual property addressed). Vegetation properties encompass varying levels of heterogeneity in time and space, allowing classification into the following major components: (i) composition (covering a topic of biodiversity), (ii) structure (such as biomass and stand structure) and (iii) status (such as phenology stage and plant stress) (cf. Randlkofer et al., 2010). Following the concept of Essential Biodiversity Variables (EBV; Jetz et al. 2019), and remote sensing enabled EVBs (Reddy et al. 2021) these components could be translated into (i) compositional diversity (EBV groups of species populations & community composition), (ii) structural diversity (EBV group of ecosystem structure) and (iii) functional diversity (EBV groups of species traits & ecosystem function). All the components cover both static and dynamic processes, with different range and dimension of the dynamics. Still commonalities within these ecosystem components can be identified. Here, we present a synopsis as a general framework of UAS-based vegetation studies allowing us to design a UAS survey according to its purpose. We support the framework by detailed schemes of individual components, as well as examples of best practices of UAS studies covering each of the vegetation components and related applications.

2. General framework of UAS-based vegetation survey

The characterization of individual components within the framework of the vegetation complexity requires a specific survey design. The decision tree in Fig. 2 represents a general framework of vegetation surveys using UAS. The studies are divided according to the component of vegetation heterogeneity addressed: (1) species composition (parameters of biodiversity), (2) ecosystem structure (stand volume/complexity), (3) plant status (phenology and stress levels), and (4) dynamics (disturbances and regeneration) (see <https://www.costharmoonious.eu/characterizing-vegetation-complexity-with-uas/> and Supplement 1 for an interactive workflow). To reach the best quality results, the design of the survey including quality of the data and selection of the processing algorithms should be driven by the purpose of research and characteristics of the ecosystem property of interest. Information on abiotic conditions (not necessarily derived from UAS surveys) are often essential for the models. Many of the processes are dynamic, so the temporal aspects related to abiotic and biotic factors



Fig. 1. Different platforms and sensors in UAS surveys; a) Lighter-Than-Air Helikite Balloon with Sony A7RII used for renaturation monitoring; b) BRAMOR ppk Fixed-Wing with Micasense Red Edge used for riparian vegetation monitoring; c) DJI Inspire 2 with zenu-muse x5s RGB camera, used for shallow water vegetation and beach cast monitoring (Palanga, Lithuania), and d) Leica Aibot AX 20 with multidirectional sensor prototype (5 Sony ILCE-QX1 RGB sensors for capturing NADIR and 4 oblique images). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

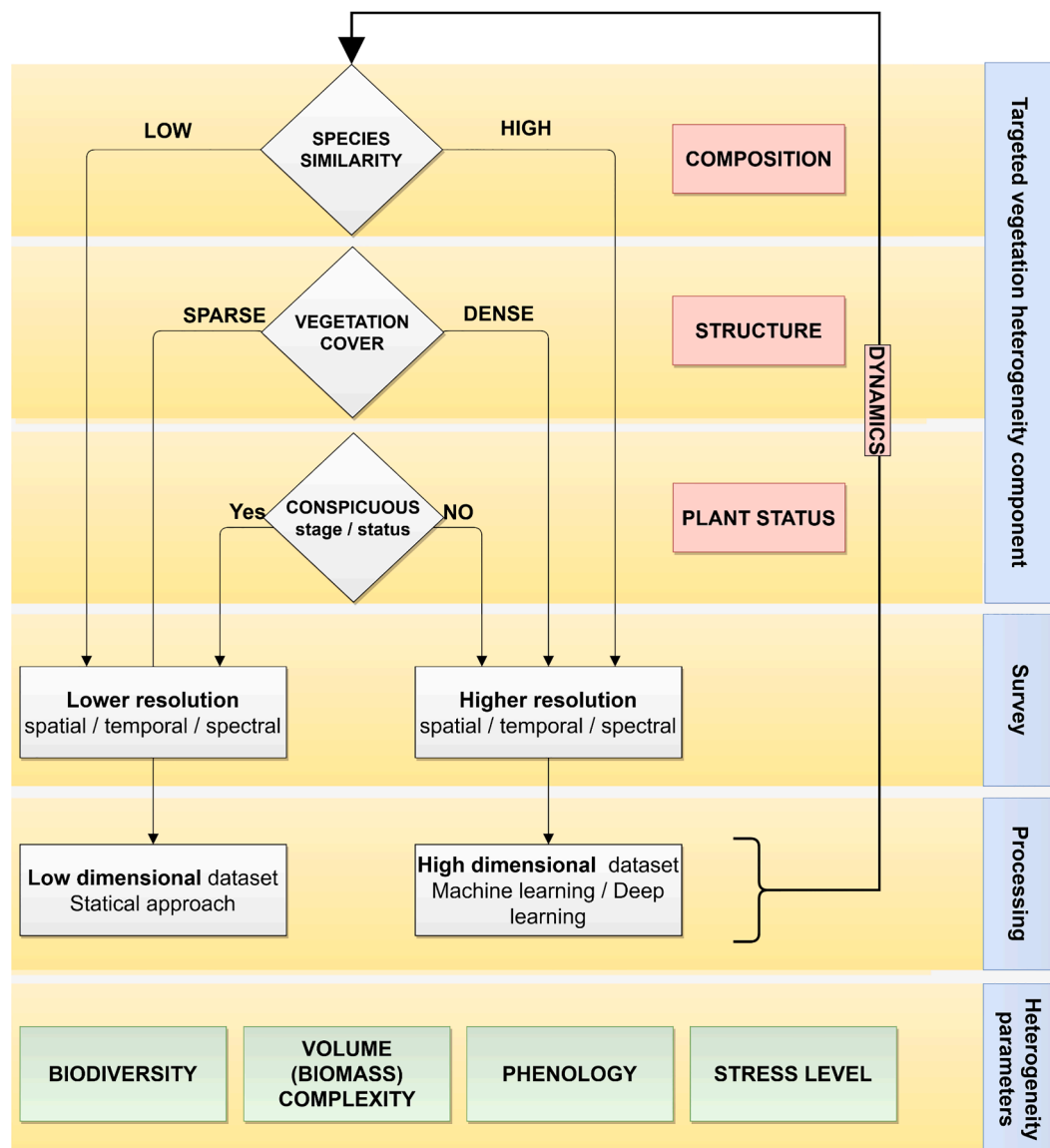


Fig. 2. Decision tree for designing the UAS-based vegetation survey according to the phenomenon/part of vegetation heterogeneity addressed. Details on each component of vegetation heterogeneity are explained in the following Figs. 3, 4 and 5, and in an interactive workflow at <https://www.costharmonious.eu/characterizing-vegetation-complexity-with-uas/> and in the Supplement 1).

need to be added to describe the changes properly. In the Fig. 2., abiotic conditions, such as geomorphology, soil properties, climatic conditions and hydrology are not included, still they all play a significant role in shaping the vegetation heterogeneity and influence the survey design (Tmušić et al., 2020).

The resolution of the UAS survey has to be adjusted depending on ecosystem characteristics, i.e. according to species and individuals' similarity and targeted heterogeneity component. The resolution, as the similarity, is hereafter considered in the following dimensions: time, space and electromagnetic spectrum. For example, when characterizing vegetation composition for the purposes of biodiversity assessment, monitoring of rare and invasive species, or understanding the processes of species coexistence and succession, it is crucial to differentiate among the species. Such differentiation will depend on the way the species occupy space through time. Furthermore, their intrinsic morphological properties will produce specific morphological and spectral signatures that can be applied for either species identification or evaluation of their status using remote sensing techniques. In case the spectral/textural characteristics of co-occurring species are similar, differentiation would require higher spectral resolution to increase their spectral separation

(Chadwick and Asner, 2016; Marvin et al., 2016). In general, the less distinct the feature is (e.g. species with a high degree of similarity to the surroundings), the more advanced sensors and the more complex methodology are required (Fig. 2). The same applies for assessing ecosystem structure, where for sparser ecosystems (e.g. sparse arid or semi-arid shrublands or tundra), photogrammetric point cloud can be sufficient, whereas for denser and more complex ecosystems such as forests, advanced LiDAR sensor becomes indispensable for most applications (Barbosa et al., 2016; Beland et al., 2019; Kent et al., 2015; Lefsky et al., 2002). The levels of conspicuousness and symptomatology of the studied phenomenon (e.g. phenological stage and/or physiological status caused by stress) influence the required level of spectral/spatial/temporal resolution (Fahlgren et al., 2015; Ghosal et al., 2018; Singh et al., 2016) and, again, the sophistication of the analytical models. In case of asymptomatic physiological status at visible range, it is very difficult to reach satisfactory results unless additional advanced hyperspectral or thermal sensors are used (Gago et al., 2017).

Insufficiently coarse resolution can decrease the accuracy, still more detail does not automatically mean better results. Whereas very high spatial resolution can be extremely beneficial for detection of small

patches or individual plants, it can tremendously increase the data complexity, processing time and data storage. Additionally, increasing spatial resolution from centimeters to millimeters can make classification extremely difficult, breaking individuals into a complex of branches and stems, green and dry leaves, individual flowers within the inflorescence, insects and soil background. Such extreme detail of UAS data also brings new challenges in the training and validation process (due to the precision limits of field Global Positioning System instruments, GPS), and proper matching of layers in case of change detection and canopy height models (Müllerová et al., 2017a). The three components of resolution, spatial, spectral and temporal, are interconnected, and certain trade-offs exist between them (Lisein et al., 2015; Michez et al., 2016). Thus, optimal resolution should be carefully chosen considering the purpose of the study as well as the target vegetation addressed.

3. The hands-on challenge: How to assess species composition, ecosystem structure and plant status by employing UASs?

3.1. Species composition: Highlighting biodiversity

Plant species composition varies along the axes of spatio-temporal heterogeneity (Lambers et al., 2008; Pugnaire and Valladares, 1999). Whereas at coarse scales it is defined by biogeographical zones and biomes, at finer scales, is determined by changes in composition as a function of abiotic conditions as well as inter-specific interactions with human management and co-occurring plant and animal species (Augustine and McNaughton, 1998; Fedele et al., 2017; Pugnaire and Valladares, 1999).

Examples where UASs have been used for specific vegetation/habitat types show that the challenges are to a certain extent case specific, depending mainly on natural characteristics. UASs were successfully applied in habitat mapping and monitoring for nature conservation purposes. Decisions on which methods and data to choose for UAS

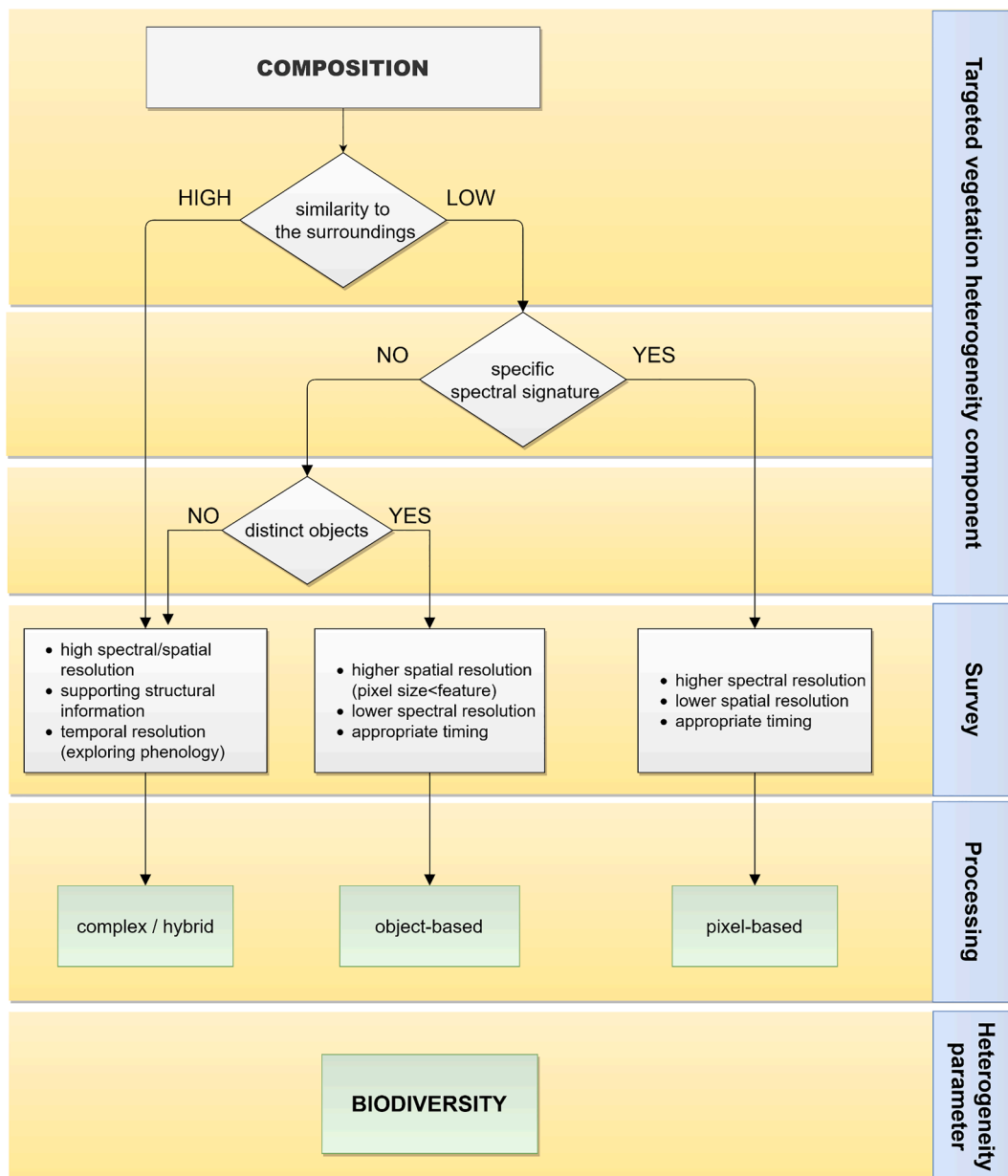


Fig. 3. Workflow for UAS-based detection of plant species composition (biodiversity, adapted from Müllerová, 2019).

assessment of plant composition shall be driven by the target species/vegetation characteristics. For species expressing low spectral and structural similarity to the co-occurring species, coarser resolution data combined with simple models would be sufficient; whereas for less distinct species, highly similar to their surroundings, a more complex approach must be applied (Müllerová, 2019). Accurate distinction between similar species is demanding in respect to the data resolution (spatial, temporal and/or spectral) and algorithms (using more complex or hybrid approaches); subtle differences in phenology or structure can help (Fig. 3).

For species that do not have a specific form (such as patchiness, and shape of individuals, inflorescences or the leaves) but are rather spectrally distinct from their surroundings, the pixel based approach might be appropriate (Müllerová et al., 2017a; Tamondong et al., 2020). Information on shape, texture and context can markedly improve precision of the species determination (Franklin, 2018; Gini et al., 2014). This is especially true for the species and/or vegetation types that have distinct shapes and/or form patches (Müllerová et al., 2017b), and for low cost digital Red-Green-Blue (RGB) cameras lacking near infrared band and with high intercorrelation of visible bands (Pande-Chhetri et al., 2017). In general, OBIA represents a powerful tool in UAS data processing that can to some extent reduce the noise and consequent “salt and pepper” effect caused by ultra high spatial resolution. However, the extreme detail leads to a large number of objects with varying spectral, morphological and proximity characteristics, which can be controlled by choosing the right spatial resolution (Yuba et al., 2021).

For complex vegetation patterns and species with a high degree of similarity, there is a need for higher spectral/spatial/temporal resolution data, multiple data sources, three-dimensional (3D) information on stand height and structure and/or advanced algorithms (e.g. Kattenborn et al., 2020; Martin et al., 2018; Michez et al., 2013). Machine and deep learning algorithms are particularly helpful to map complex vegetation, and can overcome the problem with laborious collection of training samples and ultra high spatial resolution (Liu et al., 2018).

To summarize, provided that the methodological workflow of the mission follows the species/habitat characteristics, UASs represent a powerful tool to be employed in biodiversity monitoring schemes, enabling assessment of species diversity and detection and mapping of individual species and/or habitat types. Thanks to very high spatial and temporal resolution, either repeatedly throughout the phenological season or using the optimal time window for the data acquisition, it is possible to map even the species that are difficult to distinct from the surroundings, especially in case information on 3D structure is added, several sensors combined and/or sophisticated algorithms of machine and deep learning deployed.

3.2. Ecosystem structure: Measuring biomass, volume and stand complexity

The structure belongs among the main drivers of resource variability. Particularly in forest environments, fine-scale information on canopy structure derived from UAS like canopy cover, gaps, vertical and horizontal structure and spatial aggregation are important since structure drives many ecological processes such as understorey diversity, seed establishment, and forest regeneration, and shapes important ecosystem services (Bagaram et al., 2018; Getzin et al., 2012; Kent et al., 2015).

Examples of assessing structure can be found for various ecosystems, such as shrublands (Cunliffe et al., 2016; Swetnam et al., 2018) and riparian areas (Meneses et al., 2018), but most UAS studies regard forests. In the latter, vegetation structure is addressed to analyse the stand complexity or quantify its volume/biomass (Fig. 4). 3D information is generated by different sensors and stored as point clouds for further processing. Normalization of ground using precise Digital Terrain Model (DTM) is greatly recommended (Aguilar et al., 2019). For 3D information, both passive (optical) and active (e.g. LiDAR) sensors can be used (Camarreta et al., 2020). While 3D information describing the upper

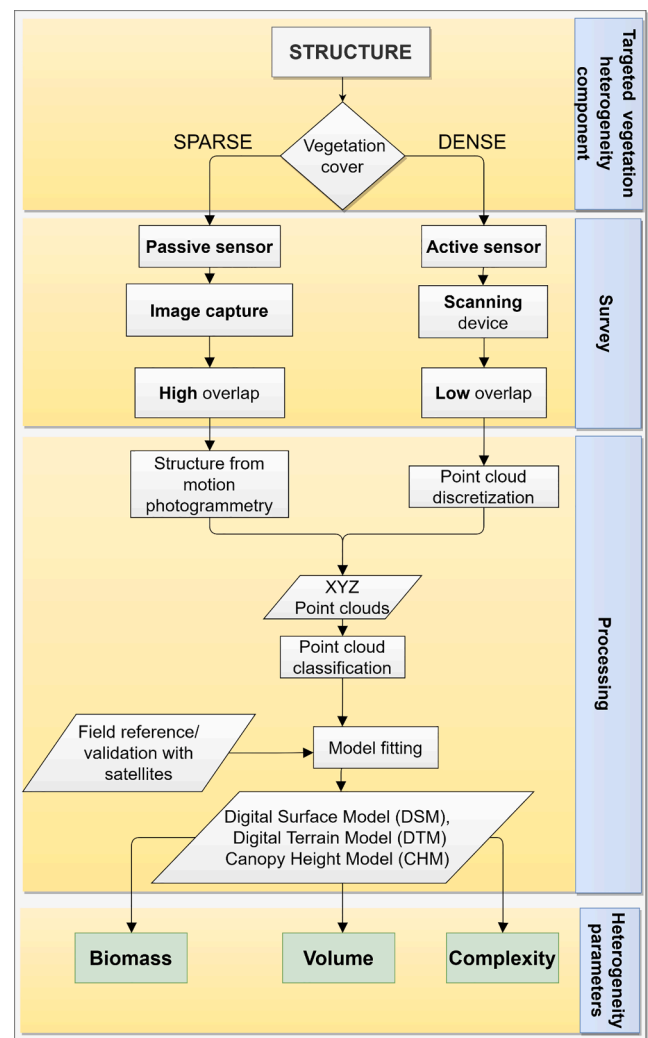


Fig. 4. Workflow for UAS-based ecosystem structure assessment.

most canopy layer can be acquired by various sensors, LiDAR sensors are necessary for the generation of DTM under the forest canopy and assessment of structural layers that is intrinsically related to the stand density and complexity.

Laser scanning provides the most accurate information on structural components including height, canopy dimensions, gaps, and biomass, and if mounted on UAS it can provide very high spatial details. However, its application is still limited due to the high costs and the fact that the sampled area is substantially smaller compared to the aerial LiDAR. In case of dense stands with complex multidimensional structure, active sensors (LiDAR) or DTM-independent approaches are an option (Gianetti et al., 2018), whereas passive sensors are not able to penetrate the canopy (especially during leaf-on season) to reach the inner structural layers and the ground (Kašpar et al., 2021). Still, for less dense and complex stands, passive optical sensors represent a low cost and simple solution to provide information on forest attributes including height, canopy dimensions, and biomass (Baltasvicius et al., 2008; Dandois and Ellis, 2010; White et al., 2015). Photogrammetric point clouds are derived from overlapping imagery by using the digital imaging photogrammetry approach such as Structure from Motion (SfM) algorithm (Westoby et al., 2012), preferably with high overlap and lower flight altitudes (Seifert et al., 2019).

Still, many issues remain using passive instead of active sensors, especially related to closed or vertically complex canopy and shadows (Dandois and Ellis, 2013). Precision of results is also species specific;

while for evergreen single-stemmed tree species, photogrammetric products are comparable to LiDAR in capability to capture forest structure and estimate the biomass (especially for regularly designed forest plantations and open forests), it is less reliable for deciduous trees (especially during leaf-on period) and for canopy cover above 60 to 80% (Guerra-Hernández et al., 2017; Wallace et al., 2016). To overcome these problems, the data sources can be joined, such as adding spectral properties to LiDAR, or combining LiDAR-derived DTM and a series of photogrammetrically-derived DSMs to assess changes in the canopy (Lisein et al., 2013; Wallace et al., 2016). However, in such cases, precise co-registration is required. Alternatively, analyses of forest structure and gaps can be based solely on optical properties of UAS imagery, using the effect of darker objects (shaded gaps; Bagaram et al., 2018; Getzin et al., 2014). Nevertheless, such approach might bring even more imprecision with dense and/or highly vertically heterogeneous canopies.

As summarized in Fig. 4, from the examples proposed from different communities and environments, the choice of the sensor (active vs passive remote sensing) is particularly important for the structural assessment, and should respect the complexity of the stand to be sampled.

3.3. Plant status: phenology and plant stress

Plant status is driven by phenological stage and physiological status in response to endogenous (circadian and seasonal rhythms) and exogenous factors (abiotic stressors). High spatial and temporal resolution of

UASs provide an unprecedented detailed insight into the ecosystem's response to (a)biotic stress (D'Odorico et al., 2020). Most of the papers using UASs to assess plant stress are performed in agricultural and forestry applications focusing only on a single species at a time, while for species rich natural ecosystems, such studies are largely lacking (but see e.g. Banerjee et al., 2020; Zhang et al., 2017).

Studied phenomena can range from distinct and well defined phenomena by spectral properties that can be assessed using relatively low spatial, temporal and spectral resolution, to the less conspicuous/symptomatic phenomena, where the most sophisticated hyperspectral and thermal sensors coupled with complex modelling are needed (Fig. 5). In addition, even defining specific factors affecting the particular plant physiological status might be difficult due to the fact that the plant response to different types of stress is often indistinctive (Jones and Vaughan, 2010).

For example, UASs thermal imagery and the related leaf energy balance model estimations can be used to detect (a)biotic stress early since stomata are highly reactive to any stress, from abiotic stress such as drought (Gago et al., 2017) and herbivory attacks (Smigaj et al., 2019). In addition, stomata closure promotes general increase in canopy temperature that can be used as a physiological stress indicator (Smigaj et al., 2019). Very high spatial resolution of UAS data opens the opportunity to assess drought stress at individual level.

As for phenological stage, UASs provide both very high spatial detail and possibility of right timing of the data acquisition to capture a particular phenomenon, e.g. flowering (Carl et al. 2017; Müllerová

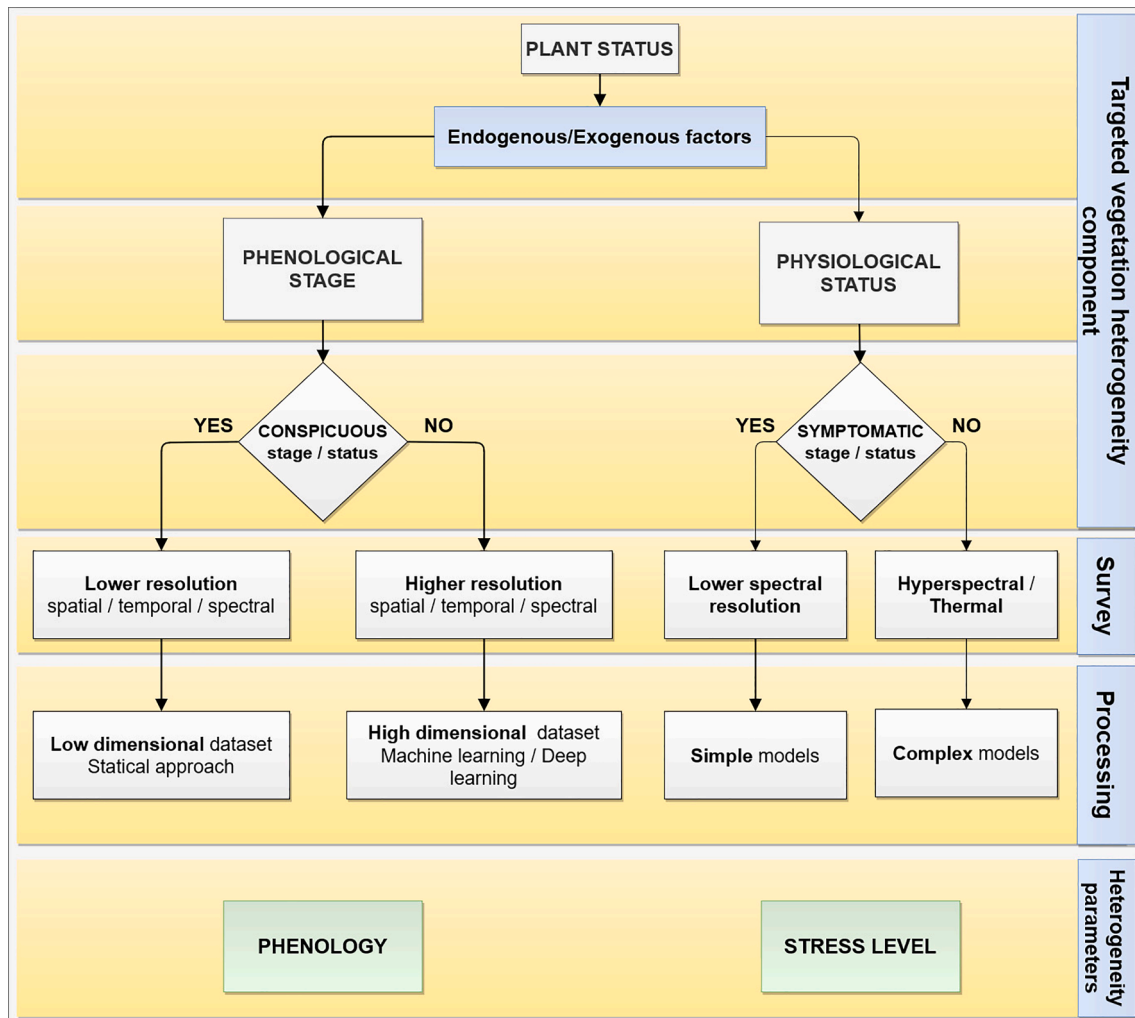


Fig. 5. Workflow for UAS-based assessment of plant status.

et al., 2017b; de Sá et al. 2018). Unlike the satellite data, UAS surveys allow data acquisition on demand and enable to zoom on individual plants within the stand, and therefore to study variation within plant populations and/or trace the very first or last individuals of particular phenophase (Fawcett et al., 2020). Improvements of sensor resolution and/or ability of UAS to fly very close to the canopies obtaining sub-cm resolution (such as for nano and micro-UASs) are still not widely employed even though the spatial information they provide is tremendous. For instance, ultra high spatial resolution enables the detection of flowering individuals without the need for higher spectral resolution sensors, opening a new opportunity to use micro-UASs to characterize ecosystem dynamics (Gago et al., 2020).

3.4. Ecosystem dynamics: Disturbances and regeneration

Many natural processes are dynamic, addressing plant composition, ecosystem structure or plant status from a temporal perspective. Whereas data collection itself follows the workflows suggested in previous sections depending on the type of ecosystem/phenomenon and heterogeneity addressed, a change detection approach is adopted for repeated UAS measurements to study the changes in time. Still, we have to bear in mind that for different components of heterogeneity (composition, structure and status), the dynamics can show different ranges and dimensions that must be reflected by the survey design.

To assess dynamic processes, such as phenological development or stress response, the temporal dimension is indispensable. Operational satellite data are the most commonly used for this purpose, however due to lower spatial resolution they are suitable mostly at global and landscape scales and for large homogeneous stands (Berra et al., 2019), and their temporal coverage is limited by their revisiting frequency. On the contrary, UAS can provide very high spatial and temporal resolution (revisiting time), and flexible, frequent and “ad hoc” data acquisition. Thus, UASs allow to explore the phenological cycle in unprecedented detail, e.g. individual-level phenological patterns and intraspecific variation (Fawcett et al., 2020; Park et al., 2019). Because of unprecedented fine scales, UAS are also very appropriate for dynamic ecosystems such as riparian areas and river ecosystems (Laslier et al., 2019; Michez et al., 2016).

In case of dramatic events, absence of data is common. Here, flexibility provided by UAS brings immediate revenues, since the surveys need to be conducted as soon as possible after the disturbance to support the decision-making and prevent further damage. Flights can be conducted immediately, eliminating the risk of injury linked to field surveys, such as in case of forest fires and windthrow (Mokros et al., 2017; Yuan et al., 2015). UASs was also shown to assist in monitoring post-fire regeneration (Fernández-Guisuraga et al., 2018; Larrinaga and Brotons, 2019).

Insect disturbances in forests act at varying spatial and temporal scales, and understanding local dynamics as well as early detection of infestation onsets, which can be both facilitated by UAS, are very important (Senf et al., 2017). A variety of approaches and sensors were applied in UAS analyses of forest infestation dynamics; not only sophisticated hyperspectral sensors (Näsi et al., 2018) but also simpler sensors, such as multispectral or even low cost consumer grade cameras (Cardil et al., 2017; Minařík and Langhammer, 2016). UAS can also serve to study natural regeneration of forest after the outbreak (Röder et al., 2018). UAS assessment allows more cost-effective monitoring compared to the field surveys, and enables to acquire data at very high frequency providing observation data about the gradual spectral change after the attack. It can therefore be used to estimate the impacts of forest defoliation in spatial and temporal terms, for better assessing outbreak spread patterns and providing guidance in forest management programs. For possible extension of monitoring over larger areas, integration of UAS and satellite data is to be considered.

4. Research gaps and future perspectives

Exploring the capabilities of different statistical, spatial, temporal and textural settings, UAS represent a huge potential for assisted vegetation assessment. There is no doubt that recent technical advances significantly increase capabilities and accessibility of both platforms and sensors. One such example is the geometrical precision of UAS orthomosaics. Geometric distortions, particularly significant in forest or other complex environments (see Ludwig et al., 2020), can to a large extent deteriorate reproducibility, complicate the assessment of dynamic processes and decrease the power of change detection in general. Even though the number and design of ground control points are still an open debate in the scientific community (Padró et al., 2019), recent advances in affordable miniaturized GPS and on board UAS (such as Real-time kinematic - RTK) push the boundaries towards automation and increased geometric accuracy without (or with severely limited amount of) field work.

In addition, technological progress is opening brand new opportunities, such as extraction of meaningful information through standardized procedures without a need to be a specialist in the remote sensing field, mechanistic models and/or on-the-fly incorporation of ground and plant measurements to calibrate the remote sensing models, different flight modes (flying closer to the target, longer flights covering larger area, penetrating the forest canopy to assess the forest herb layer, Hyypä et al. 2020; Ryddel et al., 2020), autonomous/real-time sensing (improving temporal resolution to assess plant stress, detection of non forested and eroded areas in tropical rainforest, Cruz et al. 2016), or targetless workflows to capture accurate reflectance values (Schneider-Zapp et al., 2019).

However, even though technological advances are expected to overcome many limits of current technologies and methodologies, some constraints will certainly remain, such as UASs regulations and restrictions. Recent harmonization of UASs regulations within the EU will definitely foster collaborative efforts and promote competitive development in the field.

5. Concluding remarks

UASs offer products and applications never imagined just a decade ago. However, optimizing the workflow is still a matter of discussion. In our review, we summarized and generalized the procedures of UAS-based vegetation research. Aiming to provide a framework for optimal workflow to characterize vegetation complexity with UAS, we divided it by the major components of vegetation complexity: biodiversity, structure and status, covering also the dynamic processes. We propose a general framework and detailed decision trees for each component including examples, and synthesize that any UAS survey must be built respecting the following steps: (i) get familiar with the phenomenon to be studied; (ii) choose suitable UAS and appropriate temporal, spatial and spectral resolution; (iii) select either simple or more sophisticated processing, classification algorithms and models depending on the complexity of the studied phenomenon; and (iv) carefully interpret the results considering the weaknesses and limits of UASs methods. During the process one must bear in mind that the simpler the procedure, the more robust, repeatable, applicable and cost effective it is; proper design minimizes the efforts and maximizes the best results, and appropriate temporal, spatial and spectral resolution are essential key-points. The experimental design must thus be adapted to the studied phenomenon and not the other way around. Still, even if UAS technology is capable and widely available, a combination of profound ecological background (Goddard et al., 2021) and robust knowledge on the limits of UAS technology are indispensable to avoid misinterpretation of the findings.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contribution

JM conceived and co-ordinated the writing, RK and XG supported formulation of the framework and the paper outline, and all authors took an active part in writing the paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108156>.

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Appendix 2.

PAPER 2. **Müllerová**, J., Brundu, G., Große-Stoltenberg, A., Kattenborn T., Richardson, D.M. (2023a). Pattern to process, research to practice: Remote sensing of plant invasions. *Biological Invasions* 25: 3651–3676. <https://doi.org/10.1007/s10530-023-03150-z>



Pattern to process, research to practice: remote sensing of plant invasions

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Abstract Processes that drive plant invasions play out across multiple spatial and temporal scales. Understanding individual steps along the introduction-naturalization-invasion continuum and its drivers is crucial for management. This review, targeting the broad audience of invasion scientists, field ecologists and land managers, summarizes the state-of-the-art and potential of remote sensing (RS) in plant invasion science and management. It identifies challenges and research gaps, discusses the discrepancies between

technology, science and practice, and suggests ways of addressing some of these issues. Mapping, modelling and predicting invasion processes across scales is a major challenge since they are dynamic and highly complex. Integration of RS data collected at different spatial and temporal scales (“rocking” across scales) has the potential to elucidate the dynamics of invasions and to reveal its drivers, thereby improving the efficiency of control measures. Increasing spatial/temporal resolution of imagery from satellites and drones has much potential to (i) precisely identify even less conspicuous invasive species; (ii) map invasion dynamics; and (iii) provide information on

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environmental variables and landscape structure at scales fine enough to capture underlying ecological processes. Until now, RS research has focussed primarily on spatio-temporal patterns of plant invasions. Other more challenging topics, such as early monitoring, and revealing the invasion mechanisms and impacts have received less attention. Despite the power of RS technology and recent developments, large discrepancies remain between possibilities and actual implications in research and practical management of invasions. Although recent technological advances, such as powerful algorithms, cloud solutions, and data streams from citizen science, might overcome some limitations, the mutual dialog among field ecologists, managers, invasion scientists and RS specialists remains crucial; our review contributes to such communication.

Keywords Invasion ecology · Invasion science · Monitoring schemes · Remote sensing · Spatio-temporal dynamics

Introduction

Biological invasions are a major threat to biodiversity and cause economic damage worth billions of dollars every year (Diagne et al. 2021; Zenni et al. 2021). Processes that drive plant invasions involve multiple steps, from introduction, establishment, survival, persistence, dispersal and landscape-scale invasion (Theoharides & Dukes 2007). Prevention and effective management of invasions demands an understanding of the dynamics at different scales that drive progression along the introduction-naturalization-invasion continuum (Hulme 2006; Richardson & Pyšek 2012; Haccou and Serra 2021). Invasions show spatio-temporal patterns that depend on both the invader and the invaded habitat (Pyšek and Hulme 2005). The perception of these patterns and processes can also change with the scale of observation (Richardson 2011).

Remote sensing (RS) is an important data source for spatio-temporal information about plant invasions that has the potential to reveal new insights on invasion dynamics. Applications of RS in the domain of plant invasions range from mapping and monitoring invasion patterns (including retrospective analyses) to the provision of information on the landscape and environmental characteristics for studies on invasion

processes, such as dynamics, mechanisms, drivers and impacts, and from invasion science to the practical management of invasions at different spatial and temporal scales (Fig. 1, Table 1).

The level of utility of RS in practical management of plant invasions is determined by the characteristics of the plant and the stage of the invasion. To benefit fully from the technology we need to define appropriate spatial and temporal scales to adequately address different phenomena related to plant invasions, and specify possible contributions of RS during individual invasion phases that can be separated into prevention, early detection and rapid eradication, and restoration (Regulation (EU) no. 1143/2014 on invasive alien species) (Fig. 2).

Recent research on RS and mapping of plant invasions has benefited greatly from the rapid development of technology and data availability. Key innovations have included increased spatial and temporal resolution, coverage, availability and accessibility of RS data, platforms, sensors, software and enhanced computational power. These advances open opportunities to develop new approaches to (i) precisely detect even the first onset of invasion and/or small and fairly inconspicuous invasive species; (ii) map invasion dynamics from multi-temporal series of RS data; (iii) help to assess and quantify invasion impacts; (iv) support risk assessment and the development of predictive models; and (v) improve our understanding of invasion mechanisms by providing spatially continuous information on the invaded environment (environmental variables and landscape structure) at scales fine enough to capture underlying ecological processes. This paper, targeted to the broad audience of both invasion ecologists and land managers, outlines the potential and challenges of RS, discusses the discrepancies between science and practice, and proposes solutions on how current technological developments could alleviate some of these issues.

From patterns to processes—rocking across scales

Ecological systems are characterized by cross-scale interactions in time and space (Peters et al. 2007), and describing and understanding these interactions has always been crucial in ecological research (Turner et al. 1989). Neglecting the fact that ecological patterns and their underlying processes are

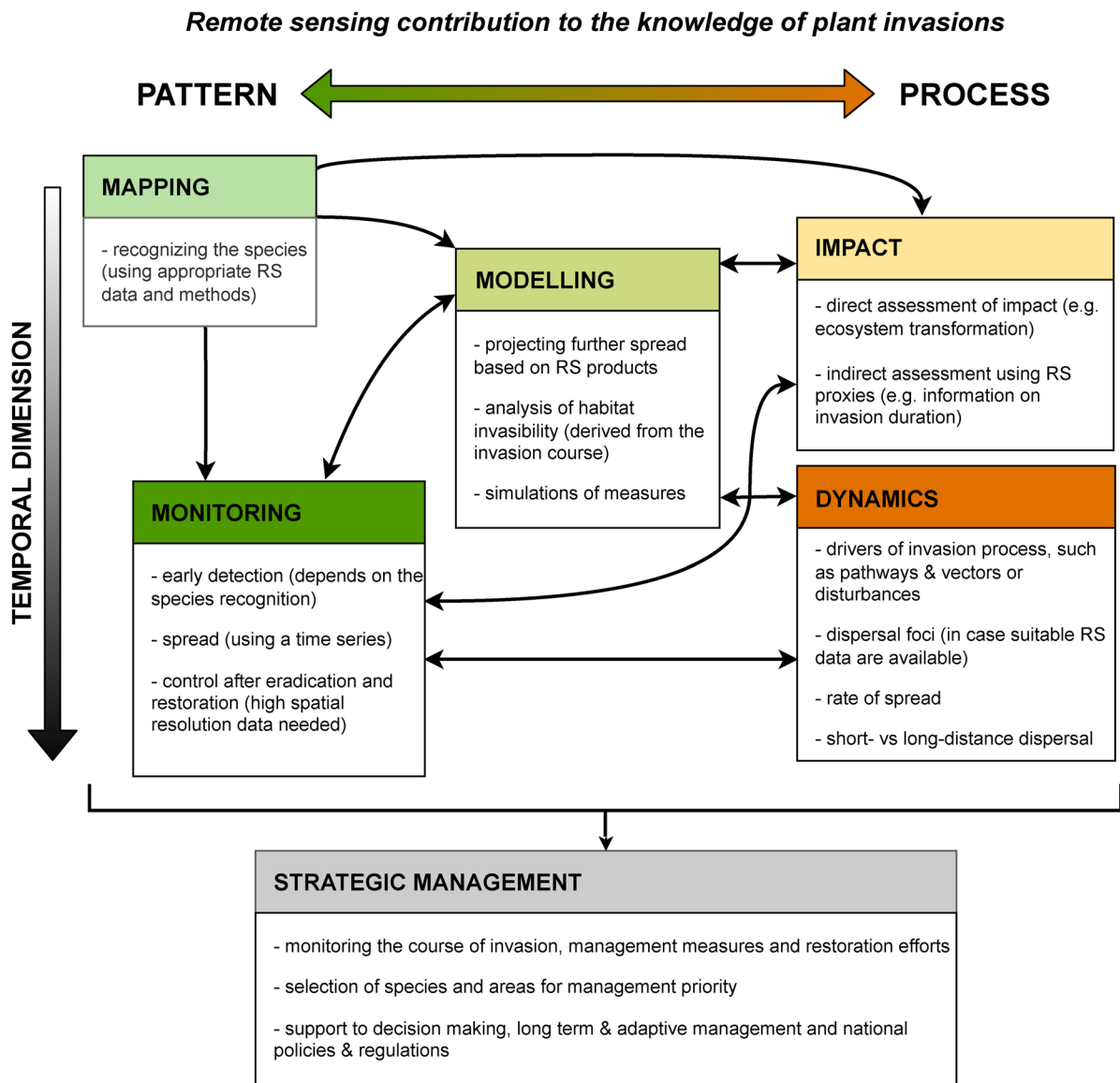


Fig. 1 A conceptualization of the contribution of remote sensing to the knowledge of plant invasions (for examples see Table 1)

scale-dependent might lead to conclusions with limited interpretation value (Chase 2014; Chase et al. 2018). Likewise, plant invasions are characterized by processes with clear spatio-temporal aspects and dimensions (Latombe et al. 2021). Therefore, some processes may be only discernible at certain scales (Bailey 1985), and a thorough understanding of ecosystem properties at one level may be insufficient to understand the whole phenomenon (Odum and Barrett 1971). Remote sensing has huge potential to

bridge spatio-temporal scales in ecological studies (Kerr and Ostrovsky 2003), and to contribute to a better understanding of invasion processes and dynamics by improving the sampling and observation of important parameters related to occurrence, spread and impact of invasive plants at multiple scales (c.f. Latombe et al. 2017). Ideally, such approaches facilitate the assessment of the start of invasions at fine scales (individual plants) as well as patterns and processes at broader spatial scales, while also allowing

Table 1 Examples of the contribution of remote sensing to the study and management of plant invasions (related to the conceptual diagram at Fig. 1)

Topic	Objective	References (examples)
Mapping	Recognizing the species	Andrew & Ustin (2008); Carter et al. (2009); Dai et al. (2020); Evangelista et al. (2009); Gholizadeh et al. (2022); Große-Stoltenberg et al. (2016); He et al. (2011); Huang & Asner (2009); Huang & Geiger (2008); Lopatin et al. (2019); Müllerová et al. (2017a, 2017b); Niphadkar & Nagendra (2016); Pu et al. (2008); Ramsey et al. (2005); Resasco et al. 2007; Sandino et al. (2018); Shouse et al. (2013); Silván-Cárdenas & Wang (2010); Singh et al. (2015); Skowronek et al. (2018); Vaz et al. (2018, 2019); West et al. (2016); Wilfong et al. (2009)
Monitoring	Early detection	Asner & Vitousek (2005); Dash et al. (2019); Glenn et al. (2005); Lass et al. (2005); Slingsby et al. (2020)
	Spread	Bazzichetto et al. (2018); Gavier-Pizarro et al. (2012); Müllerová et al. (2005, 2013); Ren et al. (2021)
	Control after eradication and restoration	Lishawa et al. (2017); Meng et al. (2012); de Sá et al. (2018); Sankey et al. (2016)
Dynamics	Drivers of invasion process	Bazzichetto et al. (2018); Cunliffe et al. (2016); Hastings et al. (2005); Hellmann et al. (2017); Hobi & Ginzler (2012); Lefsky et al. (2002); Pyšek et al. (2008)
	Dispersal foci	Civille et al. (2005); Müllerová et al. (2013)
	Rate of spread	Andrews & Ustin (2010); Müllerová et al. (2005); Pyšek et al. (2008)
Modelling	Short- and long-distance dispersal	Andrews & Ustin (2010); Pergl et al. (2011)
	Projecting further spread	Ahmed et al. (2020); Barona & Mena (2014); Huang et al. (2008); Nehrbass et al. (2007)
	Analysis of habitat invasibility	Andrews and Ustin (2010); Bazzichetto et al. (2018); Mouta et al. (2021); West et al. (2016); Zimmermann et al. (2011)
Impact	Direct assessment	Asner et al. (2008); Ewald et al. (2018); Horn et al. (2017); Ren et al. (2021); Rosso et al. (2006)
	Indirect assessment using RS proxies	Asner & Vitousek (2005); Barbosa et al. (2017); van Cleemput et al. (2020); Dostál et al. (2013); Große-Stoltenberg et al. (2018); Hellmann et al. (2017); Helsen et al. (2020); Hughes et al. (2014); Jandová et al. (2014); Ren et al. (2021); Shiferaw et al. (2021)
Transfer to management	Monitoring the course of invasion, management Measures and restoration efforts	Bedford et al. (2018); Dahal et al. (2022); Doody et al. (2014); Lishawa et al. (2017); Rebelo et al. (2021); Rodgers et al. (2018)
	Selection of species and areas for management priority	Morisette et al. (2006); Mouta et al. (2021)
	Support to decision making, long term & adaptive management, national policies & regulations	Andrews & Usting (2010); Dahal et al. (2022)

for assessment over time. The idea of exploiting multiple scales or zoom-levels is neither new nor limited to the field of biological invasions. According to Richardson (2011), bird watchers frequently zoom in and out with binoculars (they use the term “rocking”) to identify key features of bird species that are difficult to identify. The same principle of rocking, i.e.

moving back and forth across scales, can be applied in RS by using multi-temporal data or data at different spatial scales that are becoming increasingly accessible to bring new insights to our understanding of the invasion process.

Remote sensing observations provide the means for moving across space and time (rocking) by scaling

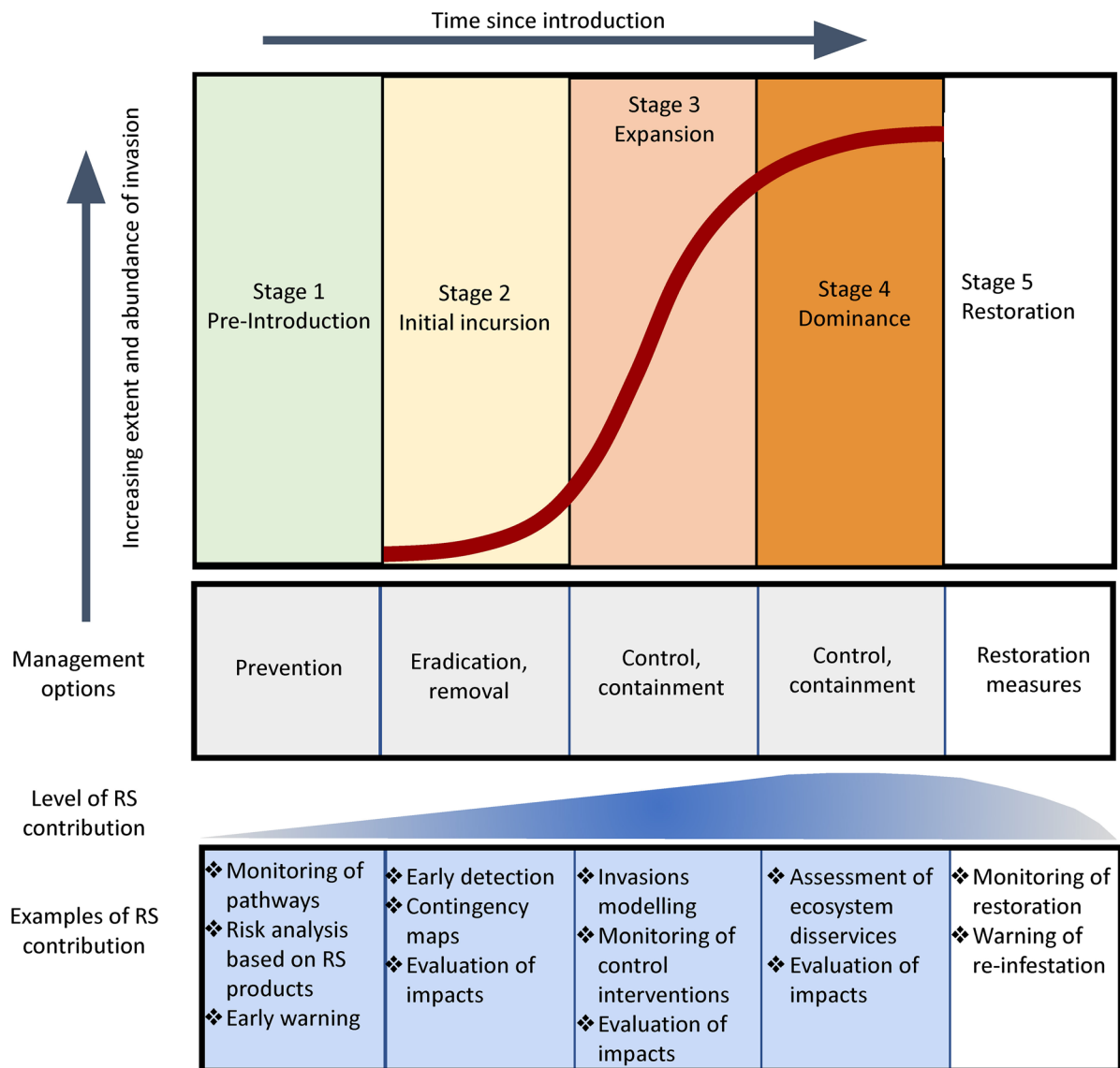


Fig. 2 Potential contribution of remote sensing to different management options during the course of plant invasion. The red line in the top section indicates the extent and abundance

of invasion. The background diagram (invasion curve) was inspired by van Wilgen et al. (2014)

up and down in space between site-and landscape scales by making use of drones (unmanned aerial systems, UAS, unmanned aerial vehicles, UAV, or remotely piloted aerial systems, RPAS), aerial and satellite imagery, and back and forth in time, utilizing the growing archives of analysis ready data (Giuliani et al. 2019) from, for example, the Landsat Archive (Dwyer et al. 2018), fused Landsat and Sentinel data (Frantz 2019; Lucas et al. 2019), the

Brazilian CBERS data cube (Picoli et al. 2020), national archives (Dhu et al. 2019) historical data-sets such as the SPOT World Heritage Programme (Nosavan et al. 2020) and up-to-date, high-resolution data from nano satellites (Boshuizen et al. 2014; Kopacz et al. 2020). Such repeated data acquisition over broad scales at appropriate intervals, e.g. across seasons, can facilitate capturing wall-to-wall key phenological phases of invasive species across

heterogeneous landscapes (Andrews and Ustin 2010; Royimani et al. 2019). Combining RS data with different spectral, spatial and temporal resolution can be challenging (but see e. g. Harmonized Landsat Sentinel-2 data product, Pastick et al. 2020). Such combinations nonetheless allow for tweaking the focus on different spatio-temporal aspects of plant invasions (rocking) to achieve a more complete picture of the invasion dynamics (Fig. 3).

By moving (rocking) across spatial and temporal scales, RS can widen the perception, enabling not only mapping of plant distributions more precisely (Kattenborn et al. 2019a), but also opening opportunities for exploring invasion processes, monitoring invasion dynamics and studying impacts at different levels and scales (Große-Stoltenberg et al. 2018). Such changes in perspective can provide the context required to fully understand the driving forces behind aspects such as the site history in terms of temporal scales, or the links between the behaviour of invasion (meta) populations at the site level with landscape features, such as disturbed sites or corridors that serve as pathways. There is a need for more RS-based studies on plant invasions across multiple scales and for studies that go beyond simple description of the invasion state towards understanding of the invasion processes, such as the impact of invasion (Vaz et al. 2018). Hence, land managers will need to adapt their skills to benefit fully from a multiple-scale approach by utilizing, in new ways, spatially and temporally rich datasets. Improved coverage of RS data over space and time is increasing the power of rocking. Such increased power is opening many new opportunities to explore the roles of diverse biotic and abiotic variables in launching and sustaining plant invasions. These advances offer new insights into invasion patterns and processes, but are also creating options for testing ecological concepts, and paradigms and for developing new management tools.

From research to practice

Remote sensing contribution to the invasion framework

Following the typical invasion curve (Fig. 2), expansion and dominance stages are the phases most commonly addressed using RS, employing a

variety of sensors, platforms and algorithms at different spatial and temporal scales with the choice depending mainly on the size and conspicuousness of the invader (e. g. Bolch et al. 2020; Huang and Asner 2009). On the other hand, initial stages of invasion, measures of prevention and early warning/early detection of invasion onset, evaluation of invader impact and inspecting the efficiency of control, eradication and restoration measures are rather difficult to address using RS (see Sect. “[New solutions](#)”). However, with growing availability of ultra-high spatial resolution data from drones, coupled with high temporal frequency of data acquisition, miniaturized powerful platforms and sensors (hyperspectral and Light Detection and Ranging, LiDAR; Dash et al. 2019), sophisticated algorithms, such as deep learning (see Sect. 5.1), and automation of drones (autonomous flights, real time monitoring), the possibilities for detecting even small patches of invasive plants are increasing. Nonetheless, the limited coverage of these kinds of data means that they are not particularly suitable for operational monitoring; they are more useful for targeted screening (e.g. of vulnerable habitats or sites of high nature conservation value). This means that the efficient use of drones for early detection requires coupling with modelling tools, such as habitat suitability and predictive modelling to identify target areas for detailed drone screening. Another possibility of early warning is via change detection, where rather rapid change in the spectral signature of a pixel or structural variables such as biomass increase may indicate invasion that is often pronounced by rapid growth (Asner and Vitousek 2005; Slingsby et al. 2020). Such a method is rather imprecise; the derived information therefore only provides a trigger for field surveyors and land managers to conduct more targeted surveys. On the other hand, it can be used rapidly and relatively easily without the need for expert knowledge of the situation. It is also applicable almost irrespective of the invasive species if the revisitation time of the satellite or other RS platforms is frequent enough. For inspecting the efficiency of eradication, control, and restoration measures, similar tools as for early detection could be applied, although this facet of RS application remains underrepresented [but see examples of tamarisk (Meng et al. 2012; Sankey

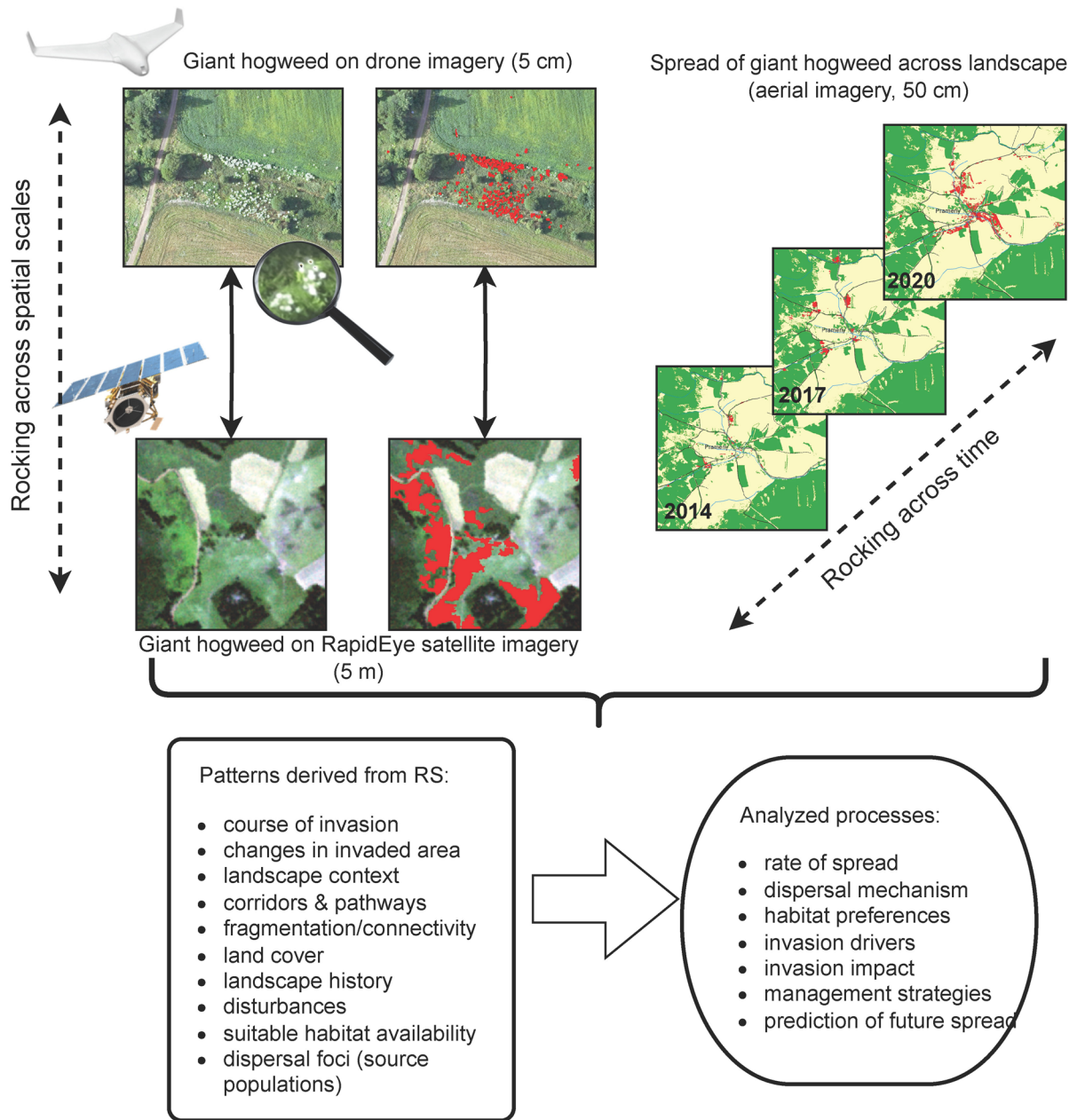


Fig. 3 An example from an invasion of giant hogweed (*Heracleum mantegazzianum*) illustrates how rocking across space and time can help to better understand invasion dynamics. Rocking from the finer to coarser and from the current to archival imagery enabled the reconstruction of the invasion process at the landscape scale, and deriving multiple invasion patterns

that later served to analyse invasion processes (based on works of Müllerová et al. 2005, 2013, 2017b; Nehrbass et al. 2007; Pyšek et al. 2008; Pergl et al. 2011; Dostál et al. 2013). Areas shaded in red indicate giant hogweed presence classified using drone and satellite imagery

et al. 2016; Bedford et al. 2018) and *Acacia longifolia* biocontrol (de Sá et al. 2018)].

The contribution of RS to plant invasion science spans a variety of life forms/domains, and applications along the introduction-naturalization-invasion

continuum (Fig. 2), offering insights on both invasion patterns and processes, ranging from single dimension to spatially and temporally multi-scaled approaches and from scientific knowledge of invasion processes to the practical management of plant invasions (Fig. 1 and Table 1). Adoption of a particular RS approach is driven by the characteristic of the species or the phenomenon to be explored, as well as the overall aims of the study (for details see decision trees in Müllerová et al. 2021). Table S1 in Supplementary Material provides illustrative examples of RS application for different species, life forms and purposes, including technical details.

The core of RS applications lies in mapping and monitoring the invasion progress to inform management. Remote sensing technology can both provide information on invasions and assess aspects of invasion dynamics. The occurrence of the target species can be directly mapped from RS data from a single or multiple dates (Bolch et al. 2020; Evangelista et al. 2009; He et al. 2011; Huang and Asner 2009; Müllerová et al. 2013; Niphadkar and Nagendra 2016; Vaz et al. 2018, 2019). Plant invasions can also be detected indirectly; for example the rapid growth of invasive plants can be monitored as an increase in vegetation greenness by using vegetation indices (Pu et al. 2008).

Spatial heterogeneity of landscapes greatly affects the spatial spread of invasive species (Hastings et al. 2005), and the landscape parameters and dynamics derived from RS data can help to disentangle and describe the invasion. Important parameters pertaining to spatial heterogeneity can, for example, be derived from airborne LiDAR data (Bazzichetto et al. 2018; Lefsky et al. 2002; Hellmann et al. 2017; Potgieter et al. 2019), using photogrammetric methods based on drones (Cunliffe et al. 2016), or aerial (Price et al. 2020) and satellite stereo imagery (Hobi and Ginzler 2012).

Both direct and indirect approaches are subject to types of uncertainty. Direct recognition of particular invasive species/or lower taxa depends largely on its similarity to the surrounding vegetation driven by the species' characteristics and local context (Andrew and Ustin 2008) and depending largely on the spatial, spectral and temporal resolution of the RS data. Consequently, both direct recognition and similarity are rather specific to the site, case and data used, and may vary widely even for a single species. The approach

of indirect mapping is more robust to the individual characteristics of particular invaders but can also bring confusion due to the fact that a sudden increase in vegetation greenness can be attributed to many processes including uncommonly high precipitation or local fertilization. Such problems make it hard to formulate generally applicable recommendations on how to use RS for invasive plant species mapping.

In cases where the invader is distinct enough and archival data are available, RS can be used in retrospective analyses using the rocking approach detailed above (Gavier-Pizarro et al. 2012; Müllerová et al. 2005). To reconstruct the course of invasion, archival remote sensing data can be combined with oral histories, museum records, and a variety of publications (scientific journals, newspapers and popular magazines)(Civille et al. 2005). Such information can be used to identify spread dynamics and develop hypotheses concerning dispersal mechanisms and drivers (Pyšek et al. 2008). RS can also support invasion science, conservation practice and management decisions indirectly by providing input data for various types of models for simulating current and future distribution, management measures, risk assessment, or invasion dynamics (Nehrbass et al. 2007; Zimmermann et al. 2011; Rocchini et al. 2015; West et al. 2016; Mouta et al. 2021; Große-Stoltenberg et al. 2023). One popular approach for modelling the spread dynamics between the individual time steps involves the use of cellular automata. Cellular automata are simple spatio-temporal models in which cells (pixels) change their state over time according to some user-defined rules (Hui and Richardson 2017). Such rules can be optimized using multiple reference time-points where the states are known. Successful applications of cellular automata in combination with RS-based maps are provided by Huang et al. (2008) and Barona and Mena (2014).

Unlike detection and monitoring, the impact of invasive species on ecosystem functioning or services is difficult to assess, measure or monitor using RS. Impacts are scale-dependent and can vary greatly across space and time (Ricciardi et al. 2013) depending on invader abundance (Latzka et al. 2016), cover (Barney et al. 2013), spatial extent (Barney et al. 2013), spatial heterogeneity of the landscape (Thiele et al. 2010; Hellmann et al. 2017; Ren et al. 2021) and complex interactions between features of the invader and the provision of ecosystem services (Potgieter

et al. 2019; McInerney et al. 2021). Although methods have been developed for spatial upscaling of invader impacts on ecosystem functioning using RS data (e.g. Hellmann et al. 2017), the temporal dimension is often addressed by studying gradients of invasions (Hellmann et al. 2017) and relating cover to impact (Große-Stoltenberg et al. 2018; Shiferaw et al. 2021). In ecology, the common challenge of acquiring sufficient data with appropriate temporal resolution and quality is often addressed by using space-for-time substitution (SFTS) (Pickett 1989). However, this approach has been criticised, as inferring ecological processes from snapshot data might lead to inaccurate conclusions. New approaches are required that combine time-series with spatial data in causal ecological models (Damgaard 2019). Rocking in space and time using RS data can provide an appropriate framework for unravelling ecological impacts of invasive species on ecosystem functioning. RS-based information on the spatial patterns of the invader could potentially be used, for example, to assess resource competition between native and invasive species (c.f. Gioria and Osborne 2014) or to test models and theories of biological invasions (c.f. Shigesada and Kawasaki 1997) to gain insights into invasion success (Theoharides and Dukes 2007). This requires a multiscale approach (rocking) as interpretation might differ between scales (Knight and Reich 2005). RS-derived spatially explicit information on the course of invasion can be used to assess the dynamics of invader impact in time, such as changes in plant-soil feedback during the invasion progress (Dostál et al. 2013). However, while methods are available for assessing the spatial impact on ecosystem functioning, the temporal dimension of invader impacts, essential for management, remains a challenge. For example, the spatial impact of the N-fixing invader *Acacia longifolia* on N-cycling, mapped at plot level, can be upscaled to the landscape level and across invasion gradients using a combination of RS-assisted information on invader distribution (Große-Stoltenberg et al. 2018), LiDAR-derived vegetation cover and topographical metrics as predictors and stable isotope composition ($\delta^{15}\text{N}$) as a response variable in a mixed effect modelling approach (Hellmann et al. 2017). The use of stable isotopes allows us to understand invader-ecosystem interactions (see also Hellmann et al. 2016). Thus, invader impact can be assessed along an invasion gradient, making the interpretation of the

temporal dimension of the impact possible by substituting space for time. In line with the limits of the SFTS approach, mapping stable isotope ratios allows us to better understand the ecological process behind static spatial datasets. Further, the most important predictors in Hellmann et al. (2017), namely invader cover, native vegetation cover and topographical metrics, can all be captured using novel RS technologies at various scales. This means that RS-based rocking could fill important data gaps that reduce the utility of the SFTS approach (see Damgaard 2019); by doing so it could be the basis for confirming important predictors, identifying confounding variables, and assessing the scale- and context-dependency of invader impacts. We suggest that RS-based rocking is an appropriate framework to address the challenges of the SFTS approach (see Damgaard 2019) in the context of plant invasions and their impacts on ecosystem functioning.

Clearly, the utility of rocking is not limited to assessing the impacts of invasive species on nitrogen cycling. Invasive species are known to affect many key ecosystem functions (Asner and Vitousek 2005; Barbosa et al. 2017; Hellmann et al. 2016; Rascher et al. 2011b) with the potential to cause regime shifts (Gaertner et al. 2014). Using RS, the related impacts of invasive species on productivity, water-use strategies, water management and carbon storage (e.g. Rascher et al. 2011b; Nagler et al. 2012; Doody et al. 2014; Hellmann et al. 2016; Dziki et al. 2016; Le Maitre et al. 2020) can potentially be linked to key traits of ecosystem functioning derived from RS at various spatio-temporal scales like the Leaf Area Index (LAI), aboveground biomass, canopy height and foliar nitrogen content (Hughes et al. 2014; Barbosa et al. 2017; Migliavacca et al. 2021). The findings can then be integrated into monitoring schemes (Nagler et al. 2009). For example, the fast-growing invasive tree *Acacia longifolia* (e.g. Rascher et al. 2011b) can cause an increase in LAI (Rascher et al. 2011a), while at the same time LAI can be used to map the invader using satellite data (Mouta et al. 2021). Concerning canopy-height and above-ground biomass, integrating terrestrial LiDAR-derived height information with drone-borne hyperspectral data allowed for assessing the effects of the invasive *Lupinus polyphyllus* on biomass in extensively managed temperate grasslands (Schulze-Brüninghoff et al. 2021). In the case of *Spartina alterniflora* invasion,

the above-ground biomass of the invader can be mapped by combining data from satellites and drones (Zhou et al. 2018), and the invader effects on soil properties can be assessed using a time-series of spaceborne radar data (Yang et al. 2019). The invasive *Prosopis glandulosa* can be mapped across spatial scales (Mirik and Ansley 2012), and approaches exist for estimating its biomass combining aerial imagery with LiDAR data (Ku and Pupescu 2019). Multitemporal and multiresolution aerial photographs and satellite data were integrated with field measurements to estimate the effect of invasive *Tamarix ramosissima* on the water use of riparian and wetland vegetation (Nagler et al. 2009). While most studies are still based on single time data acquisitions (Große-Stoltenberg et al. 2023), and given the fact that there are numerous showcases that integrate multisource and multitemporal data, we see great potential for applying the principle of “rocking” in RS-based impact studies as technological progress will soon facilitate the acquisition of key vegetation properties across spatio-temporal dimensions (e.g. Houborg et al. 2015). Such advances will make it possible to achieve multilevel assessments of post-invasion changes of, for example, LAI, biomass, and canopy height. Additional approaches for capturing impacts of invasion using RS data include mapping effects on biogeochemical properties (Asner and Vitousek 2005; Ewald et al. 2018, 2020), gross primary production (GPP) (Barbosa et al. 2017; Große-Stoltenberg et al. 2018), ecosystem structure (Asner et al. 2008), and erosion and water drainage patterns (Rosso et al. 2006). Moreover, spectrally-derived functional traits have been applied to assess invader effects on above-ground biomass, litter stabilization and soil available phosphorus (van Cleemput et al. 2020) as well as litter composition (Helsen et al. 2020), and have been linked to the concept of trait dissimilarity and impact (Große-Stoltenberg et al. 2018).

In summary, the increasing availability of RS data is paving the way for multi-site studies and is opening new opportunities for exploring typical invasion patterns in much greater detail, for elucidating the context-dependencies of RS-based impact assessments, and for testing diverse ecological concepts and theories. Remote sensing proxies of invasion impact, based on a thorough understanding of the invasion mechanisms across levels and coupled with RS-based analysis of the spatial pattern of the invasion (c.f.

Huang and Asner 2009), represent an important step forward towards defining impact thresholds (Bartz and Kowarik 2019) in a spatially-explicit and updatable way to guide monitoring and management.

Limitations of the RS technology

Accurate recognition/identification of plant invaders is not always possible, and there is often a mismatch between invaders that can be identified and those that are critical for the region. For example, mapping of invasive plant species in the forest understorey is challenging. In case of dense canopy cover, they can either be mapped during a specific time window (e.g., before leaf emergence of overstorey tree species or after the senescence for broadleaved forests) (Resasco et al. 2007; Wilfong et al. 2009; Shouse et al. 2013; Müllerová et al. 2017b), or indirectly by detecting, for example, changes in structure (Singh et al. 2015), or a fraction of shades and green vegetation (Lopatin et al. 2019; Dai et al. 2020). In some cases, only supra-species level recognition is achievable, e.g. *Fallopia* taxa (*Fallopia japonica*, *F. sachalinensis* and *F. ×bohemica*; Müllerová et al. 2017b). Using different spatial or temporal scales (or a combination of both) can help to increase recognition success, such as where *Lepidium latifolium* mapping accuracies of ~90% were achieved by zooming into one specific area (Andrew and Ustin 2008). However, when choosing a wide-angle view and comparing different sites, the accuracy decreased due to lower phenological separability and possibly higher site complexity. Another possibility for increasing the recognition success is to use advanced sensors, such as those that analyse a wide spectrum of light instead of just assigning primary colours (i.e. hyperspectral; e.g., Gholizadeh et al. 2022), or by combining several different sensors, such as fusion of Sentinel-2 and Landsat 8 multispectral with Synthetic Aperture Radar Sentinel-1 data to detect *Rubus cuneifolius* (Rajan et al. 2018). Photogrammetric digital surface models, created as a by-product of drone imagery processing, are an interesting option for improving detection accuracy (Müllerová et al. 2017a; Kattenborn et al. 2020).

Spatial resolution can be a severe limiting factor for detecting smaller species, and specifically for small patches or even individual invasive plants during the early stage of invasion. In some cases these limitations can be overcome by sub-pixel mapping

and spectral unmixing (Ramsey et al. 2005; Silván-Cárdenas and Wang 2010). However, the often reported moderate accuracies of this approach may not suffice for operational applications (e.g., Padalia et al. 2013; Somers and Asner 2013). On the other hand, ultra-high spatial resolution may also create challenges and is not necessarily optimal for mapping a given target species. For example, Müllerová et al. (2017b) showed that in centimetre-resolution drone data, the compound inflorescences of giant hogweed (*Heracleum mantegazzianum*) were separated into individual umbels, which hampered the counting of flowering individuals and decreased the accuracy of mapping. However, such high-resolution drone data can help to identify non-flowering individuals by detecting specific leaf shapes, thereby extending the time window for species mapping. Very recently, new algorithms from the field of deep learning have greatly advanced opportunities for harnessing the fine details of high-resolution spatial data (see Sect. 5.1). Nonetheless, substantial challenges remain in maintaining long-time series of such high spatial resolution data. One of the options to address this problem are PhenoCams (digital cameras that capture time-lapse images of foliage) which can systematically monitor the site over a long period but only cover very small areas (Gill et al. 2021). PhenoCams can be combined with other types of RS data to allow a multi-scale approach, such as in Nagler et al. (2012) for testing the effects of beetles on invasive Tamarix evapotranspiration and leaf phenology.

Despite repeatability of RS analyses and available time series of RS data, the temporal aspects of invasion have received less attention in RS research. This is because variability in spectral reflectance of invasive plants can hamper the transportability of trained algorithms in space and time, making it challenging to add retrospective dimensions (long-term or phenological dynamics) (Dudley et al. 2015). Furthermore, it is usually only feasible for species that can be easily separated from their surroundings and where sufficient time series are available (Müllerová et al. 2005). The spatial resolution of long-term satellite missions, such as Landsat, AVHRR or MODIS, is often too coarse. However in some cases, temporal richness of the data can alleviate the deficiency in spatial resolution, such as when the phenology of the invader differs sufficiently from that of native species (Huang and Geiger 2008).

RS-derived data are often used to support modelling of plant invasions (Rocchini et al. 2015). From a modelling point of view, care should be taken to consider the real potential of RS as well as common sources of uncertainty such as the spatial mismatch between the detail of field data and the resolution of remote sensing data (e.g., Carter et al. 2009). Predictions of invasions are limited by the fact that, contrary to when native species distribution is modelled, invading species are not always at an equilibrium and the actual occurrence is often limited by time lags, disturbances or management actions rather than by bioclimatic factors (Bradley 2013; Ahmed et al. 2020).

Fig. 4 Number of papers published each year between 1980 and 2022 on the topic of remote sensing of plant invasions. Accessed from the SCOPUS database using the search string: (TITLE-ABS-KEY (remote AND sensing) AND TITLE-ABS-KEY (invasive OR invasion*) AND TITLE-ABS-KEY (plant OR vegetation) AND (LIMIT-TO (DOCTYPE,"ar")))

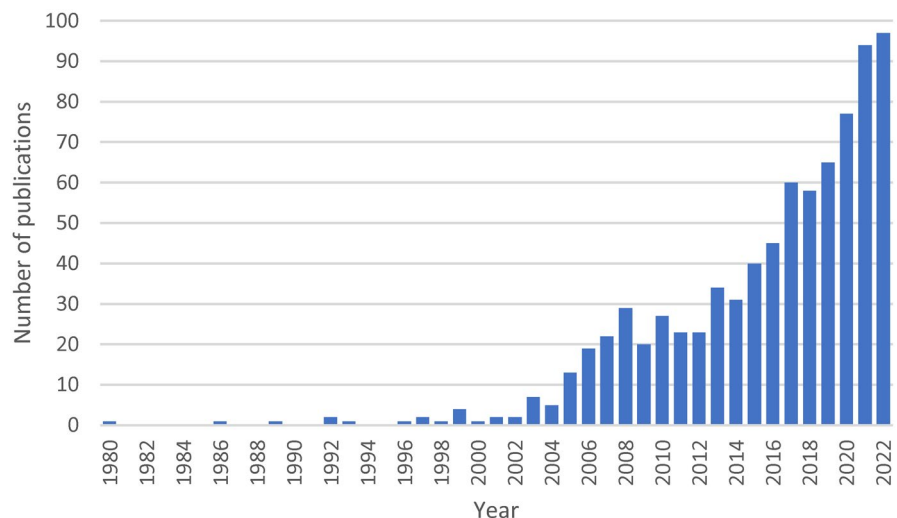


Table 2 Barriers of broad application of remote sensing in plant invasions management, and proposed solutions

Barriers			Possible solutions
Communication and engagement	Failure to communicate both potential and limitations of RS with invasion managers	Building trust in RS applications to plant invasions	Review lists of possible stakeholders Foster communication Promote networking among invasion managers and public–private partnerships Collaborate on decisions Identify key invasion process and management priorities
	Failure to anticipate and support management needs		Engage end users from the very beginning Shape the workflow according to their needs Promote pilot and demonstration projects for key invasive species and invaded habitats
	Mistrust of the community of invasion practitioners and field ecologists		Popularize RS among land managers and invasion ecologists Provide transparent assessments Report uncertainties related to RS of invasions Collaborate more with other disciplines and public
	Failure to incorporate RS into policy and strategic documents on biological invasions		Engage citizen scientists, promote hackathons Integrate RS explicitly into policies and national or regional strategies on biological invasions, pest risk analysis, protected areas and biodiversity

Table 2 (continued)

Barriers	Possible solutions
Complexity, technical issues constraining operationalization	Delivering timely and precise products and knowledge transfer Simplify and automate the workflows, and train dedicated personnel to use complex methods Foster availability of reproducible and well-documented workflows Lack of standardization Standardize the workflows Establish gold standards and examples of best practices, e.g. following FAIR Principles (https://www.go-fair.org/fair-principles/) Uncertainties and imprecision of both invasion detection and model performance Take advantage of new sensors and platforms (e. g. high-resolution satellites and drones) Low ability to transfer the established RS workflows to other sites, time, RS data or invasive alien plant species Support research and application of new powerful algorithms (machine and deep learning) Facilitate and promote data sharing to enhance the training of transferable models Employ crowdsourcing and citizen science Delay in delivering RS products, such as invasion risk maps Establish real-time monitoring protocols Deploy high-resolution satellites and drones Capitalize on cloud solutions Costs Promote policies for both open data and free and open-source software (FOSS) Provide tutorials to reduce costs of training for dedicated personnel

Certain impacts of invasive species on ecosystem functioning are easy to identify, such as the transformation of a grassland ecosystem to a shrubland or productivity-related impacts. Others are difficult to decipher (Jarić et al. 2019), such as changing interactions among native species (Myczko et al. 2017), or those that have yet to reach a particular threshold (Bartz and Kowarik 2019). In such cases, more sophisticated sensors such as hyperspectral or LIDAR might be necessary (Asner and Vitousek 2005; Ewald et al. 2018). Alternatively, the RS-based information should be interpreted as only a proxy (Große-Stoltenberg et al. 2018) or for deriving information on invasion duration (Jandová et al. 2014). The ability of optical traits such as vegetation indices related to productivity such as the Normalized Difference Vegetation Index (NDVI) to capture typical invasion patterns or syndromes (Kueffer et al. 2013) varies in time and space according to conditions that are not yet fully understood (c.f. Große-Stoltenberg et al. 2018; Horn and Clair 2017).

Transfer to practice

Technology transfer is a core principle in large parts of environmental law and international conventions, from Convention on Biological Diversity (CBD) to Sustainable Development Goals (SDGs), and it has been very clearly reaffirmed in Goal D of the Kunming-Montreal Global biodiversity framework (CBD/COP/15/L.25, December 18th 2022). It is not a simple nor a single step process (Ryerson and Haack 2016). As demonstrated above, RS can be useful for understanding the invasion process and for guiding prevention and management strategies by providing accurate, timely and site-specific data for decision support systems and land planning (Lass et al. 2005; Lishawa et al. 2017; Rebelo et al. 2021; Shaw 2005; Zimmermann et al. 2011). Conceptual frameworks on how to integrate RS in species monitoring have been suggested (Jetz et al. 2019), and requirements of data infrastructures suitable for invasive species monitoring have been identified (Hardisty et al. 2019). Yet, despite the large amount of available data and tools (Kwok 2018; Martinez et al. 2020), many well-documented case studies on the application of RS in plant invasion topic (at least 97 papers in 2022 alone; Fig. 4), and well-studied species groups such as invasive *Acacia* species (Große-Stoltenberg et al. 2023),

applications of the technology remain focussed at the experimental level, and evidence of effective implementation (operationalization) in invasion monitoring schemes and policy-making process is very scarce (Bell et al. 2023). However, following the recent technological progress towards freely available RS data of high spatial and temporal resolution, we can expect improvements in implementation of RS technology in invasion management.

Most RS research tools and workflows have not been tested in real-world conditions nor successfully transferred to practice. Among the rare success stories of operationalization of RS approach in management of plant invasions are the National Invasive Species Forecasting System in the USA that is based on habitat suitability models, realized for tamarisk (Morissette et al. 2006), or a regional-scale eradication project on giant hogweed in the Czech Republic from 2013 to 2016 (CZ.1.02/6.2.00/12.17406) that used aerial photography and satellite interpretation to support management actions (Müllerová et al. 2013). Long-term studies in the riparian corridor of the Colorado River delta using satellite time-series data revealed that the effect of the invasive tamarisk on water use is less than initially expected, and a monitoring scheme based on these data was developed to map the effect of a biocontrol agent, the tamarisk beetle, that causes defoliation in the frame of restoration measures (Nagler et al. 2020). Rodgers et al. (2018) described a multiscale invasive plant monitoring program in Everglades NP (USA) that combined visual observation during the flight and digital aerial sketch mapping. In the Framework of the Habitats Directive (which includes provision on alien species), the French Ministry of the Environment have launched the CarHAB program which aims to map terrestrial natural habitats including invasive species using Earth Observation imagery. Among other examples of successful technology transfer are works of Canada Centre for Remote Sensing (Heslop and Fadaie 2002), German GFZ working group, and the Danish Technological Institute (DTI), such as a drone-based solution coupled with artificial intelligence capable to automatically identify and spray herbicide on hogweed individuals (<https://www.dti.dk/services/drones-as-tools-flying-weed-control-can-provide-environmental-and-bottom-line-savings/42361>). The Earth Resources Observation and Science (EROS) Center of the United States Geological Survey

(USGS) uses Harmonized Landsat and Sentinel-2 data products with a vast data set of 17,536 field plot observations from the Bureau of Land Management Assessment, Inventory, and Monitoring program to create fractional cover estimates of non-native annual grass species in Western US rangelands between 2016 and 2020 based on a deep learning framework (Dahal et al. 2022). Their work contributes directly to the USGS Rangeland Exotic Plant Monitoring System, and the maps are publicly available (Dahal et al. 2022).

The problems of transferring the RS technology to practice are neither new nor are they reserved to the invasion field. Three decades ago, Bruce and Ryerson (1993) identified the main sources of failure to make the RS technology operational; although technology has evolved tremendously since then, their findings remain valid. In particular, they identified problems in linking technology development, applications and management needs. In general, there is a gap between invasion scientists and practitioners/site managers in all aspects of invasion science (Shaw et al. 2010; Funk et al. 2020), and RS is no exception. It is apparently challenging to transfer the results and potentialities into practice, and this problem needs to be solved quickly to assure that the potential of RS methods is realized. This discrepancy between the potential and practical use is partly due to technical limitations of the technology and data that is caused by complexity and variety of both the invasive species and the RS data, pronounced e. g. in a mismatch between spatial/temporal resolution of the data and the species to be studied, or in imprecision of RS products. However, the problem can be largely attributed to the failure to provide timely data products at the appropriate spatio-temporal scales and at sufficient accuracy to the respective stakeholders, and last but not least to difficulties in communication between land managers, field ecologists and RS experts (Pettorelli et al. 2014) (Table 2).

The limited number of practical applications of RS by public authorities and land managers belies the significant number of legal endorsements of the importance of both invasive species surveillance and RS. In fact, several policy and technical documents highlight the relationships between the CBD and RS, with special concern to those strategies, targets, indicators where RS can make an important contribution, e.g., for tracking progress, including the case

of invasive alien species (e.g., Secades et al. 2014). More recently, the CBD/SBSTTA/24/10 document (July 10th 2020) states that “States are encouraged [...] to monitor the spread and impact of high-ranking sleeper species, particularly in sites or regions where biodiversity and ecosystem services are likely to deteriorate rapidly under climate change. Best-practice approaches using, for example, RS or sensor networks are suggested to be undertaken”. According to European Union Regulation no. 1143/2014, Member States shall establish a dynamic surveillance system of invasive alien species of Union concern. Although the Regulation does not explicitly mention RS, it is clear that such a surveillance system would greatly benefit from RS and GIS technologies. However, European Alien Species Information Network (EASIN), appointed to facilitate implementation of the mentioned EU Regulation by providing technical and scientific support and gathering, analysing and modelling information on alien species, shows very limited use of RS data so far. On the other hand, precision agriculture is becoming an important component of landscape management practice, including (and largely based on) the use of novel RS technologies for native and alien weed mapping and control and a consequent reduction in the use of plant protection products and many other associated benefits. On top of that, the European Commission expects to publish a Communication on the long-term vision for rural areas with a prominent role of digitalization and RS in the future of rural areas and great implications for management of invasions.

For effective RS transfer, the competences of scientific method development must be combined with sustainable software development and aspects of business development, and end-users (practitioners) must be involved from the very first phase. It is crucial to bring RS technology to practice. This can be done especially by clearly communicating the results to the invasion managers and nature conservation practitioners, and making the outputs operational and useful for the managers. It is also important to provide clear and well documented workflows to make the analyses reproducible (West et al. 2016). Underestimating the challenges related to awareness and confidence of practitioners, mentioned by Bruce and Ryerson (1993), is still common. The attitude of the invasion community and practitioners to RS technology often suffers either from unrealistic expectations

or scepticism. One reason could be that most RS research focuses on mapping that is traditionally done in the field, and application of RS for this task mostly mirrors the field research rather than searching for new research strategies that would leverage the full potential of RS. The potential of RS technology in addressing other aspects such as impact is less frequently addressed (Große-Stoltenberg et al. 2023). Among the serious technical limitations that hamper the practical use of RS in this field are: problematic species identification, defining optimal timing and spatial/spectral resolution of the data (Müllerová, 2019), within-species spectral variability (Große-Stoltenberg et al. 2016), early detection of individual plants or very small populations serving as invasion onsets (Glenn et al. 2005), context-dependency of both detection (Andrew and Ustin 2008) and distribution models (Skowronek et al. 2018), delays between data acquisition, processing and delivery of resulting maps to the managers (Zhu et al. 2019; Bolch et al. 2020), and especially limited and rarely tested transferability of the models across species, time, RS acquisitions and sites (but see Skowronek et al. 2018). The resulting products need to be precise enough and informative. The data uncertainties and limitations of the methods and the predictive power of the models must be explained so that they are accepted and understood by various stakeholders ranging from land managers and nature conservation practitioners, invasion ecologists and the general public. This is not only to implement RS tools into monitoring schemes, but also to build overall trust in RS methods, and make the approach as accessible and easy to implement as possible.

New solutions

Rapid advances in RS technology in recent years offer potential solutions to some of the mentioned challenges, specifically those related to sensor and computing hardware/software. Such advances include the use of photogrammetric height information derived from optical drone imagery as a predictor in detection models (Wijesingha et al. 2020; Martin et al. 2018), protocols for the analysis of multitemporal data to account for phenology (Dudley et al. 2015; Somers and Asner 2012; Masemola et al. 2019; Tarantino

et al. 2019; Liu et al. 2020), real-time monitoring using autonomous drones that would enable studying invader occurrence, drivers and impact with high-resolution data across temporal and spatial scales. Increasing spatial and spectral resolution and coverage of a new generation of space-borne systems providing very high resolution imagery on a daily basis, such as the hyperspectral missions EnMAP, PRISMA, CHIME (Seeley and Asner 2021), or microsatellites such as PlanetScope (Mudereri et al. 2019), opens new possibilities for precise mapping and especially for monitoring plant invasions. Low-cost drone technology could bridge spatio-temporal scale gaps (Tmušić et al. 2020) and coupled with advanced algorithms assure transferability of the models across sites (Sandino et al. 2018). In terms of image processing, methodologies to artificially increase the spatial resolution of a satellite image for improved object detection based on deep learning (“super-resolution”) (Shermeyer and Van Etten 2019) are very promising for mapping invasive plant species even at early stages of invasion (Chen et al. 2020). We can expect new powerful tools for image acquisition and processing to strengthen and reduce the time needed for analyses. Standardization and generalization of methods and protocols (gold standards) for new technologies such as drones (as proposed by Müllerová et al. 2021) would help to fully utilize the ultra-high spatial resolution and flexibility of the technology, and hopefully to increase practical use of RS technology in invasion management. Virtual platforms and cloud solutions, such as Google Earth Engine or OpenEO, provide access to larger amounts of data and allow for running processes that are highly computationally demanding without the need for sophisticated local hardware (Visser et al. 2014; Vanthof and Kelly 2017; Elkind et al. 2019; Xu et al. 2020; Schramm et al. 2021). Such advances are expected to rapidly increase the range and operability of RS applications, allowing for more complex tasks such as early warning, assessing impacts of invasions on ecosystem services and especially practical use in invasion management. Such advances will also help to improve the transferability of models across taxonomic groups and geographical ranges, and in scaling up applications from site- to landscape- and regional scales (Kattenborn et al. 2019a).

Powerful algorithms

An urgent prerequisite for the increased operational use of RS is effective methods to identify the species of interest in the data. In this regard, computer vision methods based on deep learning are currently in the spotlight of RS-related research. Like machine learning in general, deep learning aims to automatically identify relevant patterns in data (e.g. canopy structures of an invasive species) through autonomously learned transformations of the input data. The basic property of deep learning is the immense number of such transformations (deep), enabling it to extract (learn) potentially more information than shallower machine learning approaches (for more details see Brodrick et al. 2019; Kattenborn et al. 2021). From an applied RS perspective, this has two major advantages over previous regression and classification methods: Firstly, the target can be mapped with unprecedented accuracy (Liu and Abd-Elrahman 2018; Kattenborn et al. 2019b; Qian et al. 2020). Secondly, the huge number of data transformations renders feature engineering obsolete: Whereas former RS-analysis approaches relied heavily on extracting relevant images features (e.g. band-combinations, vegetation indices, texture metrics), the intense number of transformations in deep neural networks allows the network to autonomously extract the features relevant for the problem at hand.

A frequently applied deep learning method to harness spatial patterns in RS imagery are Convolutional Neural Networks (CNNs). CNNs are composed of consecutive filter operations that extract spatial information, e.g., characteristic canopy textures and structures of invasive and native species. CNNs were even shown to be very effective for detecting invasive species when used with low-cost drone-based RGB imagery (examples reviewed in Kattenborn et al. 2021). Such data does not contain much spectral information, but usually have very crisp spatial details, such as branching patterns or leaf forms that can be characteristic of an invasive species. This has great potential for the operationalization of RS for invasive species mapping, since such sensors are affordable, usually require little expert knowledge and do not require sophisticated pre-processing or calibration steps (Guirado et al. 2017; Qian et al. 2020; Liu and Abd-Elrahman 2018; Kattenborn, 2019b, 2020).

Despite its great potential, the use of this method is only promising if the invasive species is indeed clearly distinct (visible) from the surrounding vegetation. In addition to spatial patterns, deep learning methods have also great potential for analysing spectral and temporal patterns (Tian et al. 2020; Chen et al. 2020). While CNNs can also be used to extract patterns in spectral information (e.g. the spectral signature of an invasive plant), Recurrent Neural Networks (RNNs) or related methods like Long short-term memory (LSTM) are the current means of choice for time-series analysis. Briefly, such networks are designed to recognize the sequential characteristics in time series data, enabling to automatically extract temporal features, such as phenological characteristics of an invasive plant (Larson and Tuor 2021).

Open and FAIR data—citizen science and cloud solutions

Ample reference data are critical for developing, validating and comparing map products or spreading models, and also for assessing how transferable the models are in new, unseen domains, such as data from new sensors, new geographic areas or collected at different phenological stages. Understanding the model performance is crucial when it comes to operational monitoring. For instance, accuracy of invasive species detection is very context dependent and might differ largely due to differences in surrounding species, topography or illumination conditions. Particularly deep learning but also other statistical RS approaches benefit greatly from large amounts of reference data for model calibration and validation, i.e., RS data together with cover or abundance information of invasive species. However, the acquisition of truly representative reference data is costly, especially estimating the cover or even just the absence or presence of an invasive plant, and, thus, represent a major obstacle for individual stakeholders. The most obvious and sustainable solution is to synthesize the joint effort by involving multiple stakeholders by curating the data in databases, including available RS data and models paired with observations of invasive species. This accounts particularly for drone data which are collected by many parties but for which sharing protocols are lacking. Platforms exist where users can upload and share drone imagery (geonadir.com;

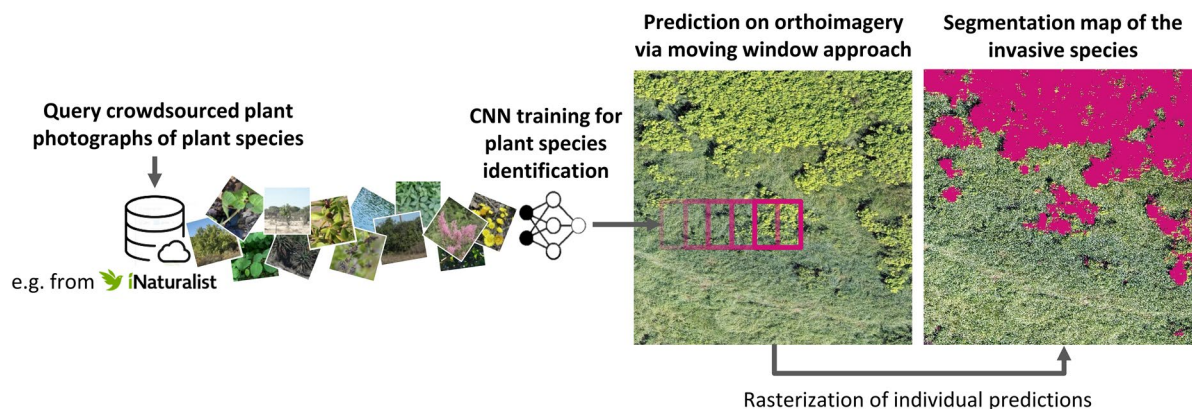


Fig. 5 Conceptual scheme illustrating the integration of crowdsourced data in the training of deep learning models (Convolutional Neural Networks, CNN) to alleviate training data scar-

city in the context of mapping invasive species (here, *Fallopia japonica*; see Soltani et al. 2022)

opendrop.com; openaerialmap.com) but they do not readily provide the option to share reference data along with the imagery as an integrated dataset. Such data would ideally be open and follow the *FAIR* principles (Findable, Accessible, Interoperable, Reusable; Wilkinson et al., 2016). In other disciplines, such initiatives have already been successfully implemented (BigEarthNet, National Ecological Observatory Network by NSF, PlantClef, etc.) (Sumbul et al. 2019). However, specifically for invasive species, such a data treasure chest remains a dream, due to missing data standards, limited capacity for data storage and limited long-term funding opportunities.

In this regard, citizen science data is increasingly contributing to the monitoring of invasive species (Johnson et al. 2020; Mesaglio and Callaghan 2021; Wallace et al. 2021). For instance, iNaturalist has already motivated more than 2 million users to contribute more than 20 million observations of vascular plants across all continents, while the project is still rapidly growing (Di Cecco et al. 2021). Many projects on invasive species already exist in iNaturalist (Howard et al. 2022). The deep learning-assisted mobile application, such as iNaturalist or Pl@ntNet, can be used to automatically identify photographed species. These plant image collections are hosted by the Global Biodiversity Information Facility (GBIF) as a survey-grade dataset, integrating photographs, geolocation and species annotations under creative commons licence. For many invasive species several thousand such

observations exist (e.g., GBIF holds 117,428 geo-referenced records of *Ailanthus altissima* as of 7 February 2023), which may contribute to monitoring invasive species in multiple ways. First, occurrence observations of invasive plants may be used to train or evaluate large-scale RS-based species distribution models and target monitoring actions. Secondly, photographs and connected taxonomic information may be used to train deep learning methods (cf. CNNs introduced above) for the identification of invasive plant species in photographs (Takaya et al. 2022). Models trained on photographs can even be used to identify the spatial distribution of such species in high-resolution RS imagery (Fig. 5, Soltani et al. 2022) even though idiosyncratic behaviour of citizen-science observers often differs largely from the “bird’s eye” perspective of RS. Nonetheless, exploiting the somewhat fuzzy, but ever-increasing and freely available crowdsourced records of invasive species distribution and merging this with RS is clearly worth pursuing (Soltani et al. 2022). This is especially true if we are able to rock between individual observers records from experimental site mapping via drone up to large-scale wall-to-wall mapping and operational monitoring using satellites (such as Planet Labs or Sentinel satellite constellations).

The increasing availability of RS data, including open and analysis-ready data together with the progress in Free and Open Source Software (FOSS) (Dwyer et al. 2018), supports skill building and

sharing regarding data analysis (Rocchini et al. 2017). Other promising options are cloud solutions such as openEO (Schramm et al. 2021) and Google assisted tools, including Google Earth (Visser et al. 2014), Google Earth Engine (Dong et al. 2020) and Google Street View (Pardo-Primoy and Fagúndez 2019). Google Street View has proven to be quite efficient along roads which often serve as corridors for plant invasion (e. g. Deus et al. 2016; Barone et al. 2021; Kotowska et al. 2021). The tremendous power of Google Earth Engine can also be combined with deep learning algorithms (Tian et al. 2020).

Conclusions

Remote sensing has taken its place, along with other new technologies such as advanced modelling methods, geographic information systems, molecular ecology, and stable isotope analysis as an essential tool in invasion science that is helping to improve our understanding of invasion processes. It is changing the ways we perceive and can monitor invasion dynamics and impacts at different scales, and potentially improves our ability to manage invasions. Yet, examples of RS applications in practical management of plant invasions are rare. Among the main reasons for the mismatch between the potential of RS and the degree of uptake in practice is the discrepancy between the needs of invasion ecologists and managers and the current availability of RS products. RS procedures are rarely transferable from experimental sites to other areas/species and/or coarser scales, and their accuracy is generally inadequate. There is a need for standardization of RS workflows for invasive plant species monitoring and assessment, including the use of new technologies such as drones. Besides such technical challenges, there are also problems in communication between RS specialists, ecologists and managers. We hope that this review will improve the dialog among RS specialists, invasion scientists, field ecologists and land managers. RS methods are still not consistently integrated into policy documents. Given its massive potential RS needs to form a fundamental part of policy and management of biological invasions. Most technical barriers are likely to be overcome soon. Fast development in the field and the potential of new powerful tools such as drones and

deep learning algorithms, coupled with open data, citizen science and cloud solutions including user-friendly interfaces, will reduce these mismatches and pave the way for improved applicability of RS tools in invasion science and practice, including the transfer of RS-assisted approach towards field ecologists and managers. The task of building trust in RS methods among field ecologists, managers and policy makers should be neither overlooked nor underestimated. Remote sensing methods can never (nor should they aspire to) replace field campaigns but improved synergy is urgently needed.

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Declarations

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Appendix 3.

PAPER 3. **Müllerová**, J., Bartaloš, T., Gago, X., Kent, R., Michez, A., Múcher, S., Paulus, G., Mokroš, M. (2023b). Vegetation mapping and monitoring by unmanned aerial systems (UAS)—current state and perspectives. In Manfreda & Ben Dor, *Unmanned Aerial Systems for Monitoring Soil, Vegetation, and Riverine Environments*, p. 93-124, Elsevier. ISBN: 9780323852838. <https://doi.org/10.1016/B978-0-323-85283-8.00008-4>

Vegetation mapping and monitoring by unmanned aerial systems (UAS)—current state and perspectives

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4.1 Introduction

Over the last years, unmanned aerial systems (UASs) have been receiving much attention, becoming essential tools for characterizing vegetation patterns and processes. Thanks to its ultrahigh spatial resolution and flexibility, UASs bear potential to bridge the gap between field surveys and satellite remote sensing (RS) studies and, to certain extent, replace or complement laborious field work. For natural vegetation, ultrahigh spatial resolution is particularly beneficial for tasks such as biodiversity monitoring, habitat mapping, or measures against ecosystem degradation via invasive species or disturbances. Additionally, the acquisition frequency UASs provide can also be much higher, and this

fact can assist in studies of ecosystem functions and services. On top of that, UAS optical data can provide spectral and structural information on ecosystems, substituting expensive active sensors. Last but not least, the availability of UASs at low costs opens new applications in vegetation research and practical management. UASs can thus serve well to derive remote sensing—enabled essential biodiversity variables (EBVs) (Reddy et al., 2021), specifically those on species and community composition, ecosystem structure, species traits, and ecosystem functions. UAS can also help to upscale the point or plot field measurements to the landscape scale and overcome limitations imposed by traditional in situ measurements and destructive sampling (Alvarez-Vanhard et al., 2020), one of the challenges in RS applications.

The variety of sensors, platforms, and procedures used to collect and process UAS data is vast. To adequately address the research questions with sufficient accuracy, it is necessary to optimize survey workflows and processing methods (Müllerová et al., 2021). In this chapter, we summarize the methods applied to ecosystem assessment and discuss selected studies divided into state, structure, status, and dynamic components. To better illustrate the different workflows, we provide several pilot study cases that offer a wide spectra of challenges in vegetation monitoring. At the end, we introduce challenges and future perspectives related to UAS applications in mapping and monitoring natural vegetation.

4.2 Methods

4.2.1 Two-dimensional mapping and monitoring

Vegetation assessment using optical imagery is one of the classic applications of RS. Similar to satellite or airborne imagery, UAS data can cover various spectral ranges from simple sensors (consumer RGB cameras, eventually accompanied by modified near-infrared (NIR) using filters), through more sophisticated multispectral to the most advanced hyperspectral, thermal, and laser scanning sensors (Yao et al., 2019). As already mentioned, the main advantages of UASs are its ultrahigh spatial resolution, allowing it to detect even very small species or fine-grain mosaic of vegetation, and its flexibility, enabling it to cover the study area frequently, promptly and/or in fixed targeted phenological phase(s). Increasing spectral information is connected to growing complexity in processing and thus increasing demand for experience level. For example, radiometric correction represents an absolute necessity for hyperspectral and thermal sensors, but it can be omitted for consumer-grade visible cameras with lower quality of sensors (Adão et al., 2017). Therefore the mission and sensors settings should be carefully selected according to the purpose of study/target of interest (Roth et al., 2018). In cases where the species, habitats, or phenomena are easily separated, the simpler sensors, which are easy to use and replaceable in case of crashes, can be deployed, whereas for targets that are difficult to distinguish, such as rare species, early detection of invasion or inconspicuous phenological or physiological status might require more sophisticated hyperspectral sensors, and/or frequent temporal coverage (Müllerová et al., 2021). Naturally, the distinctness of the target plant does not depend solely on its own properties but also on the context, that is, its surroundings.

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In general, methods used for UAS processing follow traditional RS workflows with some modifications (e.g., [Tmušić et al., 2020](#)). Still, the processing must consider the common problems, such as the noise and errors due to radiometric irregularities and geometric distortions ([Fernández-Guisuraga et al., 2018](#)). Object-based image analysis (OBIA) and machine and deep learning (ML and DL) algorithms are among the methods capitalizing on UAS ultrahigh spatial resolution (see Section 4.2.3.3). According to the OBIA paradigm, such fine resolution UAS imagery makes it inefficient to classify each pixel separately but rather as pixel clusters or segments, where higher semantic information can be assigned ([Blaschke et al., 2014](#)). Thus OBIA does not rely solely on the spectral values of the pixels but also considers variation in spectral patterns that describe the texture and patterns of objects, similarly as the human mind takes into consideration during visual interpretations. OBIA and DL can even be combined ([Liu and Abd-Elrahman, 2018](#)) for classifying wetlands. This way, they help to overcome the difficulties arising from the spatial detail itself, where the millimeter to centimeter resolution breaks the response of the target plant into the separate pixels of leaves, branches, flower heads, background soil, etc., generating the so-called salt-and-pepper effect when using a traditional pixel-based approach ([Müllerová et al., 2017b](#)). Vegetation shows substantial intraannual dynamics, and this fact can be employed in analyzing selected phenomena. The analyses can thus be supported by multitemporal data, or proper timing can be selected to capture the feature in the most conspicuous situation ([Müllerová et al., 2017a](#)).

4.2.2 Three-dimensional mapping and monitoring

Structural variables including vegetation height is mentioned as one of the remotely sensed (RS-enabled EBVs) as shown by [Skidmore et al. \(2015\)](#) to support the measurement of the EBV “ecosystem structure.” While land cover has been an operational RS product for decades, vegetation structure and height are still challenging to measure remotely. Combined with spectral information, these parameters can help to identify specific ecosystem or vegetation types ([Ficetola et al., 2014](#)). As an example, the regular monitoring of vegetation height would help to identify processes such as shrub and tree encroachment. [Noss \(1990\)](#) describes the different levels of information that can be considered for biodiversity and ecosystem studies, which are the compositional, structural, and functional aspects of ecosystems. The importance of habitat/vegetation structure is emphasized by [Bunce et al. \(2013\)](#), who demonstrate that there are strong links between vegetation structure and the occurrence of species. Moreover, only a minimal number of species can be directly monitored from RS, compared to vegetation structure and habitats that can be used as a flagship for many species ([Mücher et al., 2017](#)).

Two major options to produce three-dimensional (3D) information are currently available with UASs. Firstly, it is the photogrammetric approach using Structure-from-Motion (SfM) algorithm ([Fig. 4.1](#)), and in recent years also the UAS-borne LiDAR (light detection and ranging). Both provide information about the vegetation 3D space, where multiple structural parameters can be derived, for example, tree position, height, and volume (see [Chapter 3](#) for more details on SfM). The information about complex forest ecosystems or other types of vegetation available from UAS is not limited only to 3D structural information. It can be expanded by

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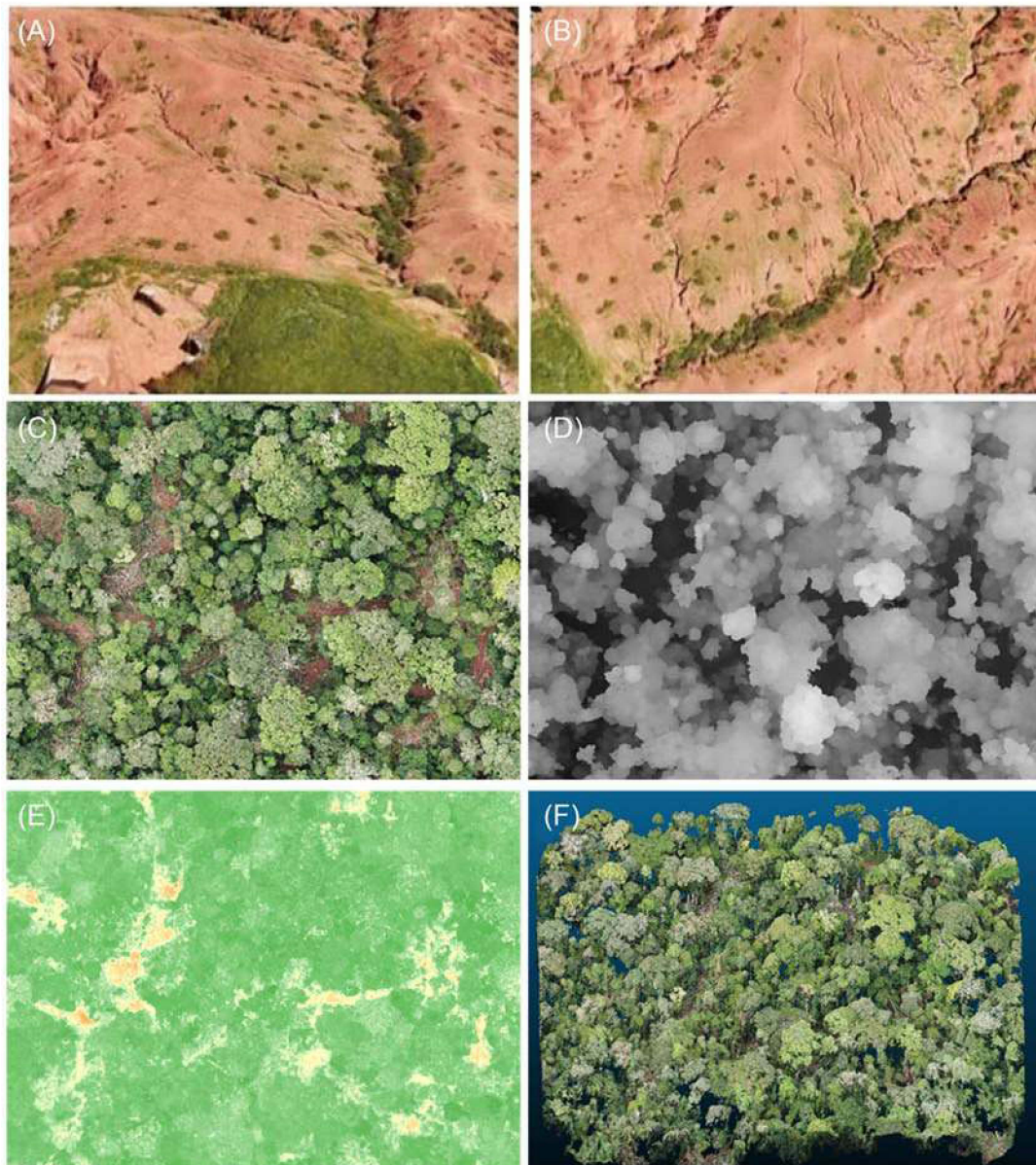


FIGURE 4.1 Unmanned aerial system (UAS) photogrammetric outputs obtained by RGB and multispectral cameras for two contrasting biomes: sparse (open shrubland; A, B) and complex (tropical rainforest; C–F). The first row (A, B) shows 3D models of semiarid shrubland in the Talhiant subcatchment of the Khenifra Region (Middle Atlas Range, Morocco) as an example of a sparsely vegetated ecosystem where most of the terrain is not covered by vegetation. The second and third rows show tropical rainforest in South-East Cameroon through four different maps: (C) visible orthomosaic, (D) canopy height model, (E) NDVI, and (F) 3D point cloud. 3D, Three-dimensional; NDVI, Normalized Difference Vegetation Index.

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combining with other sensors; for example, a combination of LiDAR scanner and hyperspectral camera can produce both 3D information on the structure from LiDAR (height, volume, etc.) and spectral information on plant species from hyperspectral imagery (Sankey et al., 2017).

Both methodologies produce raw 3D information stored as discrete point clouds. The initial information is usually derived in a digital surface model (DSM) describing the absolute altitude of the top vegetation canopy layer. When the DSM is combined with a digital terrain model (DTM), UAS optical sensors can deliver a canopy height model (CHM) at unprecedented spatial resolution and extent beyond comparison with other approaches. However, to generate DTMs and consequently CHM solely from UAS photogrammetric surveys, vegetation cover must be open enough to detect bare ground pixels. In the case of dense vegetation, it is impossible to generate points on the ground, and the solution is then either to combine UAS optical survey with an ancillary data source describing the ground relief, being LiDAR, or to use an active sensor such as UAS-born LiDAR (Lisein et al., 2013). As most UAS LiDAR systems can record several returns from a single laser pulse, they can simultaneously describe the 3D structure of the ground as well as the canopy layers (i.e., DSM, DTM, and CHM).

The main limitation for UAS LiDAR remains its relatively high cost as well as the weight of the sensor itself (>1 kg). Considering these limitations, photogrammetric approaches are the most used to produce 3D information with similar accuracy as LiDAR while using consumer-grade cameras mounted on low-cost UASs (when treetops and crown delineation are considered) (Kwong and Fung, 2020; Cao et al., 2019). In case of deciduous vegetation, the leaf-off season can be used to produce photogrammetric DTMs (Jurjević et al., 2021). Still, with the technical advancements and miniaturization of sensors, we can expect affordable and low-weight LiDAR sensors in the near future.

4.2.3 Novel approaches

4.2.3.1 Combining or fusing 2D and 3D approaches

The above-described possibilities of two-dimensional and 3D approaches can be widened with combination or fusion, and such integration of structural information can help the mapping process. The most used combination is 3D point clouds combined/updated with optical information from multi- or hyperspectral data. For example, Prošek and Šímová (2019) combined UAS multispectral data with 3D point clouds derived from RGB images using SfM to classify and map shrub vegetation in Central Europe.

The fusion of 3D point clouds captured by UAS LiDAR with UAS hyperspectral data was performed by Sankey et al. (2017). Point clouds from UAS LiDAR were used to estimate tree height, crown diameter, and total tree canopy cover. Hyperspectral data were used to derive tree species. When the fusion was used, they achieved higher accuracies by reducing vegetation pixels that were misclassified when only one data source was used. The same combination was explored by Lin et al. (2019) for the purpose of quantifying tree crown damage severity by pine shoot beetles. Also, in this case, the authors confirmed that such fusion increased the accuracy of detection.

Another example is a combination of outputs from the same data source. For instance, Gonçalves et al. (2016) used very-high-resolution images (6 cm) for feature extraction and to generate a detailed DSM (10 cm). Together with random forest (RF) classifiers, they

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characterized fine-scale dynamic vegetation mosaics of heathlands. Adding structural information into the classification process particularly assisted in the mapping of wet heath habitat types with complex patterns with mixed dominants. [Palace et al. \(2018\)](#) increased the power of classification of heterogeneous subarctic peatland vegetation by applying ML algorithms (specifically artificial neural networks) to a combination of spectral and textural information (by using a moving window) derived from a low-cost RGB imagery of ground sampling distance (GSD) of 3 cm.

4.2.3.2 Combining with other techniques

Combining 3D/2D data derived from UASs with terrestrial, airborne, or spaceborne data is needed in cases where UAS data is not sufficient or needs ground truthing. It is mainly when the goal is to cover large-scale areas and when high spatial resolution under canopy structures is needed within dense vegetation (e.g., DTM or trunk parameters).

[Mikita et al. \(2016\)](#) combined terrestrial and UAS photogrammetry to measure tree diameters and heights. Terrestrial photogrammetry can cover only the lower part of the trunks, which is sufficient for tree diameter estimations, but it is insufficient to estimate heights. Therefore UAS photogrammetry was used to reconstruct tree crowns and, with the combination of DTM created using terrestrial photogrammetry, it was possible to estimate height with high accuracy. Other examples of such combinations are within the study of [Navarro et al. \(2019\)](#), where authors combined UAS photogrammetry with Sentinel-2 and Sentinel-1 for aboveground biomass estimation of mangrove forests, or the construction of the Digital 3D Twin of a forest within the temporary art installation “FOR FOREST” by fusing terrestrial laser scanning (TLS) and UAS imagery ([Paulus et al., 2020a](#); see pilot case study 4).

[Schmidt et al. \(2017\)](#) transferred existing field monitoring schemes for mapping *Calluna* heathlands (Natura 2000 dwarf shrub habitats) to the RS approach. In their study, they integrated hyperspectral aerial imagery of 3 m GSD with UAS RGB imagery and CHM of 0.3 m GSD using support vector machines (SVMs) and partial least square regression. These data were used to assess the conservation status of *Calluna* heathlands, as expressed by the habitat structural diversity, cooccurring key species, and degradation. The authors showed that the UAS-assisted approach can improve the efficiency and transferability of monitoring schemes and indicated that the adaptation of the field mapping guidelines to the capabilities of RS remains an important issue. These data were used to assess the conservation status of *Calluna* heathlands, as expressed by the habitat structural diversity, cooccurring key species, and degradation.

4.2.3.3 Machine and deep learning

UAS imagery provides very fine information about the sampled surface. Unprecedented detail (up to millimeter resolution) brings large amounts of information not only on plant spectra, but also on the shape of plant organs (leaves, inflorescences), that potentially allows UASs to distinguish vegetation to the species level, or even further (e.g., health status). However, this can only be possible with powerful algorithms (possibly coupled with cloud processing) for full automation and fast processing of such a large amount of information. The new and technical approaches toward this problem lie in artificial intelligence. This popular approach receives a lot of attention, finding application in many different fields including

vegetation sciences. This is due to an increasing capability of computers with potentialities which were previously only possible with connotations of the human mind.

In this sense ML and DL algorithms make a revolutionary change in the UAS-borne RS. ML classifiers, such as RF or SVM, are based on the idea that machines can access data and learn by themselves from that data in a similar way as humans do. SVM can handle high-dimensional data and perform well with limited training samples (Mountrakis et al., 2011), whereas RF classifiers are easy to use, being relatively insensitive to classification settings (Belgiu and Drăguț, 2016).

Nowadays, ML methods, primarily RF, are among the most common algorithms in UAS-based vegetation classification. Among others, Abdollahnejad and Panagiotidis (2020) proposed a workflow to map tree species and assess the tree health using SVM and a combination of spectral and textural information derived from UAS multispectral imagery. Durgan et al. (2020) tested SVM and RF combined with OBIA approach to successfully map a large number of wetland plant species.

DL is based on the principle that multiple layered neural networks can learn from large datasets. Examples of commonly used DL algorithms are convolutional neural networks (CNN). These algorithms markedly help to refine the results in terms of accuracy and open new possibilities especially in UAS applications (Schiefer et al., 2020). Still, they require massive training datasets. This drawback can be partly overcome by enriching the training dataset automatically using multiview data (Liu and Abd-Elrahman, 2018), or by capitalizing on available databases and Citizen Science (Kattenborn et al., 2021). On the other hand, the use of large and diverse datasets facilitates a high degree of generalization and fosters the transferability of the method to other areas (Schiefer et al., 2020). DL classifiers are new to vegetation science but are getting more popular (and accessible) in recent years (Kattenborn et al., 2021). Among the most common in UAS-borne vegetation applications is CNN, such as in Kattenborn et al. (2019) for different herb, shrub, and tree species or Higgsion et al. (2021) for semiarid wetlands, Qian et al. (2020) for plant invasions, or Schiefer et al. (2020) for mapping nine tree species in a temperate forest. Wang et al. (2021) compared the performance of ML (RF, decision tree) and DL algorithms (residual network and CNN—AlexNet) for early detection of *Juniperus virginiana* encroachment in the United States. Both DL algorithms outperformed the ML ones.

4.2.3.4 Open-source software

The increasing number of applications using UASs for land monitoring stimulated the development of several free and open-source software (FOSS). In addition, a wide portfolio of commercial (proprietary) software packages is often combined with available FOSS tools, or even fully open-source workflows are being developed (Mattivi, 2021; Lehmann et al., 2017), especially in studies testing low-cost UASs with the aim to demonstrate an affordable mapping solution.

In some domains, such as GIS processing, FOSS tools have already become serious alternatives and programmes such as GRASS, QGIS (including plugins such as SCP, semi-automatic classification), or SAGA are being used widely. In other domains, such as image processing, the offer is not so rich, but still, several relevant tools and packages are available, such as the ImageJ/FIJI with a wide range of plugins. Specifically, for UAS flight planning, ArduPilot is considered an advanced full-featured autopilot (but others such as LibrePilot can

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be mentioned). Once imagery is acquired, orthomosaic generation using preferably SfM algorithm can be generated, where OpenDroneMap or MicMac reveal promising results. Classification algorithms are often part of the mentioned GIS systems (both unsupervised and supervised), or additional tools such as R or utilization of OpenCV libraries are documented. Finally, OBIA can be also performed using FOSS tools. Compared to pixel-based approaches, the OBIA domain is still dominated by proprietary software utilization (De Luca et al., 2019), but several examples of utilizing FOSS OBIA elements can be also found (R SegOptim, GRASS, InterImage, Python and QGIS) (Bankert et al., 2021; Lam et al., 2021; Wijesingha et al., 2020). They differ significantly in complexity since no ready solution is available and proposed approaches rather rely on a combination of several tools and libraries. In many cases, the setup of such a system is not straightforward or shows several limitations (typically image size constraints). Nevertheless, the FOSS field is evolving rapidly and has a strong support from active user/developer community, and with increasing availability of UAS we can expect more powerful and elaborated solutions soon.

4.3 Vegetation mapping and monitoring, examples of the best practices

Nature conservation management requires spatially explicit information on species/habitats/vegetation types and their status. Conventional field inventories can provide accurate and detailed information but are often time-consuming, laborious, and cost-intensive, which is especially true for inaccessible areas such as swamps. UASs have made possible to capture and analyze the detail in ways never possible before.

According to Noss (1990), Randlkofer et al. (2010), and Müllerová et al. (2021), vegetation studies can be divided into the four categories: (1) *state*, such as biodiversity, habitats, plant composition, and species of particular interest such as rare or problematic species; (2) *structure*, including the vegetation complexity and structural diversity and its impact on source availability, biomass, canopy height, and openness; (3) *status*, such as physiological state of vegetation and plant stress; and (4) *dynamics*, that is, monitoring the ecosystem development, catastrophic events, resilience and regeneration after disturbances, as well as the changes in phenology, dynamics of flowering, and shifts in course of vegetation season. Within these four categories, the types of UAS data and processing methods differ according to the purpose (Müllerová et al., 2021; Fig. 4.2). We elaborate on each category to illustrate the different workflows and choose several examples (case studies) to serve as benchmark studies, some being accompanied with the study material including data and codes to enable readers to run the analyses on their own.

4.3.1 State—biodiversity mapping

The most common application of RS in general, and specifically UASs, is mapping and monitoring ecosystem state for the purposes of biodiversity and habitat mapping, often to support management (e.g., invasive species control, degradation or restoration efforts). Many authors show that the UAS-assisted approach can improve efficiency and transferability of mapping schemes and indicate that adaptation of the field mapping guidelines to the capabilities of RS remains an important issue (Schmidt et al., 2017).

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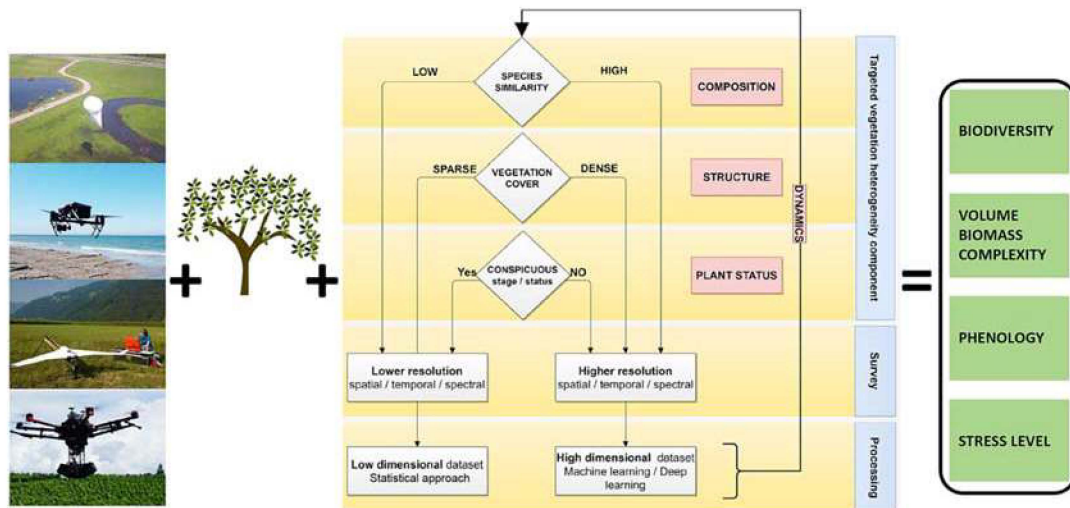


FIGURE 4.2 UAS-based vegetation surveys need to be designed according to the phenomenon/part of vegetation heterogeneity addressed. Source: Adapted from Müllerová, J., Gago, X., Bučas, M., Company, J., Estrany, J., Fortesa, J., et al., 2021. Characterizing vegetation complexity with unmanned aerial systems (UAS) – a framework and synthesis. *Ecol. Indic.* 131, 108156. See the paper for more detailed workflows on each vegetation component.

For the purposes of mapping (and potentially monitoring), the distinction of the target plants, habitat types, or degradation state is a necessity. The accurate distinction between similar species as well as their direct mapping can be problematic especially in cases when they do not show distinct form or spectrum, or the data quality is insufficient regarding the resolution (spatial, spectral, and/or temporal). In such cases, more sophisticated multi-temporal, and/or object-based approaches must be adopted, such as shown by Müllerová et al. (2017a). However, the level of sophistication needed largely depends on the target species/habitat. In some cases, even the simple three-band RGB imagery classified by the maximum likelihood algorithm was shown to be capable of distinguishing between coarse vegetation types and evaluating the effects of a rehabilitation program (spraying of invasive weed followed by planting the native species in Eastern Australia; Hamylton et al., 2020). Some authors used very low flight height to acquire subcentimeter GSD, such as Hao et al. (2021) studying the spatial patterns of the desert vegetation by applying the maximum likelihood algorithm on RGB imagery flown at 10 m with GSD 0.4 cm. The same algorithm was successfully used for mapping the marine submerged vegetation (Tamondong et al., 2020). For classification of forest tree species, pixel-based algorithms showed lower accuracy compared to the OBIA that helped to delineate the tree crowns (Gini et al., 2014; Franklin, 2018).

Pande-Chhetri et al. (2017) compared the performance of pixel- and object-based algorithms for the classification of wetland vegetation using a consumer RGB camera, with OBIA greatly increasing the accuracy. Müllerová et al. (2017b) demonstrated the benefits of OBIA for mapping invasion dynamics, yet, for such a task, the appropriate timing of the data acquisition was necessary (see case study 1). In coastal dunes, De Giglio et al.

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(2019) concluded that the required level of detail determines the choice among the pixel- and object-based approaches.

Laliberte and Rango (2011) concluded that using a consumer RGB camera and a transferred rule set, mapping of arid rangelands at the structure-group level (grasses, shrubs, trees) is more repeatable than mapping at the species level, especially in case of small and/or less spectrally distinct grass species. A workflow of radiometrically calibrated color infrared imagery, multistage segmentation, and supervised ML classifier enabled Chabot et al. (2018) to monitor emergent and submerged vegetation with very high accuracies. Husson et al. (2016) demonstrated that OBIA coupled with an RF algorithm could classify nonsubmerged aquatic vegetation to the species level, and the classification accuracy was negatively affected by the vegetation complexity.

Adding temporal dimension can in many cases ease the determination of individual species as well as the habitat types, such as shown by Yaney-Keller et al. (2019) who used the phenological dynamics of Normalized Difference Vegetation Index (NDVI) in the dry and wet seasons to distinguish different species of mangrove estuaries. Van Iersel et al. (2018) found increasing classification accuracy of river floodplain vegetation by using multitemporal UAS imagery combined with a CHM. Invasion ecology is the field substantially benefiting from high temporal resolution provided by UASs, whereas the temporal heterogeneity of the invasion process (e.g., high seasonal variability, rapid growth of biomass during the season, or particularly distinct phenophase) can be employed to increase the detection accuracy (Müllerová et al., 2017b, see pilot case study 1). Many studies combine the structural and temporal information provided by UASs (Lu and He, 2017; Carl et al., 2019), including CHM and/or the surface roughness parameters (Müllerová et al., 2017a; de Sá et al., 2018; Wu et al., 2019). For example, Martin et al. (2018) integrated the rapid growth of invasive knotweeds into the monitoring process by using repeated UAS acquisition. Lisein et al. (2015) and Michez et al. (2016) showed that the increase in temporal resolution helped leveraging phenological differences among deciduous tree species in temperate European forests, even if using low spectral resolution off-the-shelf cameras (see case study 3).

4.3.1.1 Pilot case study 1. Monitoring the plant invasion using consumer camera and OBIA

Plant invasions represent a major threat to biodiversity, and early and precise monitoring is crucial for effective control. Giant hogweed (*Heracleum mantegazzianum*) is a noxious invader herb in temperate regions. The herb is huge with stems of up to 4 m and forming round white inflorescences of compound umbels (Fig. 4.3). Such characteristics make the plant a perfect candidate for OBIA approach in the case of proper timing, segmentation enabling identification of the whole object of the plant beyond the spectral characterization itself.

The presented case study aims to demonstrate an effect of the right timing of the data acquisition (testing three phenophases), the effect of spatial resolution (UAS and satellite data) on the accuracy, and possibilities of FOSS approach in comparison to the proprietary state-of-the-art OBIA software (eCognition). Two study sites in the Western part of the Czech Republic were surveyed at different phenological phases (i.e., peak of flowering, end of flowering, start of the fruit ripening, postflowering Table 4.1) using self-designed

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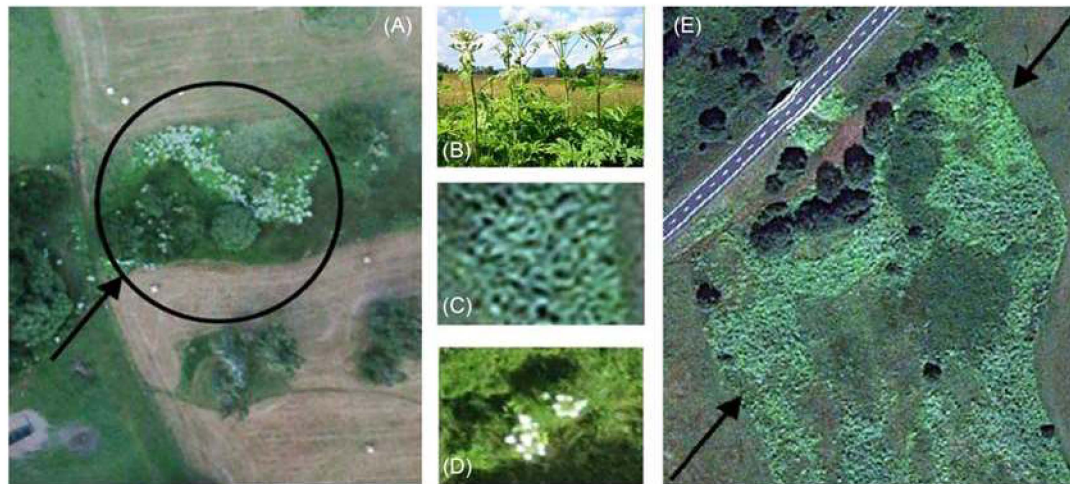


FIGURE 4.3 Flowering giant hogweed (B) on UAS image [GSD 5 cm, (A) hogweed marked with black circle and arrow, detailed in (D), the lower middle] and Pleiades satellite [GSD 2 m, (E) hogweed marked with arrows, detailed in (C), the middle] (Müllerová, 2019). Source: Adapted from Müllerová, J., 2019. UAS for nature conservation—monitoring invasive species. In: Sharma, J.B. (Ed.), *Applications of Small Unmanned Aircraft Systems: Best Practices and Case Studies*, CRC Press, pp. 157–178; ISBN 9780367199241.

TABLE 4.1 Overview of study sites and imagery.

Site No	Name	Area	Imagery		Phenological stage
			UAS (5 cm)	Satellite (Pleiades, 2 m)	
1.	Domoušice	59 ha	Jul 15, 2015	17-07-2015	end of flowering
			Jul 20, 2016	-	start of the fruit ripening
2.	Anenská Ves	70 ha	Sep 04, 2014	-	post-flowering
			Jul 09, 2016	-	peak of flowering

fixed-wing UAS equipped with standard and modified consumer cameras of RGB and NIR and Pleiades satellite, and testing both OBIA and pixel-based approaches coupled with RF algorithm (Müllerová et al., 2017b). The resulting accuracy as well as the best classification workflow depended on the phenological stage of the plant as well as the data GSD. The best results were achieved during the peak of flowering by Pleiades satellites (85% overall accuracy, Table 4.2). The results demonstrate the importance of right data timing as well as the fact that the dinner resolution is not necessarily better. In case of hogweed forming large inflorescences of up to 2 m in diameter, resolution of UAS can be too high, breaking inflorescence into individual umbels (Fig. 4.3 lower middle) and decreasing classification accuracy.

The FOSS-based implementation relied on separate OrfeoToolbox/SAGA tools and R package SegOptim (Gonçalves et al., 2019) enabling the utilization of various segmentation

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TABLE 4.2 Detection accuracy of giant hogweed at different phenological stages from UAS and satellite imagery using RF algorithm. OBIA detecting distinct white round inflorescences (multiresolution segmentation using eCognition software) was used except for September where hogweed was out of bloom, and thus pixel-based approach had to be applied (PCI software).

Data Site	UAS				Pleiades 1
	2	1	1	2	
Acquisition date	July 9, 2016	July 15, 2015	July 20, 2016	September 4, 2014	July 17, 2015
Overall accuracy	84	76	75	60	85
Producers accuracy of hogweed class	75	64	58	44	70
Users accuracy of hogweed class	90	83	88	64	99

Adapted from Müllerová, J., Brišna, J., Bartaloš, T., Dvořák, P., Vítková, M. & Pyšek, P., 2017b. Timing is important: unmanned aircraft vs. satellite imagery in plant invasion monitoring. *Front. Plant. Sci.* 8:1–13.

algorithms available in other FOSS systems (as OrfeoToolbox, GRASS or SAGA), followed by supervised classification (RF). Both proprietary and FOSS follow similar rules and parametrization. As seen from Fig. 4.4, using various segmentation algorithms in combination with comparable classifiers, input data, and features may result in reconcilable outputs. Slight under/overestimation is inevitable, but object-based approach overperforms simple pixel-based classification and eliminates undesirable artifacts. Nevertheless, single end-to-end OBIA application and image size remain the main issues for FOSS-based alternatives.

For the purpose of practical exercise, all mentioned data and scripts are made available at Bartaloš et al., (2022) for the readers to run the workflow and detect g. hogweed invasion themselves. Links to the software mentioned in the present section can be found in Appendix D.

4.3.1.2 Pilot case study 2. Detection of sea grass on Dutch sea coast using deep learning

Within this pilot case study, researchers examined to what extent it is possible, based on different types of UAS imagery, to accurately distinguish between dwarf eelgrass (*Zostera noltii*), common eelgrass (*Zostera marina*), beaked tasselweed (*Ruppia maritima*), and other types of cover such as algae and bare soil (Mücher et al., 2020). Coverage of sea-grass could then be determined based on these classifications. This innovative method may eventually be used to support or replace the traditional regular field surveys.

Two study sites in Oosterschelde, The Netherlands were selected: an area of 32 ha near Krabbendijke (here, *Z. noltii* occurs in different cover classes, Fig. 4.5), and an area of 18 ha at Plaat van Oude Tonge (here we can find *Z. marina* and sporadic *R. maritima*, albeit on a small scale and in a very low cover). RGB and multispectral UAS imagery was acquired on July 21, 2020 under favorable weather and tide conditions (wind 3bft NNW, 23°C, cloud 1/8). In the same week, a conventional field survey was carried out by Eurofins (Mücher et al., 2020).

Two types of UAS were tested: a fixed-wing Ebee-X RTK and a Phantom 4 Pro (multicopter) (Fig. 4.6). With the Ebee-X RTK, images were taken with two modular camera types: an RGB camera (Sensor Optimised for Drone Applications—S.O.D.A.) and a multispectral camera (Parrot Sequoia) measuring reflections in four spectral bands: green (530–570 nm), red

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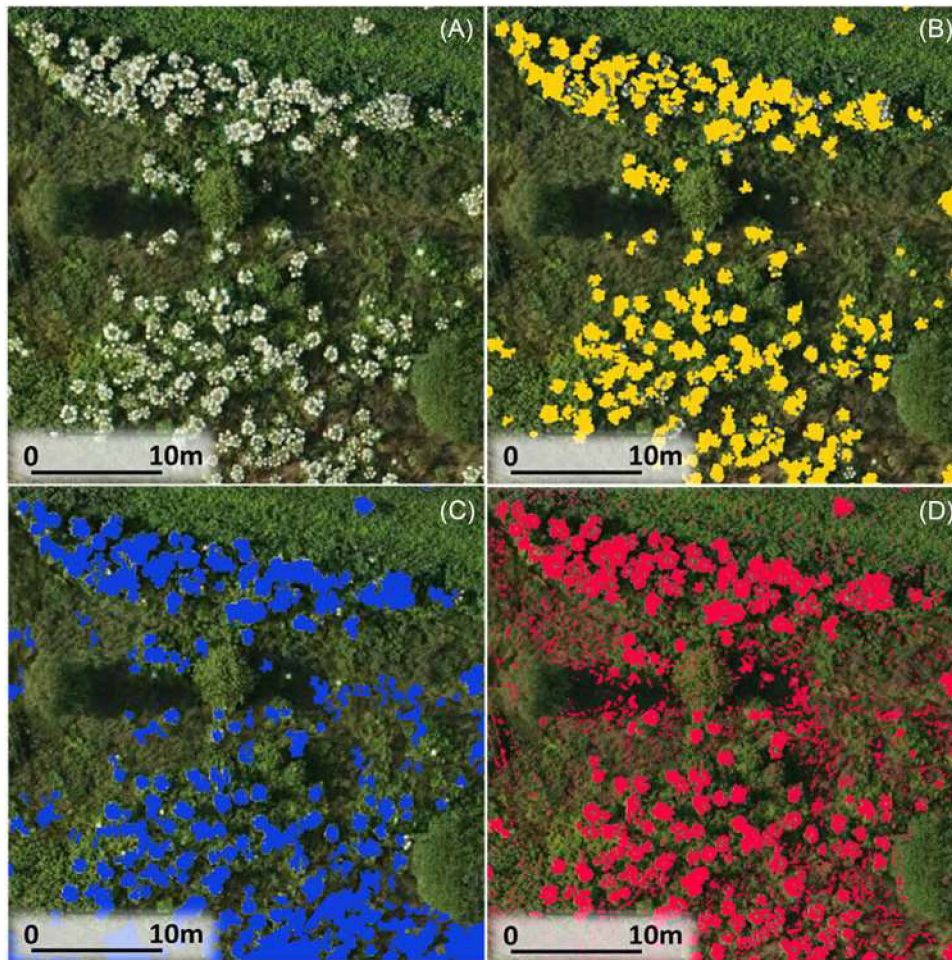


FIGURE 4.4 Comparison of pixel- and object-based random forest classification of giant hogweed (both proprietary and FOSS). From upper left: (A) original image (RGB); (B) yellow—eCognition multiscale segmentation/RF classifier; (C) blue—OrfeoToolbox segmentation (mean_shift) and RF classifier; (D) red—RF pixel-based classifier. Source: UAS imagery from July 15, 2015.

(640–680 nm), red edge (730–740 nm), and near infrared (770–810 nm). From a height of approximately 60 m, the sites were sampled in a preprogrammed flight plan in squares with a 70%–80% overlap. This generated orthomosaics with a pixel resolution of about 1.5 cm for the RGB and about 5 cm for the multispectral images (Mücher et al., 2020).

In addition, the Phantom 4 Pro was used for the RGB recordings of the Plaat van Oude Tonge. On the 3 mm resolution images of the Phantom 4 (10-m height), different vegetation types (sea grasses, algae, and bald mud) were visually located to be used for both training and validating the classification, along with the RGB orthomosaic. This arrangement assured the optimal thematic accuracy, georeferencing, and ground truthing (Mücher et al., 2020).

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FIGURE 4.5 Study area of Krabbendijke with *Zostera noltii*.



FIGURE 4.6 UASs used for detecting seagrass. Left, a fixed wing EBEE X RTK, right, a Phantom 4.

This training dataset was used in the DL module of ENVI software. The reason for this choice of DL algorithm over the often used OBIA was that the segmentation process within OBIA is so computationally demanding that segmenting images at the given level of detail (such as for large seagrass and *Ruppia*) for large areas were not considered workable, and it was DL techniques that were expected to serve the purpose more efficiently.

To test the results of the DL classification (Fig. 4.7), a validation was performed for Krabbendijke based on independently collected ground truth data (manually interpreted points based on 3 mm resolution detail Phantom UAS images at 10 m height at 414 locations). The classification accuracy for small eelgrass at Krabbendijke was good for high abundances but dropped with lower coverage (Table 4.3). For the other test site, common eelgrass (not present in Krabbendijke) did not reach good results since it only occurred on a few locations, and therefore the ground truth was too limited (#8) for running a DL model. Overall, the DL techniques performed better on 1.5 cm RGB orthomosaic than on 5 cm multispectral orthomosaics. Obviously, spatial resolution outperformed the spectral one (Mücher et al., 2020).

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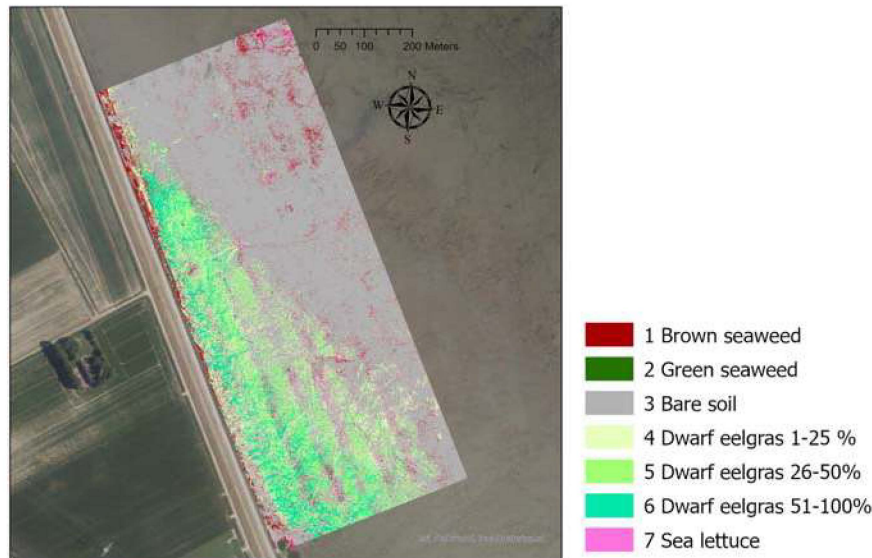


FIGURE 4.7 Deep learning classification of sea grass on Dutch sea coast. Source: From Mücher, C.A., de Jong, J., Kramer, H., Reitsma, J.M., Los, S., 2020. Pilot innovatieve inwinning zee gras Oosterschelde. Bureau Waardenburg Rapportnr. 20–323. Bureau Waardenburg, Culemborg i.s.m. WENR, Wageningen. In opdracht van RWS-CIV Delft.

4.3.1.3 Pilot study case 3. Temperate forest species mapping using multitemporal imagery

This study case addresses the question of how and particularly when UAS imagery should be used in order to efficiently discriminate deciduous tree species. In this study, Lisein et al. (2015) took advantage of one of the most promising features of small UASs: their capability to acquire dense time series.

A time series of high-resolution UAS imagery was collected using a fixed-wing to cover the growing season, 10 acquisition dates from leaf flush to leaf fall over a 1.3 km² forest in Wallonia (Southern Belgium). For each survey date, visible and multispectral datasets were collected. Using a reference database of 577 delineated tree crowns (from five species groups), different classification schemes were tested to highlight the best time window to capture UAS imagery: one-date, two-date, and three-date scenarios. The classification was performed at the tree crown scale using OBIA metrics and an RF classifier Fig. 4.8.

The end of leaf flushing was the most efficient single-date time window (84% overall accuracy), while multitemporal datasets definitely improved the overall classification accuracy (89% and 92% for two-date and three-date combinations). Single-date high-resolution orthophotomosaics, acquired on optimal time-windows, resulted in a very good classification accuracy (with an error of 16%). While for human eyes, the disparity in forest tree phenology seems maximal during early spring and late autumn, for the RF algorithm, the end of leaf flushing period was highlighted as the optimal monotemporal time window. This is because this period minimizes the spectral variation within tree species groups and, at the same time, maximizes the phenological differences between species (Fig. 4.9).

TABLE 4.3 Confusion matrix of deep learning eelgrass classification in Krabbendijke (The Netherlands).

In situ	Classification							Total	User's accuracy
	Brown seaweed	Green seaweed	Bare soil	Dwarf eelgrass 1%–25%	Dwarf eelgrass 26%–50%	Dwarf eelgrass 51%–100%	Sea lettuce		
Brown seaweed	46	—	1	1	—	4	2	54	85%
Green seaweed	3	0	—	—	—	—	1	4	0
Bare soil	—	—	98	16	—	—	—	114	86%
Dwarf eelgrass 1%–25% cover	2	—	15	31	19	2	12	81	38%
Dwarf eelgrass 26%–50% cover	1	—	—	5	36	10	10	62	58%
Dwarf eelgrass 51%–100% cover	4	—	—	—	3	43	—	50	86%
Sea lettuce	3	—	—	4	—	2	2	11	18%
Total	59	0	114	57	58	61	27	376	—
Producer's accuracy	78%	0%	86%	54%	62%	70%	7%	—	68%

The significance is marked in bold.

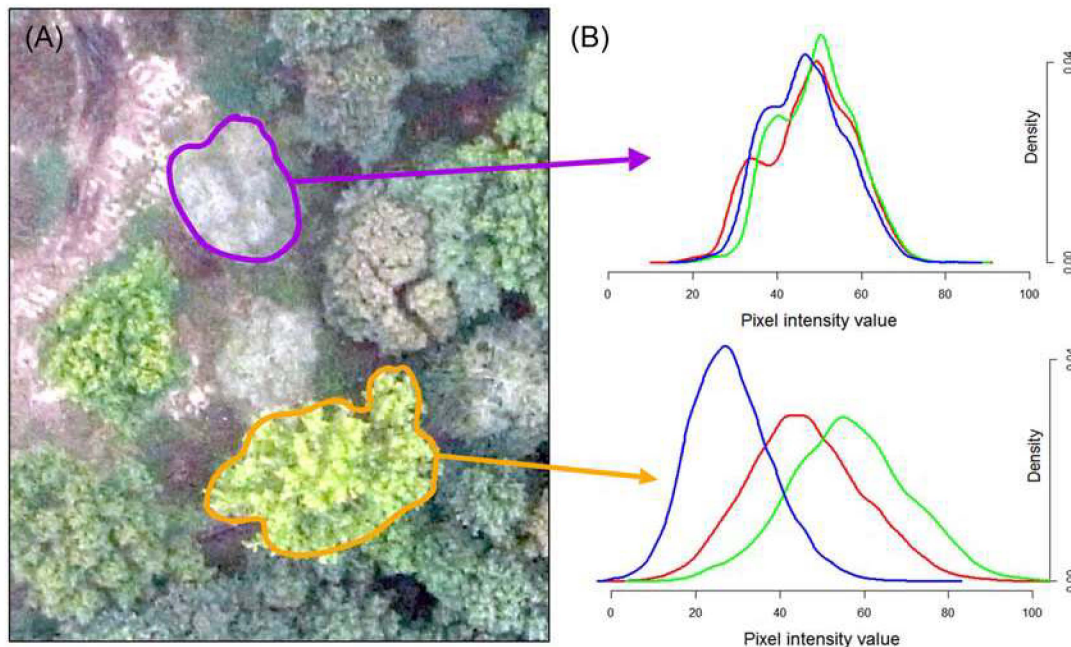


FIGURE 4.8 (A) Differences in spectral response captured with a compact camera mounted on an UAS for two tree crowns (birch and poplar species). (B) Density curves for the red, green, and blue band are depicted on the right (Lisein et al., 2015).

A simplified dataset of the time series used in this research as well as the [R] script used to process the image metrics and build the RF classifier are available at: <http://hdl.handle.net/2268/180873>.

4.3.2 Structure—assessing stand complexity and biomass

Ecosystem structure and complexity is an important variable, providing information on biomass as well as other ecosystem functions. Covariates such as canopy cover, gaps, vertical and horizontal structure, and spatial aggregation regulate spatial variation of light, microclimate, soil quality, and consequently forest regeneration and compositional and structural biodiversity variables in the forest (Valladares and Niinemets, 2008; Getzin et al., 2012; Lelli et al., 2019). Fine-scale information on canopy structure is important since it drives many ecological processes such as understory diversity, seed establishment, and forest regeneration after the disturbances (Kent et al., 2015; Bagaram et al., 2018). This canopy heterogeneity shapes important ecosystem services such as forest productivity and resilience to global change because it supports nutrient cycling, soil formation, and primary production and is crucial for regulating the hydrological cycle (Aznar-Sánchez et al., 2018). It is also probable that the canopy structure can substantially mitigate the impact of climate change on forest plant diversity (Stevens et al., 2015).

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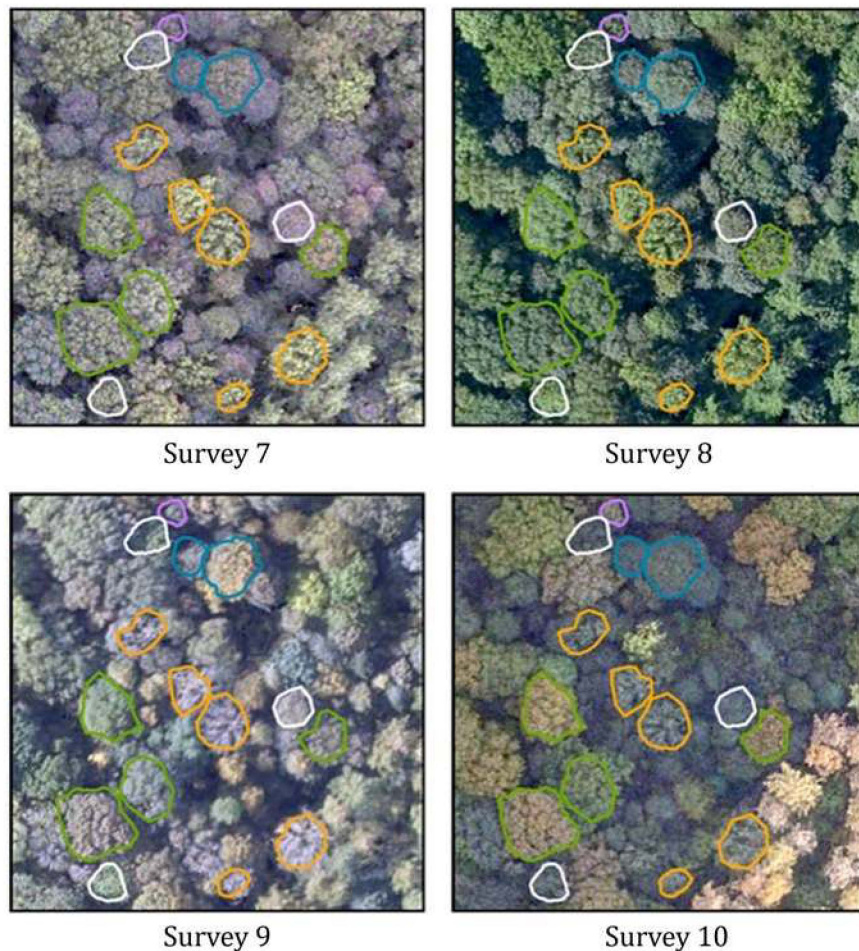


FIGURE 4.9 Effect of phenology on discrimination of deciduous tree species on a time series of high resolution forested RGB orthomosaics (20 cm GSD). Delineated trees are colored by species: English oak: green; poplars: orange; sycamore maple: blue; common ash: white; birches: purple (Lisein et al., 2015).

UAS-based structural assessment can also be applied to open ecosystems such as measuring biomass and carbon stocks in a spatial context in a gradient of semiarid ecosystems from grasslands to shrublands in Central New Mexico (United States) (Cunliffe et al., 2016) or estimating the height of woody stands in Northern Namibia (Mayr et al., 2018). Swetnam et al. (2018) compared three different platforms (ground-based, small UAS, and manned aircraft) for assessing the structural state of shrublands in Arizona, United States. Another example was done by Meneses et al. (2018) where they measured the volume of reeds in shallow parts of a lake using both copters and fixed-wing UASs. The experiment was done in Lake Chiemsee (Germany), and thanks to sparse reed stands in the area, 3D reconstruction showed low vertical mean error 0.76 m and root mean square error (RMSE) of 1.05 m (with a copter). Thiel and Schnullius (2017) showed that the use of

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photogrammetric point cloud actually slightly improved tree detection, providing more geometrical details compared to the LiDAR.

4.3.2.1 Pilot case study 4. Fusion between terrestrial laser scanning and photogrammetric-UAS-derived point clouds

Major research goal of this case study was to create a “Digital 3D Twin” of the temporary art installation “FOR FOREST - The Unending Attraction of Nature.” This unrivaled temporary art intervention of a real forest established at the former soccer stadium in Klagenfurt (Austria) (Fig. 4.10) gained worldwide attention in the fall of 2019. FOR FOREST by Klaus Littmann (based on a pencil drawing of the Austrian artist Max Peintner) created not only the largest art intervention in public space in Austria but also a unique controlled experimental geospatial laboratory in the context of forestry, high-resolution multisensor surveying, sensor fusion, spatial analysis, and 3D visualization (Paulus et al., 2020a).

TLS and high-resolution UAS imagery, photogrammetric processing, and sensor fusion were combined and innovative virtual visualization techniques explored. Multisensor data capture took place in two stages from mid-August to early September 2019. Based on a detailed concept, the first step was to measure the exterior of the soccer stadium using TLS, and once the construction of the forest in the stadium was completed, terrestrial laser scans were carried out from various positions inside the stadium. In total, 4 days of TLS measurement, the use of 30 Black and White targets for coregistration, and 8 measurement jobs within total 577 different TLS positions were performed. At the same time, very-high-resolution and highly overlapping aerial images were taken from the air at different angles using a fully certified high-



FIGURE 4.10 Temporary Art Installation FOR FOREST by Klaus Littmann (September 8– October 27, 2019, Klagenfurt, Austria).

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performance UAS [Multicopter Leica AIBOT AX 20 with Sony Alpha 7R III (42 MP) RGB Sensor]. Reference measurements for validation and quality assurance were carried out both for the exterior and for the interior of the stadium and the forest using survey-grade DGNSS.

Photogrammetric processing was performed with AGISOFT Photoscan (1.4.5) software with 573 images resulting in a DSM with an overall RMSE of 1.17 cm. TLS data processing was performed with Leica Cyclone Register (9.4.2) for Cloud2Cloud registration. The total fused UAS-TLS point cloud (577 TLS positions and 573 UAS images) consists of 27,419,265,887 individual points (Fig. 4.11). Leica Cyclone3Dr (1.9.1) was used to calculate the difference (Iterative



FIGURE 4.11 Integrated UAS – TLS 3D colored point cloud (27,419,265,887 points).

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Closed Point Distance Method—ICP) between the UAS 3D photogrammetric point cloud and the TLS 3D point cloud. Very small spatial differences, that is, a very good positional match between the photogrammetrically derived UAS point cloud and the TLS-point cloud can be observed for the higher part of the tree canopy. “Holes” in the lower part of the tree structure represent areas where no UAS point cloud data are available as such lower parts are not visible from the aerial UAS perspective and therefore no distance calculation can be performed. This clearly shows the advantage of complementary point clouds captured by different sensors and perspectives to achieve a holistic tree structure representation (Fig. 4.12). The average registration accuracy in all 10 control points has an average positional accuracy of 8 mm and an average height accuracy of 12 mm. A final revision plan and a CHM were generated (Fig. 4.13). A fully digital representation of the fused point clouds was finally presented in the impressive Deep Space 8K visualization environment at the Ars Electronica Festival 2020 (Paulus et al., 2020b).

4.3.3 Status—assessing phenology and stress

An ecosystem status represents the response of plants to seasonal changes (phenology) or a/biotic stressors. Following Jones and Vaughan (2010), the sophistication level of data and analysis is driven by the level of conspicuousness/symptomaticity of the phenomenon to be studied. For example, bud sprouting, leaf emergence, and subsequent chlorophyll content dynamics can be monitored using structural and chlorophyll-sensitive spectral indices (D’Odorico et al., 2015), such as NDVI (e.g., Fawcett et al., 2020). In this sense, as compared to other conventional and widely used methods of estimating vegetation phenology, such as tower and ground-based sensors, UASs provide similar estimates of the timing of canopy greening in temperate forest with superior spatial coverage and resolution (Atkins et al., 2020).

In ecosystems dominated by evergreen species, the mapping strategy should be different compared to that of deciduous ones as the seasonal fluctuations in chlorophyll content of conifers are minor (Lambers et al., 2008). For instance, at high latitudes dominated by coniferous forests, evergreen species keep the chlorophyll all year around, even if in winter light captured cannot be used for photobiochemistry because of low temperatures, and detection based on chlorophyll is thus not informative. However, assessment can be focused in other pigments that become important for plants under stress conditions as xanthophylls and carotenoids. At short timescales, VAZ (violaxanthin—V, antheraxanthin—A, and zeaxanthin—Z) cycle dissipates the energy excess by heat through the de-epoxidation of V to the photoprotective xanthophyll pigments A and Z. At longer timescales, photoprotective carotenoid pools change their proportion in respect to the chlorophylls, thus decreasing their light capture capacity, increasing photoprotection (Gamon et al., 1992, 2016; Wong et al., 2019). Both photoprotective responses in relationship with chlorophyll pools are directly linked to photosynthetic capacity, physiological performance, and stress status and can be assessed using UASs. Traditionally, the photochemical reflectance index was employed to assess plant stress because it reflects the changes in the VAZ cycle (Gamon et al., 1992). It was subsequently successfully studied using hyperspectral and multispectral sensors for different species, both airborne and of UAS origin (Hernández-Clemente et al., 2012). Recently, a new index was proposed to assess the changes in the proportion of chlorophylls and carotenoids (Chlorophyll Carotenoid Index; Gamon et al., 2016). Furthermore, D’Odorico et al. (2020) demonstrated the potential to use UASs along the season

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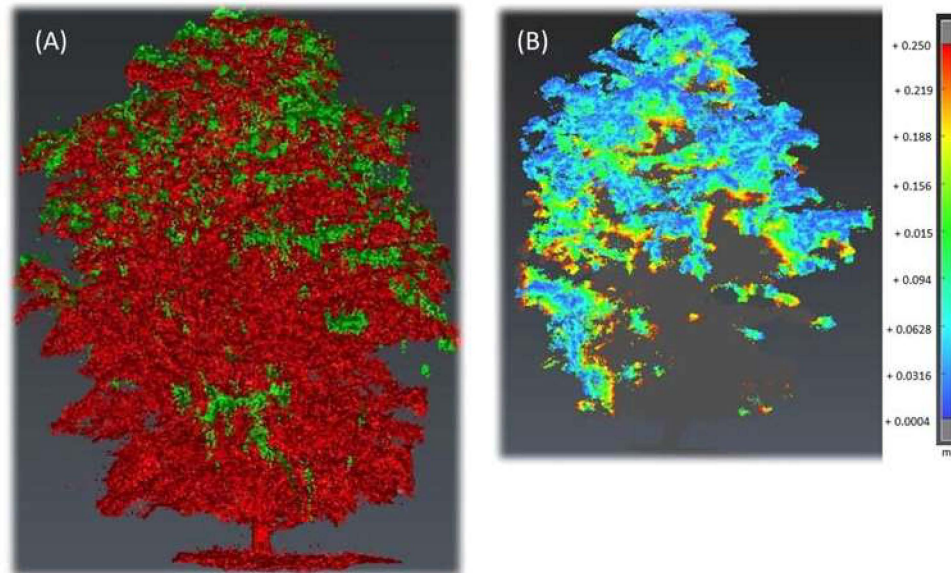


FIGURE 4.12 (A) Single Tree 3D fused point cloud. Green: UAS—derived photogrammetric point cloud; Red: TLS—derived point cloud; (B) Iterative Closed Point Distance (ICP) between UAS and TLS point clouds for an individual tree (Zebedin, 2020).

to assess photosynthetic capacity and stress physiological status in thousands of field-grown conifers through 19 campaigns along a year and with a spatial resolution lower than 2 cm/px.

Also, the canopy temperature obtained by thermal imagery can be employed to assess plant stress in forests; beyond stomatal closure due to reduced water availability (Gago et al., 2015; Smigaj et al., 2017), biotic diseases can affect canopy temperature by leaf damage, necrosis, and loss of cellular integrity or also affect directly the vascular system. For example, it was employed to detect the red band needle blight in *Pinus* plantations at six different times a day. Stronger correlations between canopy temperature and disease levels were observed at midday, which coincides with the highest solar radiation (Smigaj et al., 2019). Additionally, canopy temperature can be combined with meteorological data if they are available for the experimental site, through the leaf energy balance model being possible to estimate the canopy conductance per individual and species. Thus, based on their surface temperature, they can be employed to assess water and carbon balances in the ecosystem (Sun et al., 2019).

4.3.4 Dynamics—monitoring the development

UASs are a perfect tool to assess the dynamic processes thanks to their flexibility and possibility to be frequently or readily deployed in case of fast changing processes. For example, UAS-derived DSMs are applied to study erosion (Glendell et al., 2017) and loss or redistribution of key plant-limiting nutrients such as nitrogen (Westergaard-Nielsen et al., 2020). Likewise, vegetation can act as a sediment trap on steep slopes because its storage capacity illustrates a cubic dependence on effective plant width and an inverse dependence on local

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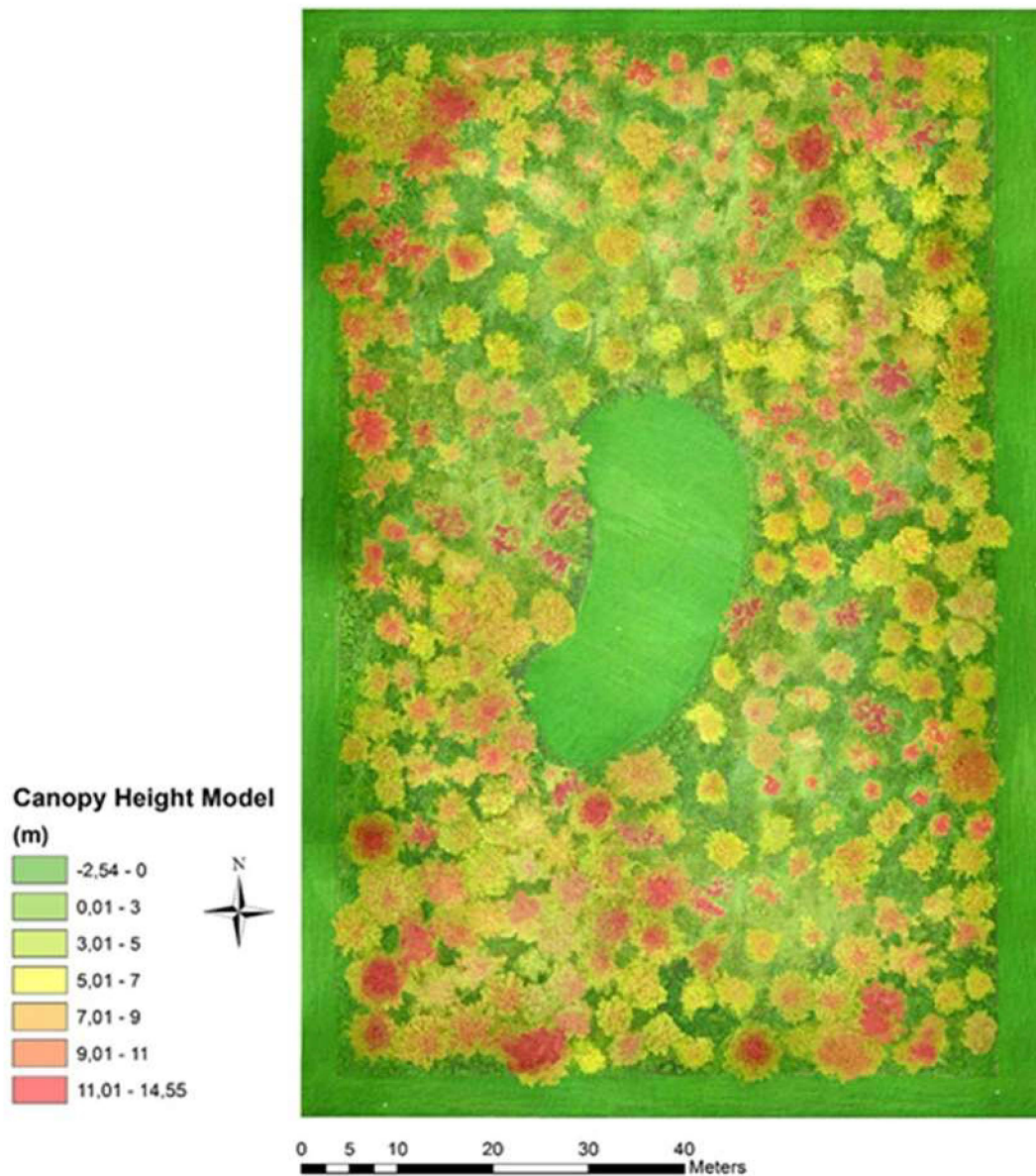


FIGURE 4.13 Canopy height model (CHM) derived from the fusion of UAS and TLS on FOR FOREST. *CHM*, Canopy height model; *TLS*, terrestrial laser scanning. From Kainbacher, J., 2020. UAS-basierte quantitative Analysen von forstlichen Parametern am Beispiel der Kunstintervention, FOR FOREST Unpublished Bachelor Thesis, Department of Geoinformation and Environmental Technologies, Carinthia University of Applied Sciences, Villach, Austria.

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slope. Using a UAS survey, [Estrany et al. \(2019\)](#) assessed the relationship between vegetation vigor by the Blue Normalized Difference Vegetation Index and sediment pathways by deriving a sediment connectivity index, observing how sediment pathways induce direct effects on vegetation growth at hillslope and catchment scale, and most particularly after a wildfire.

For forest fires and disturbances, flexibility of UASs is particularly important to provide timely information to the managers ([Mokroš et al., 2017](#)). Real-time automatic detection of forest fires (see [Yuan et al., 2015](#); for a comprehensive review), mapping fire severity ([McKenna et al., 2017](#)), monitoring postfire regeneration and assessment of potential postfire erosion ([Larrinaga and Brotons, 2019](#)), as well as mapping windthrow damage ([Mokroš et al., 2017](#)) can benefit from ultrahigh spatial and temporal resolution provided by UASs mounted with optical sensors (either RGB or RGB + NIR). [Larrinaga and Brotons \(2019\)](#) showed that spectral indices can be a better proxy to postfire regeneration than CHM.

To study degradation related to grazing and burning in a dryland ecosystem in Cyprus, [Themistocleous et al. \(2014\)](#) assessed seasonal changes of vegetation cover combining UAS and satellite imagery. The study of [Lorah et al. \(2018\)](#) showed how data collected by UASs can serve as conservation management of high-quality prairie habitat. In the latter, management practices included a series of prescribed burns and the use of UASs aimed at revealing the relationship between fire behavior and landscape features.

Another field is insect outbreak dynamics. [Näsi et al. \(2015\)](#) used a UAS-mounted hyperspectral sensor to detect bark beetle infestation of Norway spruce at the tree level to assist early monitoring of new focal points that could serve as dispersal foci. But even simple RGB cameras can serve as a capable means to detect infestation, as shown by [Minařík and Langhammer \(2016\)](#) for bark beetle damage of spruce, [Lehmann et al. \(2015\)](#) on the example of oak splendor beetle, and [Cardil et al. \(2019\)](#) assessing spatial dynamics of infestation by pine processionary moth. Authors found the use of UAS to be robust, allowing high accuracy in differentiating healthy, infested, and completely defoliated trees with accuracies comparable to field-based measurements.

[Röder et al. \(2018\)](#) used photogrammetrically derived DSM to study establishment of new tree cohorts (regeneration) following bark beetle damage in spruce forest. They concluded that UAS-based inventory is useful especially for sites with sparse understory, but it cannot fully replace field surveys in case of dense regeneration.

UAS approaches have also been deployed for riparian ecosystems at the scale of standing dead trees ([Michez et al., 2016](#)), beaver activity ([Puttock et al., 2015](#)), or postflood vegetation recruitment patterns in braided-channel rivers ([Hervouet et al., 2011](#)).

4.3.4.1 Pilot case study 5. Windthrow detection—comparison of LiDAR and photogrammetry

In case of a sudden extreme event, it is important to quickly provide accurate information about the extent of the forest damages to sufficiently plan the forest measures. The information must be as precise as possible, but at the same time rapidly acquired. Using a fixed-wing UAS is one of the best solutions for such an application ([Mokroš et al., 2017](#)).

In May 2014 in Slovakia, a windthrow event called Žofia caused great amounts of damage across forests. A portion of this area of approximately 200 ha was studied by [Mokroš et al. \(2017\)](#), where four damaged forest sites were identified covering approximately 25 ha altogether. The available data were acquired by SenseFly eBee Plus fixed-wing UAS (SenseFly,

Cheseaux-sur-Lausanne, Switzerland) with GNSS RTK/PPK technology. This technology was proven to be the same or even better positionally accurate compared to the use of ground control points (Tomašík et al., 2019). Flights were done in 2018 during leaf-off and leaf-on seasons (Fig. 4.14). The flight path was in two perpendicular directions to assure the best quality of the point cloud. Additionally, airborne laser scanning (ALS) data from prior to the event (2012) were used to prepare DTM and DSM.

To detect the windthrow-damaged areas, we used a combination of DTM derived from ALS and DSM derived from UAS photogrammetry. Furthermore, we tested the possibility to derive DTM from UAS photogrammetry from the leaf-off season acquired by 3D S.O.D.A camera which is capturing image simultaneously in nadir and oblique directions (Fig. 4.15).

Next step was to estimate the damaged areas. For the study site, two options were available. Firstly, we tested the combination of data from ALS and UAS and secondly, using only data from UAS. The drawback of UAS photogrammetry within forested areas was the difficulty to produce precise DTM under closed tree canopies. To reduce the problem, we have used a nadir and oblique images within the leaf-off season, as mentioned in the previous paragraph. Fig. 4.16) shows the difference in results from multiple sources. The detection was quite successful even in case solely the UAS data were used, although such approach would not be suitable for more subtle changes in canopy height.

For the purpose of practical exercise, all mentioned data and R scripts are made available for download at <https://doi.org/10.5281/zenodo.7303781> for the readers to run the workflow and detect the windthrow damage within the study site. This dataset includes DTM and DSM from ALS data acquired in 2012, DTM and DSM acquired in 2017 and 2018 by eBee Plus fixed-wing UAS with SenseFly S.O.D.A. RGB camera, and DSM acquired in 2020 by eBee Plus fixed-wing UAS with SenseFly S.O.D.A. RGB camera.



FIGURE 4.14 Orthomosaics from leaf-on (left) and leaf-off season (right) created from images acquired by a fixed-wing UAS.

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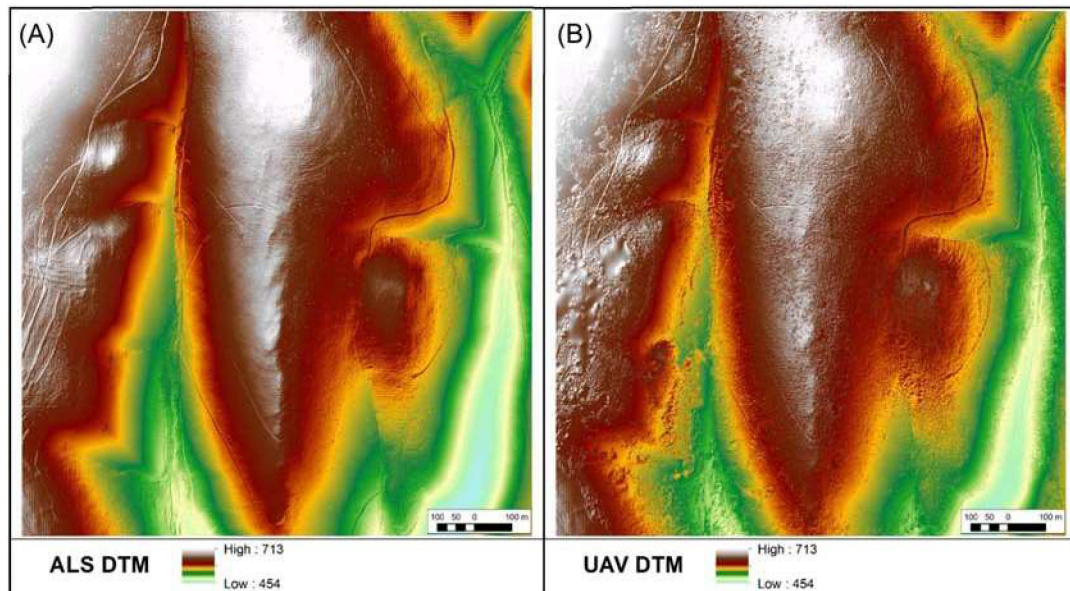


FIGURE 4.15 Digital terrain models derived from ALS (A) and from UAS photogrammetry (B). *ALS*, Airborne laser scanning.

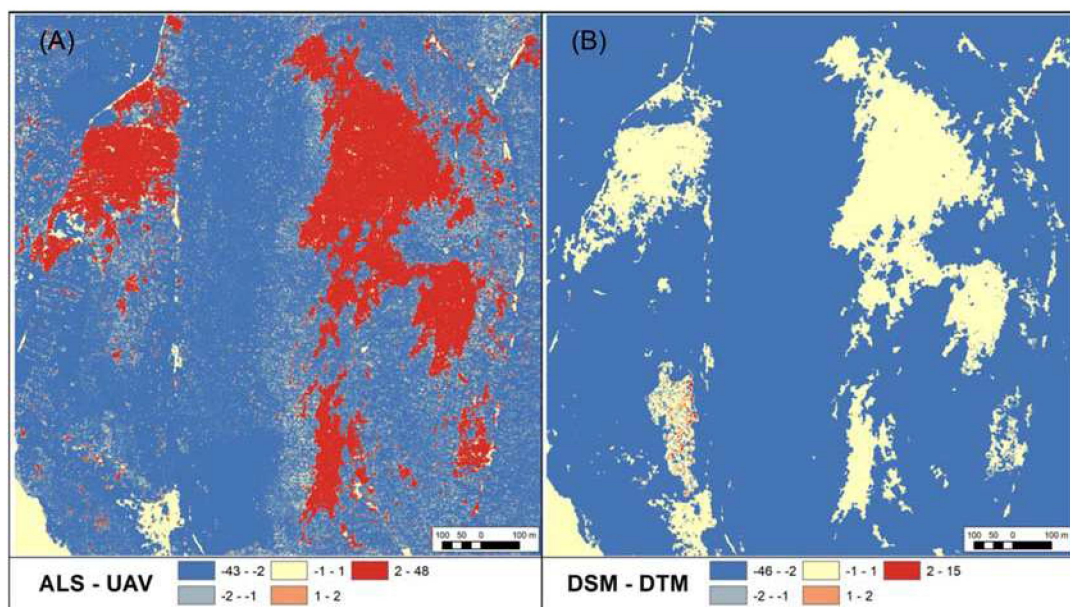


FIGURE 4.16 The comparison of windthrow-damaged area detection using a combination of ALS (DTM) and UAS (DSM) data (A), and solely UAS data (B). The differences are in meters. *ALS*, Airborne laser scanning; *DSM*, digital surface model; *DTM*, digital terrain model.

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4.4 Challenges and perspectives

In this chapter, we showed the tremendous potential of UAS in monitoring natural ecosystems processes, functions, and services.

Technological advances constantly increase the capabilities and accessibility of both new systems, opening new possibilities in ecosystem studies. Albeit UAS potential for vegetation studies is obvious, there are still technical challenges that need to be addressed. These limitations are expected to be partly addressed with the technological advancement in sensors, platforms, processing software, and positioning systems. Still, considering the ultrahigh spatial resolution and complexity and heterogeneity of the natural vegetation, the imprecisions of data could still be larger than some part of heterogeneity and subtle changes we would like to detect with the technology.

The way ecosystem properties can be addressed using UASs greatly differ from both RS from satellite and field perspectives. Still, so far, UAS studies are mostly mirroring either traditional field surveys of RS approaches. One of the main challenges is to develop original research strategies that would fully reflect specificities of UAS data and leverage on its advantages. There is an urgent need to prepare standardized workflows in UAS-assisted ecosystem studies that would assure a balance between the survey accuracy and its laboriousness and complexity, and this book is meant as a contribution to solving such a task. Still, we must bear in mind that UAS technology can expand the portfolio of addressed vegetation types, environmental problems, and research questions, and thus the advancements in technology and methods must go along with modification of the concepts and paradigms in vegetation science.

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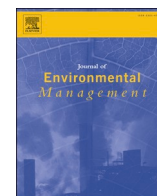
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2. Vegetation monitoring

Appendix 4.

PAPER 4. **Müllerová**, J., Kent, R., Brůna, J., Bučas, M., Estrany, J., Gago, X., Michez, A., Mokroš, M., Tsiafouli, M., Manfreda, S. (2025). Understanding spatio-temporal complexity of vegetation using drones, what could we improve? *Journal of Environmental Management* 373: 123656. <https://doi.org/10.1016/j.jenvman.2024.123656>



Review

Understanding spatio-temporal complexity of vegetation using drones, what could we improve?

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ABSTRACT

Unraveling the intricate spatial and temporal complexities of vegetation represents a crucial key to understanding ecosystem functioning. Drones, as cutting-edge technology, hold immense potential in bridging the gap between on-ground measurements and satellite remote sensing data. Nonetheless, a multitude of challenges still looms, with one of the foremost being the nuanced identification of scales that strike a balance between capturing maximum complexity while minimizing measurement errors. To explore how current research deals with the above-mentioned challenges, we carried out a literature survey on research studies employing drones to characterize natural and semi-natural vegetation. We selected papers related to the role of spatial and/or temporal complexity in ecosystem state, function and/or services. Our result showed that most studies focused on ecosystem state, whereas function and services were barely addressed. Similarly, the effects of spatial or temporal scales on vegetation heterogeneity (complexity) are rarely studied even though drone technology seems ideal for this task. Since heterogeneity differs between ecosystems and its comprehension is greatly influenced by the features of the survey, careful design is important to maximize the efficiency and the range of complexity captured by the survey. However, in reality, most studies do not follow any specific planning of the drone survey according to the case study characteristics. In fact, we found a positive trend between spatial resolution and extent of the study area, and no significant relationship between spatial resolution and accuracy, regardless of the characteristics of the given ecosystem type. Specifically designed studies need to be carried out to further explore the effects of changing spatial and temporal resolution on complexity captured across ecosystem gradients, and establish the optimal resolution for different ecosystem types to assure transferability and operational use in land management. Despite the mentioned challenges and research gaps, drones represent a powerful and effective tool to explore vegetation complexity in new ways and dimensions. Nevertheless, there is an urgent need to define the appropriate methods for each scope.

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1. Introduction

1.1. Ecosystem complexity and remote sensing

Natural ecosystems exhibit continuous change, driven by biotic and abiotic forces at both spatial and temporal scales (Davis, 2001; Turnbull et al., 2012; Pecl et al., 2017). Resource heterogeneity is reflected by vegetation structure and composition, and such complexity also supports biodiversity by providing resources for other taxa (Kolasa and Pickett, 1991; Rozenzweig, 1995; Bar-Massada et al., 2014; Manfreda et al., 2017). The intrinsic spatio-temporal complexity of an ecosystem holds substantial information on its properties, indicating the ecosystem state, functioning and services as well as ecological integrity (Angermeier and Karr, 1994; Ward, 1998). Spatial and temporal variations can also indicate a loss of ecosystem resilience, aka spatial resilience (Cumming, 2011; Sankaran et al., 2019). Perception of complexity changes depending on the organism, and varies across spatial and temporal scales (Tzanopoulos et al., 2013).

According to Müllerová et al. (2021), vegetation complexity can be classified into four major components: (i) composition, covering the topic of biodiversity (c.f. compositional diversity, in Remote Sensing Enabled Essential Biodiversity Variables, RS-EVBs, Reddy et al., 2021), (ii) structure (c.f. structural diversity, RS-EVBs), including the vegetation complexity and structural diversity, biomass and stand openness, (iii) status, e. g. phenological stage or physiological state including the plant stress (c.f. functional diversity, RS-EVBs) and (iv) dynamics, such as disturbances and changes in phenology (cf. Randalhofer et al., 2010; Jetz et al., 2019). Each component shows a different range of variability and characteristic dimension, which imposes the definition of the appropriate scale(s) is essential to understand the changes in an ecosystem and employ appropriate management measures (Levin, 1992; Henle et al., 2010). Measuring ecosystem complexity in the field is a complicated and laborious process, and remote sensing (RS), particularly drones, offers a powerful alternative to field surveys (Cunliffe et al., 2016; Marvin et al., 2016; Wachendorf et al., 2017; Wang and Gamon, 2019). Complexity of vegetation can be captured either directly via mapping species composition, functional traits or ecosystem structure and spatial arrangement, or indirectly by spectral diversity itself (Rocchini et al., 2010, 2022; Perrone et al., 2023).

Generally, because ecological patterns are often simultaneously driven by multiple processes running at different scales, they also need to be examined at multiple spatial and temporal scales (Anderson, 2018). The issue of scale is relevant for many disciplines, and spatial resolution and/or the size of the study area are among the fundamental characteristics of RS (Woodcock and Strahler, 1987; Marceau and Hay, 1999). One of the challenges in studying heterogeneous ecosystems is to identify the appropriate spatial and temporal scales for a stated objective (Wiens, 1989; Levin, 1992; Kent et al., 2011, 2014). Following the definition by Wiens (1989), the scale consists of three components: grain, extent and focus. While spatial resolution normally refers to grain (i.e., pixel size) and extent (i.e., overall area covered by sampling), temporal resolution refers to extent and focus in time (i.e., how frequently the area is sampled, and so to what extent the temporal variability is covered).

Minimal spatial unit of RS data (i.e., a pixel) determines the power of the data to address ecosystem complexity; decreasing spatial resolution reduces the amount of variance of reflectance within the same surface type, and hampers recognition of detailed processes and phenomena by generating a smoothing effect at the same time (Woodcock and Strahler, 1987). On the other hand, addressing fine scale ecosystem variability by using high resolution RS imagery is a challenging task (Spanhove et al., 2012; Wang and Gamon, 2019). This is because very high spatial resolution tends to override general patterns (e.g. environmental gradients, Huston, 1999; Dufour et al., 2006), and with increasing spatial resolution of RS data, heterogeneity introduced by both the measurement errors and high variability of natural ecosystems becomes more

apparent and difficult to disentangle (Treitz and Howarth, 2000). Such a fine scale variability consists of two major components, difficult to separate - measurement and classification errors ('real noise') and variability due to the subtle heterogeneity, which may be highly relevant for understanding the ecosystem's functioning (Woodcock and Strahler, 1987).

The accuracy of the RS surveys is thus driven by the agreement between the used scales and the part of complexity intended to address. At the two hypothetical extreme conditions, i.e., complete homogeneity and complete heterogeneity, the survey performance is expected to be independent of sampling resolution. In case of a perfectly uniform pattern, optimal survey performances should be irrespective of the survey resolution and scale. In the opposite case of absolute heterogeneity, performances will unequivocally equal to zero. These two cases are theoretical and impossible to find in nature, still, both are useful to build constraints for our hypothesis. In between these two extremes, we find a variety of real ecosystems of different degrees of complexity and spatial organization. In addition to the mentioned conditions, we also assume that there is a need to increase spatial resolution with increasing spatial complexity, and, at the same time, with increasing resolution, the analyses suffer from increasing noise in the data. This underlines the importance of optimizing the survey, since not only too coarse but also too fine resolution hampers the survey performance (cf. Steenvoorden et al., 2023).

A similar conceptual analysis can be applied to spectral resolution, which refers to both the number of wavelength bands and their spectral amplitude. A great diversity of sensors is used in ecosystem RS, ranging from panchromatic visible range sensors to hyperspectral sensors detecting hundreds of very narrow spectral bands throughout the visible, near-infrared, and mid-infrared ranges. With increasing spectral resolution, both the intricacy of the data itself (noise) and the power to address ecosystem complexity grow, as for spatial resolution. For the case of hyperspectral analysis, the data intricacy is so important that state-of-art procedures include denoising (Rasti et al., 2018) and dimensionality reduction in relation to the targeted feature (Zhao and Du, 2016).

Vegetation displays strong temporal complexity, reflecting general seasonal cycles as well as specific weather conditions of a given year or season, and the timing and duration of the survey can induce artificial heterogeneity, or noise, e.g., changes in sunlight conditions during the survey and comparing surveys from different phenological stages. Optimal timing and/or revisit time (temporal resolution) of data acquisition are therefore crucial to capturing the heterogeneity of vegetation, whereas the proper timing can, to a certain extent, substitute the measurement frequency (Cole et al., 2014; Schmidt et al., 2014; Dudley et al., 2015; Müllerová, 2019).

Until the 2000s, most RS solutions suffered from a *scale gap* (Kerr and Ostrovsky, 2003), hampering the identification of species assemblages/individuals and ecosystem processes at relevant scales (Turner et al., 2003). In case the properties of interest are scale-dependent, there is a need for up/downscaling (Gunton et al., 2014). The emergence of drones (unmanned aerial systems, UAS, or vehicles, UAV) introduced new opportunities to characterize the ecosystem complexity (Manfreda et al., 2018; Müllerová et al., 2021).

According to the concept mentioned in the previous subchapter, we hypothesize that for each drone survey, an optimal resolution can be defined in order to achieve the best performance. This optimum is determined by the ecosystem type and its characteristics, such as size of individuals, clumping/patchiness, species diversity and temporal dynamics. We expect negative correlation between the size of the smallest targeted unit (individual) and spatial resolution of the drone survey, and positive correlations between ecosystem clumping/patchiness and the survey extent, between species diversity and spectral richness of the RS data, and between temporal dynamics of the ecosystem and temporal resolution of the data (cf. Müllerová et al., 2021). For example, temperate forests formed by large individuals are expected to demand

lower spatial resolution but larger survey extent, patchy Mediterranean shrublands changing rapidly over short distances to require medium spatial resolution and larger survey extent, desert ecosystems with small patchy vegetation and irregular temporal patterns to demand both high spatial and temporal resolution and rather high survey extent, and species rich grasslands with tiny dominants and high intra-annual dynamics to demand very high spatial and medium temporal resolution but small survey extent (Fassnacht et al., 2022). Still, we have to keep in mind that the limitation exists in the survey extent that declines with increasing spatial resolution, and, at the same time, the mentioned factors are at interplay and can, to a certain extent, either improve or complement each other (Müllerová et al., 2013; Sotille et al., 2022).

We carried out a systematic literature review of drone-based studies addressing spatial, spectral and/or temporal complexity of natural to semi natural vegetation. Our main objectives were to evaluate how vegetation spatial and/or temporal complexity and related above discussed challenges are actually addressed using drones, and to what degree the system's complexity/characteristics are actually considered when designing and planning a drone survey. Since the use of drones for environmental purposes is increasing exponentially in recent years, our goal was not to provide an exhaustive and systematic overview of all articles applying drones to study vegetation. Instead, we targeted our search to drone studies related specifically to the role of vegetation spatial and/or temporal complexity in ecosystem state and function. We aimed to answer the following questions.

- What are the common aspects of heterogeneity that are addressed in current drone-based studies?
- What part of complexity is more commonly addressed (spatial or temporal one)? Are the advantages of drones exploited enough?
- To what extent is the design of drone surveys respecting the ecosystem properties and study aims, are the differences in ecosystem complexity reflected in the drone studies?
- In the drone studies, can we find any relationship between the surveyed area, ecosystem type, accuracy and resolution (ground sample distance)?

By discussing the principles related to the matching of scales of ecological processes with resolution of the drone surveys we aimed to identify the research gaps and missed opportunities the drones can provide, enable progress towards standardized and operational drone monitoring procedures, and thus bring the technology closer to practice to better serve the land management needs.

2. Methods

We carried out a systematic meta-analysis (Fig. 1) of articles related to the complexity of natural and semi-natural vegetation (agro-ecosystems were excluded). Specifically, we were interested in studies using drones as a means to study the role of spatial and/or temporal heterogeneity in ecosystem state and/or functioning. The papers were extracted from Scopus using the "TITLE-ABS-KEY" search field with the following keywords: "UAV", "UAS" or "drone", "vegetation", "heterogeneity" or "complexity", and the main type of ecosystem (Table A.1 in the Appendix). The search was restricted to article document types. Ecosystems were divided according to the vegetation height and density to: drylands (including deserts and savannas), aquatic (including marine and coastal submerged ecosystems), wetlands (including estuaries, mires and peatlands), grasslands (including tundra and alpine/arctic grasslands), riparian (including river deltas), shrublands (including semi-arid Mediterranean shrublands) and forests using more specific keywords (Table A.1 in the Appendix). Our search, closed by the end of 2023, produced 158 papers that were inspected and those not dealing with (semi)natural vegetation or drone surveys were excluded.

Finally, the process yielded 97 papers (database in Table A.2 in the Appendix), for which we recorded information about the ecosystem, study area, details on the drone survey, the focus and objective of the studies, the part of heterogeneity that was targeted (i.e., spatial and/or temporal), and the way challenges, benefits and limitations of the drone approach were addressed. Moreover, we recorded the maximum performance (in terms of accuracy assessment) achieved for mapping different aspects of vegetation, such as plant species composition, ecosystem structure, phenological and physiological status and dynamics (c.f. Müllerová et al., 2021). For the purpose of the analyses, ecosystem types were simplified to aquatic, dryland, forests, riparian, shrubland and wetland. Two referees reviewed each study to avoid mistakes. Some studies did not provide complete information on the drone mission. To maximize the explanatory power, we did not restrict our analysis only to articles with complete information and used all articles available for any parameter instead.

Generalized linear model (GLM) with the Gamma distribution was used to determine significance of a relationship between the surveyed area and spatial resolution expressed by ground sampling distance and an interaction effect of ecosystem/vegetation type (as nominal variable) was included. Multiple linear regression was applied to assess the relationship between the spatial resolution and the classification accuracy using the same interaction effect as in GLM. All the data of the variables was excerpted from the literature. Statistical analysis was carried out using the R software (R Core Team, 2023) and visualizations produced

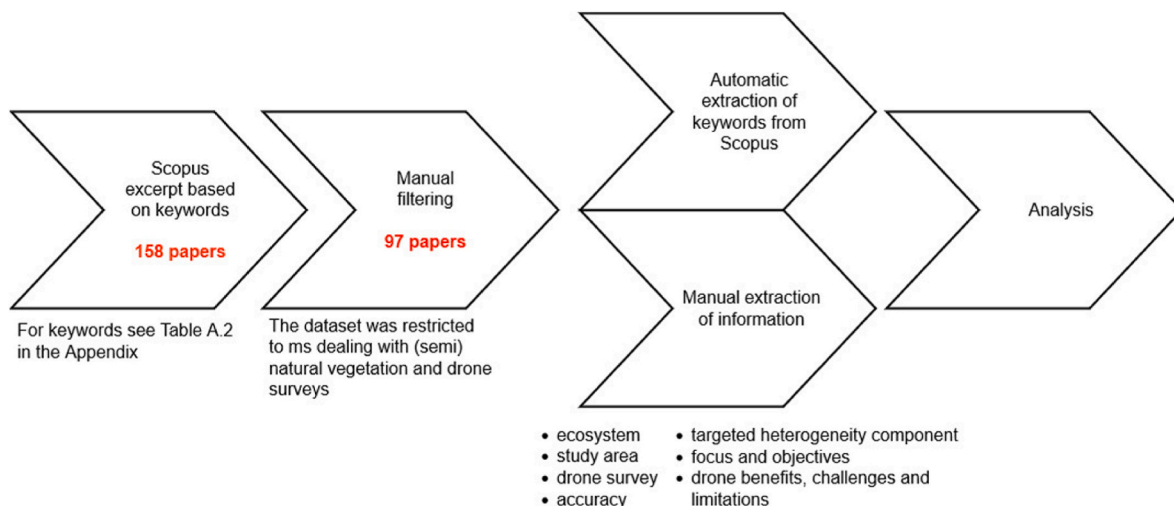


Fig. 1. Processing workflow of the meta-analysis.

by the ggplot2 package (Wickham, 2016).

3. Results

Our dataset (Table A.2 in the Appendix) covers all continents, and seven main ecosystem types (Figs. 2 and 3). Most studies were carried out in Europe (39%), Asia (23%) and North America (21%). The most commonly studied were grasslands (28%) and forests (28%), followed by wetlands (13%), drylands (13%), and shrubland (7%), while the least studied were and riparian and aquatic ecosystems (6 and 5%, respectively).

As for the technical parameters of the missions, copter drones (71%) were used more frequently compared to fixed-wing, being mainly equipped with RGB cameras (50%) followed by multispectral ones (23%; Fig. 3; Table A.2 in the Appendix). The spatial complexity was far more studied compared to the temporal one, covered only by 40% of the articles. More specifically, the vast majority of studies focused on vegetation state (84% studies focused on its spatial perspective), whereas some explored ecosystem functions (47 and 23% from the spatial and temporal perspective, respectively). Note that some of the studies addressed multiple components of heterogeneity. Studies covered a wide range of topics of vegetation monitoring, assessment of plant vigor, biomass and physiological status, species' distribution and mapping, and the effects of disturbances, whereas studies focusing on temporal dynamics were rather scarce, especially speaking about temporal aspects of ecosystem functioning (23%). Most studies dealt with ecosystem structure (52%) and/or composition (46%), whereas plant status, such as phenology or plant stress, and dynamics were far less covered (26 and 19%, respectively, Fig. 2). Studies often pursued the scale issue, exploring the ways to either upscale from field measurements (57%) or downscale to the satellite imagery (23%).

As shown in Figs. 2 and 3, drone studies cover a wide range of objectives and ecosystems spanning across a gradient of complexity. The spatial resolution expressed by ground sampling distance (GSD) ranged from <1 to 500 cm/px, and flight altitudes from 20 to 700 m. The majority of studies covered a small area (<5 ha) and reached high GSD (<6 cm). In rare cases, GSD exceeded 10 cm, and larger areas were surveyed (up to 2260 ha). There was no significant linear relationship ($r^2 < 0.01$) between GSD and the survey area (Fig. 4), except for the forests. Most studies employed GSD ranging from 1 to 10 cm irrespective of the

ecosystem type (Fig. 5).

Regarding the survey performance (classification accuracy) expressed by different accuracy metrics (Fig. 6), 80% of studies indicated the accuracy values and could be considered. Most of them exceeded 0.7 accuracy at resolution of <10 cm, with the highest average values for wetlands (0.86 ± 0.10), the lowest for riparian (0.78 ± 0.11) and shrubland (0.78 ± 0.19). The analysis did not show a significant linear relationship between accuracy and spatial resolution ($r^2 = 0.11$, $F = 1.14$, $p = 0.34$). Nevertheless, Fig. 6 highlights that irrespective of the ecosystem, most studies (63%) were clustered at very high GSD <7 cm with the first and third quartiles of the accuracy 0.75 and 0.9, respectively.

In our meta-analysis, we also reviewed the most common pros and cons of drone applications in vegetation studies mentioned by the authors in their studies. Among the most commonly mentioned drone benefits were high spatial resolution (86%) and flexibility (51%), as well as efficiency, low costs, and possibility to derive structural information from photogrammetric point clouds. Regarding the limitations, orthomosaic irregularities, limited coverage and coregistration issues related mainly to the change detection were among the most stated (Fig. 7). The intricacy of processing and the need for standardization of drone protocols were also mentioned. As for the challenges, the most emphasized were technical issues such as those related to the differentiation between the inner heterogeneity of the studied ecosystem and the data errors. Conceptual challenges related to the complexity and the ways it can be measured were briefly touched by about a quarter of studies.

4. Discussion

4.1. Drones open a new opportunity to study vegetation complexity

Drones offer an excellent opportunity to assess vegetation in detail relevant for ecological processes, making the RS approach attractive for plant ecologists (Siewert and Olofsson, 2020). They represent a flexible source of very fine spatial and temporal resolution data, and allow any kind of survey, given the actual availability of miniaturized sensors (e.g., RGB, thermal, multispectral, Light Detection and Ranging - LiDAR, and hyperspectral) that can be mounted on board (Watts et al., 2012; Manfreda et al., 2018). This provides the potential to monitor different components of ecosystem heterogeneity at very high

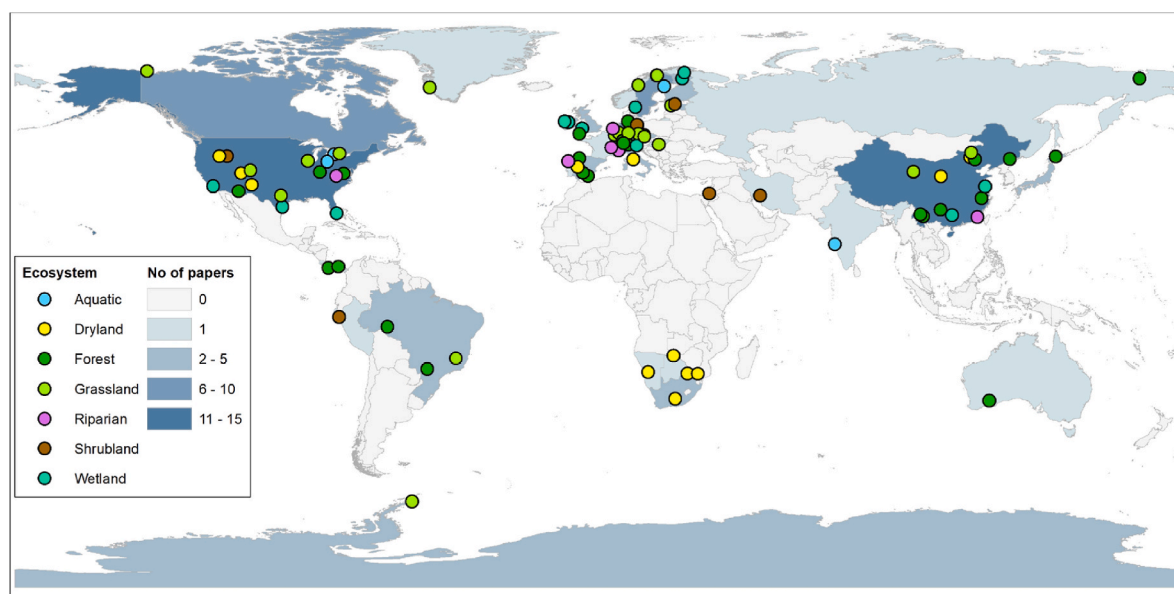


Fig. 2. Spatial distributions of the ecosystems investigated in the studies reviewed herein addressing vegetation heterogeneity using drones (referenced in Table A.2 in the Appendix). Case studies are divided according to the ecosystem/vegetation type.

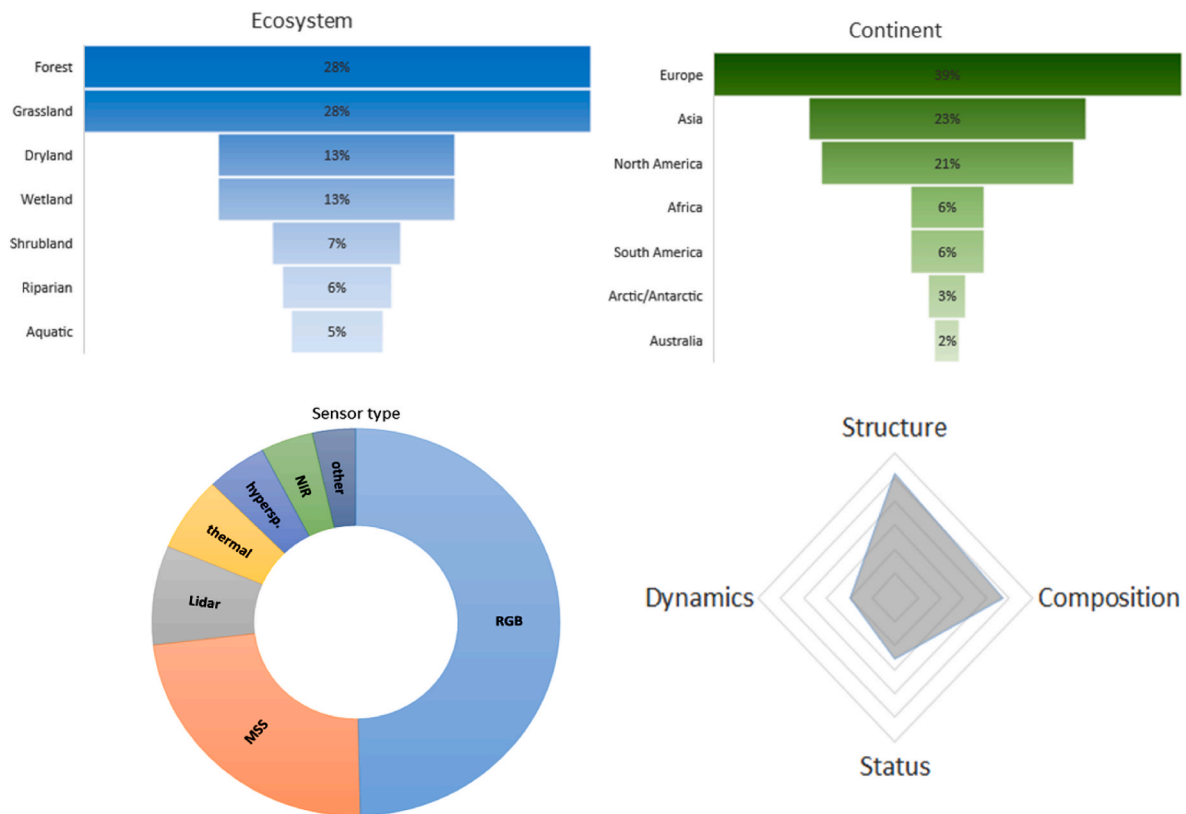


Fig. 3. An overview of drone studies divided according to the ecosystem type, continent, sensor and component of complexity addressed (for references see Table A.2 in the Appendix).

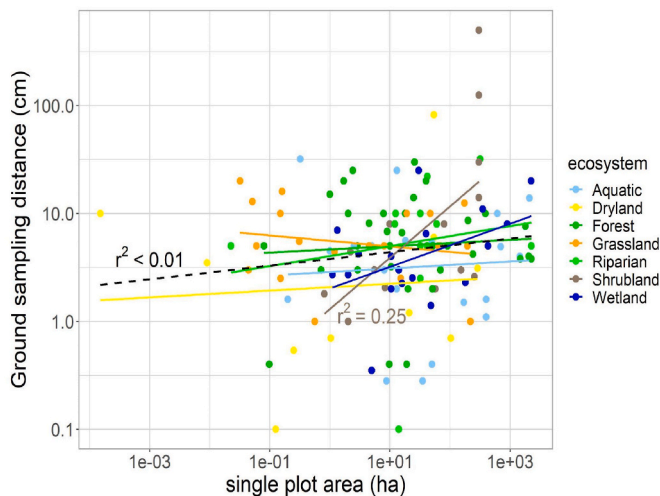


Fig. 4. Regression between the surveyed area and spatial resolution expressed by ground sampling distance according to the ecosystem/vegetation type (excerpted from the list of references given in Table A.2 of the Appendix). The data show no significant linear relationship ($r^2 < 0.01$), except for the forests ($r^2 = 0.25$, $t = 5.01$, $p < 0.01$). r^2 - coefficient of determination. Axes are in logarithmic scale.

spatial/spectral/temporal resolution and to combine different scales to study the dynamics of ecosystem change, such as phenology, plant physiological state and spatio-temporal variability (biotic or abiotic stress, evapotranspiration, biomass production), plant invasions and dramatic disturbances such as wildfires and post-fire vegetation recovery dynamics (Anderson and Gaston, 2013, Vivoni et al., 2014, Gago et al., 2015, Maes and Steppe, 2019, Estrany et al., 2019, Wang et al.,

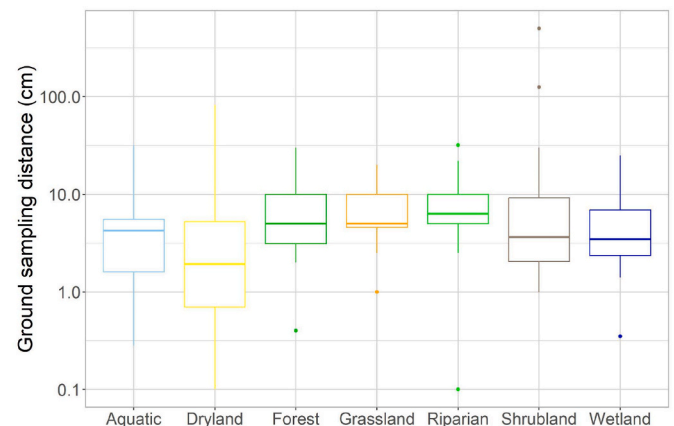


Fig. 5. Relationship between ecosystem type and ground sample distance (GSD). Boxplot shows median, upper and lower quartiles (upper and lower hinges), values as high as 1.5 times the quartiles (upper and lower whisker) and outliers (dots). The Y axis is in logarithmic scale. No significant differences in GSD among different ecosystem types were detected by the one-way ANOVA ($F_6 = 0.50$, $p = 0.80$).

2020, Cunliffe et al., 2022, Bulusu et al., 2023; Müllerová et al. 2023a, 2023b).

Our review shows that the potential of drones is not fully exploited, being especially true for operational use in environmental management and assessment of ecosystem dynamics, functions and services. Our study showed that although drones are widely used, not all the components of ecosystem heterogeneity, nor all the ecosystem types are adequately addressed. From Fig. 8, we can see disbalance in objectives, where the studies addressed mostly an ecosystem state and/or structure,

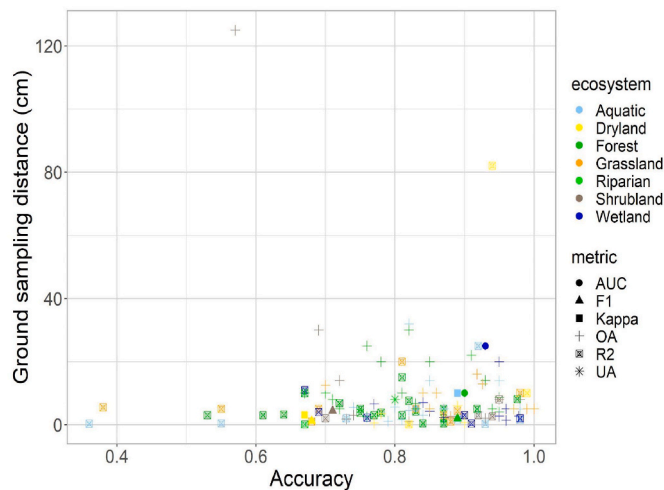


Fig. 6. Relationship between the spatial resolution and the classification accuracy excerpted from the literature (Table A.2 in the Appendix). Studies were divided according to the ecosystem/vegetation type, and the accuracy metric: AUC (area under the curve), F1 score, Kappa, OA (overall accuracy), R^2 (coefficient of determination) and UA (user accuracy).

i.e. patterns that are mapped or monitored without considering the ecosystem functions, change and dynamics. In contrast, addressing processes such as ecosystem functions, services, and dynamics can be more complex and problematic, and thus is less common. Especially in this case, transferable and well described protocols would be helpful. However, such step-by-step protocols, benchmarking datasets, high quality metadata, comparative studies and thoroughly described best practice examples are, until now, largely missing.

The design of the survey has a tremendous effect on the outcome including successful transfer to practice. Our study identified gaps in designing and standardization of drone surveys. To maximize the

efficiency and fully capitalize on the aforementioned drone advantages, carefully designing the mission according to its purpose and depending on the ecosystem studied represents a necessary step (Müllerová et al., 2021; Roser et al., 2022).

4.2. Scale matters

Ultra-high resolution of drones, in combination with other means such as field or satellite surveys, allows to better address the intrinsic spatial and temporal heterogeneity of ecosystems and related ecological patterns and processes (Marvin et al., 2016; Müllerová et al., 2023a). Still, an optimal range of scales exists to address the particular phenomena beyond which the noise, error or processing time and effort outweigh the benefits of detailed resolution. Many studies confirm that the accuracy of RS based models is strongly influenced by ecosystem homogeneity in a sense of both horizontal (patchiness) and vertical structure (Chen et al., 2016; Tang et al., 2020; Corcoran et al., 2021; Roser et al., 2022; Sotille et al., 2022).

Our study revealed that the sampling scales in drone-based environmental studies often do not match the biological phenomenon studied, and the lack of attention to scales greatly affects the ability to detect ecological processes (Gamon et al., 2020). We found no significant differences in terms of spatial resolution across the different ecosystems studied, regardless of their obvious differences. This fact can be partly interpreted as a lack of concern about the targeted ecosystem complexity, and a tendency to survey and process at the finest possible spatial resolution with little concern about the specificities among studied ecosystems, despite the fact that many examples exist in the literature illustrating that the finest resolution might not always be the best. For example, Wang et al. (2019) found that spatial resolution of 1.5 m (consistent with the canopy size) was sufficient to capture the spatial complexity of the canopy fluxes (transpiration and CO_2 assimilation) of a deciduous willow forest. Müllerová et al. (2017) showed that in case of invasive giant hogweed, centimeter resolution of drone imagery actually overwhelmed the relevant spatial patterns and hampered

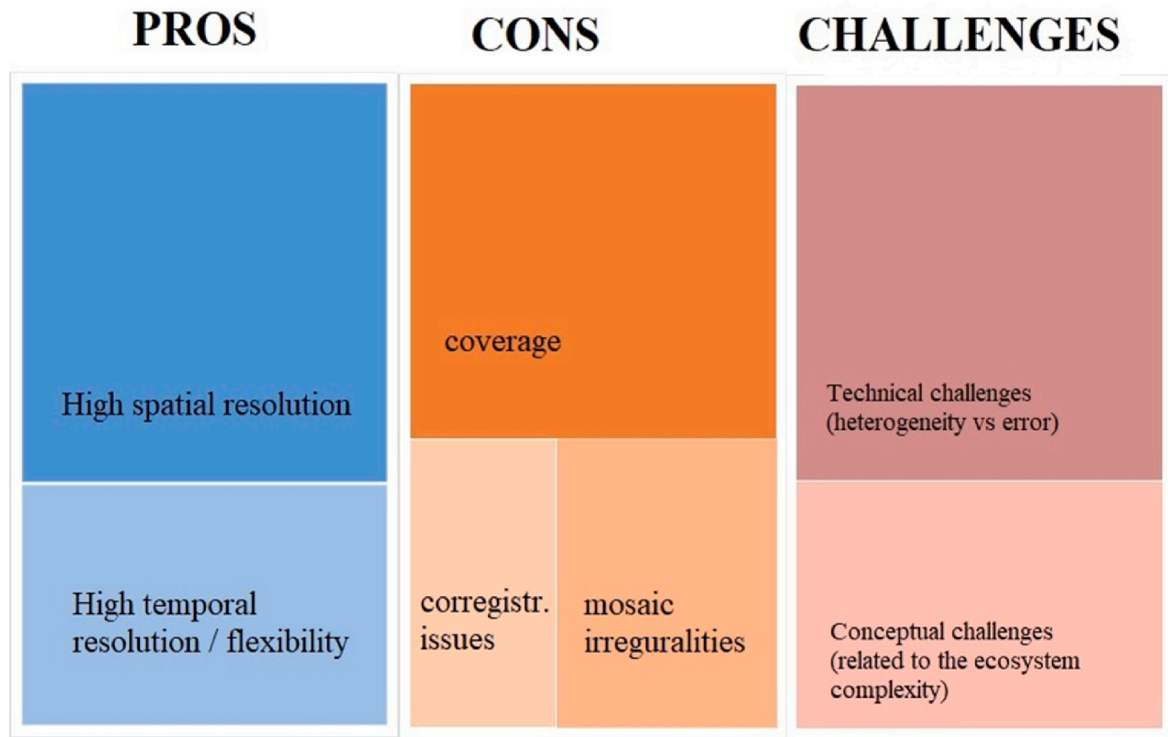


Fig. 7. The most mentioned advantages (pros), limitations (cons) and challenges related to the use of drones in ecosystem complexity assessment. Size of the box corresponds to the frequency of mention in our meta-analysis.

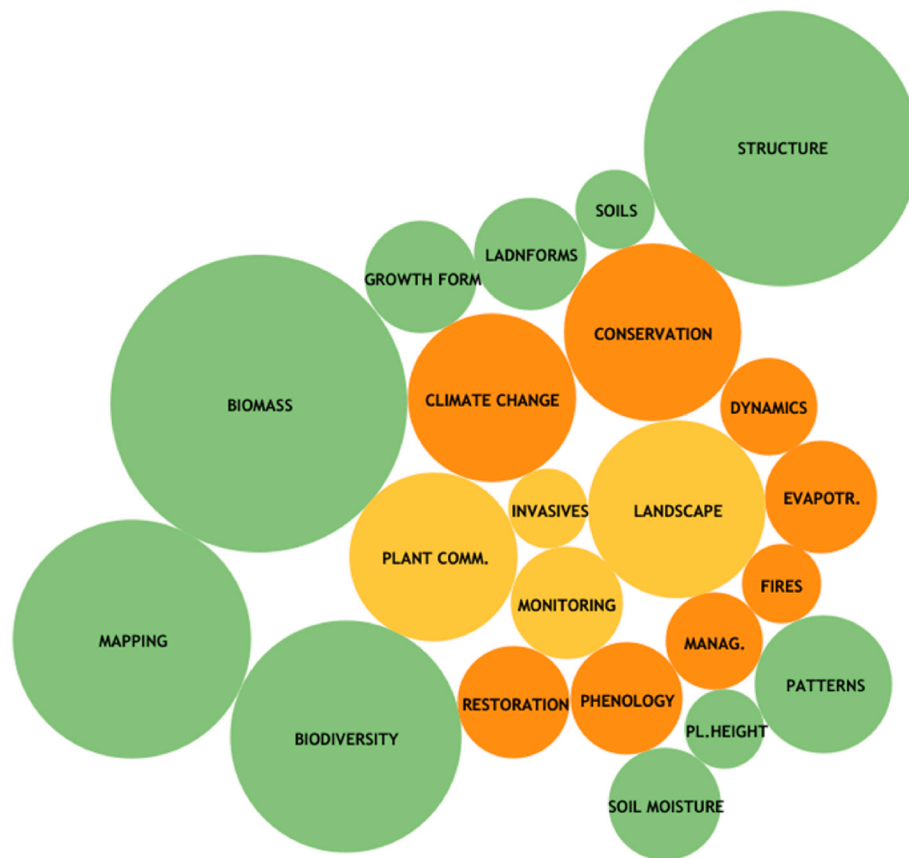


Fig. 8. Bubble plot of keywords from reviewed papers. The keywords retrieved from Scopus (both Authors and Index keywords) were manually assigned as objectives, and divided into the following groups: patterns (ecosystem state and structure) in green, and processes (ecosystem status and dynamics) in orange. Keywords that apply for both mentioned categories are in yellow. The size of the bubbles is relative to the number of keywords mentioned. Keywords only mentioned once were not considered.

the classification based flowering compound umbels, eventually decreasing the classification accuracy. [Treitz and Howarth \(2000\)](#) demonstrated that optimal resolution to characterize different forest ecosystems varies according to the density and structure of the canopy. [Albuquerque et al. \(2022\)](#) found that degradation of GSD considerably increased accuracy for detecting tree species in Amazon secondary forest. For heterogeneous grassland ecosystems, [Lu and He \(2017\)](#) were able to determine a threshold spatial resolution depending on a target species. The role of spatial resolution was confirmed even for ecosystem service models ([Bagstad et al. \(2018\)](#)). On the other hand, drone flight regulations in most cases are rather restrictive in terms of flight height ([Stöcker et al., 2017](#)), constraining drone scientists to fly relatively low. For example, the GSD suggested by [Wang et al. \(2019\)](#) would be reached by a flight height of roughly 750 m considering commonly used drones (DJI P4Pro). However, even for low drone flights, coarser spatial resolution can be reached through resampling the imagery before the processing, which would also speed up and simplify the process.

Exploring the link between ecosystem type, spatial resolution and spatial extent of the study area in published studies, we found no trend between spatial resolution and extent of the study area regardless of the ecosystem characteristics. These findings contrast with the fact that the observed complexity differs between ecosystems. In particular, in ecosystems with high complexity such as species rich temperate grasslands, the optimal spatial resolution tends to be fine ([Fassnacht et al., 2022](#)), shifting towards coarser resolutions as complexity declines (e.g. in temperate forests, [Wang et al., 2019](#)). Similarly, in patchy ecosystems such as Mediterranean shrublands ([Blondel, 2006](#)) and/or ecosystems formed by large individuals such as forests, the study area must be larger to cover the range of variability in species composition as compared to

the ecosystems that are more homogeneous and/or formed by small individuals, such as grasslands or wetlands. At the same time, the optimal resolution represents a trade-off between ecosystem complexity and signal errors, between spatial resolution and extent, and between accuracy and acquisition and processing demand and complexity ([Bradshaw and Fortin, 2000](#); [Räsänen and Virtanen, 2019](#); [Steenvoorden et al., 2023](#)). Such a concept should be used when planning data collection campaigns, but from our review it implies that these issues are rarely addressed.

Further, our meta-analysis showed no significant relationship between accuracy and spatial resolution, irrespective of the ecosystem type/characteristics. However, it is important to mention that the comparison of classification accuracy between studies remains difficult as data quality, classification scenarios and associated complexity greatly vary among studies as well as accuracy metrics, and can be further influenced by many factors related to the phenomenon studied (e.g., species/genus/family identification, health conditions), its environmental context, and the dimension considered for the accuracy assessment (e.g., leaf/branch/tree crown/forest inventory plot). The detected lack of relationship between accuracy and spatial resolution could also indicate that other major factors besides the survey design, either technical or conceptual, influence the experimental design. To be able to rigorously explore the effects of spatial resolution in drone surveys, a comparative experimental study in controlled design and spanning over broad ecosystem (environmental) gradients would be required.

4.3. Crucial role of standardization and metadata

One of the challenges encountered while studying vegetation complexity, which became even more apparent at finer spatial scales, is the ability to separate 'real noise' (i.e., data error) from heterogeneity that is informative. In this context, it is crucial to identify and standardize protocols for drone data (Manfreda et al., 2018; Buters et al., 2019; Tmušić et al., 2020; Poley and McDermid, 2020), since application of drones in ecology is particularly perceptive to the study design and methods (Frey et al., 2018; Cunliffe et al., 2022; Müllerová et al., 2023b). Several protocols were already proposed, however they are often specific for particular purposes, for example, a global protocol for assessment of the aboveground biomass from drone photogrammetric point cloud proposed by Cunliffe et al. (2022). The level of general applicability and transferability of the protocols differs according to the level of heterogeneity based on ecosystem structure. Whereas for some plant functional types, such as trees and shrubs, they can be readily transferred, for others, such as grasses or wetlands, the protocols need to be site- and/or species-specific (Cromwell et al., 2021; Dronova et al., 2021; Roser et al., 2022). As a synthesis, Müllerová et al. (2021) introduced a general framework for designing the drone-based studies according to the component of vegetation complexity being addressed.

During the review process, we noticed that studies do not often provide full details about the flight campaign, sensor characteristics, resolution, area sampled, image processing or accuracy assessment. Such metadata absence and/or poor quality makes it difficult to impossible to carry comparative studies that would allow transferability and generalization of findings. In studies capitalizing on a time series of data or combining several sources, metadata are crucial (Fawcett et al., 2021). Providing appropriate metadata remains critical for standardizing the methodology and transferability to practice, including standardized metadata protocols (Barnas et al., 2020). Comprehensive metadata represent a key step for establishing optimal study design (sampling extent, resolution, processing approach) that would reflect the study objective and characteristics of the targeted system/unit and be optimized for the purpose (cf. Müllerová et al., 2021). Such standardization would allow to fully benefit from the given technology and minimize inevitable challenges and errors related to drone surveys. It would assist continental or global comparative studies (see e.g. Cunliffe et al., 2022; Mienna et al., 2022), transfer to practice or integration drones in citizen science (Paneque-Gálvez et al., 2014; Pocock et al., 2018; Ierodiaconou et al., 2022).

4.4. Underexploited temporal flexibility of drone surveys

It is important to note that studies taking advantage of the improved drones' temporal resolution (re-visiting sampling frequency) are not very common (but see e.g., Michez et al., 2016; Müllerová et al., 2017, van Iersel et al., 2018a,b, Bulusu et al., 2023). This is despite the fact that this direction seems to be particularly promising since flexibility of drone surveys holds great potential to help understanding of dynamic changes. Drones are particularly helpful for studying disturbances and following recovery after pest outbreaks, wildfires, windthrow and soil erosion (Yuan et al., 2015; Mokroš et al., 2017; Röder et al., 2018; Laslier et al., 2019), detecting rapid growth (e. g. herb invasions, Martin et al., 2018, and measuring intra-annual biomass dynamics, Doughty and Cavanaugh, 2019). They bear great potential for assessment of natural cycles along the seasons and fluctuations under environmental stress, such as seasonal or diurnal water deficiency, phenological dynamics, or an intra-annual competition in space that results in a sort of a dynamic mosaic (Lu and He, 2017, Tóth, 2018).

We can infer that with automation of the drone operation, cloud based/real time processing and other technological advancement, the temporal aspect will be increasingly addressed using drones, including a combination of ultra-high spatial resolution data collected by the drone surveys with comprehensive archives of satellite data (Francis et al.,

2024).

4.5. Disbalance in ecosystems

We detected uneven coverage of ecosystem types; according to our analysis, the vast majority of studies were developed between 40° to 60° latitude in the northern hemisphere, specifically in Europe and North America, and focused on cold and temperate ecosystems, mainly temperate forests and grasslands. Other latitudes and ecosystems, such as arctic and alpine ecosystems, shrublands, savannahs, and deserts remain largely understudied. One of the reasons for such a disbalance might be related to the technical issues. For example, there is typically high phenotypic plasticity in shrub species (e.g. Lev-Yadun and Ne'eman 2004; Gratani, 2014; Khadka et al., 2018; Michelaki et al., 2019), which makes their identification more complex. Dryland ecosystems express extremely high spatio-temporal variability (Roser et al., 2022). In such heterogeneous ecosystems, vegetation is usually sparse, making its assessment from a distance a challenging task (e.g., Elbaz et al., 2021). Drylands are often characterized by a large fraction of bare soil, contributing to high levels of soil reflectance in images, creating a saturation effect which substantially reduces classification accuracy (e. g., Tian et al., 2016). Even more serious impediment in using drones in arid ecosystems is the ephemeral nature of plants in such ecosystems (Lev-Yadun and Ne'eman 2004). Individual plants may be dormant for prolonged periods of time with dead plants difficult to discern from dormant ones, making quantification of vegetation cover and state difficult (Hamada et al., 2019). On the other hand, deployment of photogrammetrically derived structural measures bears high potential in drylands (and shrub encroached grasslands) thanks to the sparsity of vegetation cover and often contrasting size of shrubs as compared to other vegetation (Cunliffe et al., 2016; Howell et al., 2020; Zhao et al., 2021).

4.6. Implications for management

Drones are highly relevant for nature conservation and land management because understanding spatiotemporal patterns of vegetation in depth and detecting changes early are critical for operational monitoring of ecosystem status and restoration efforts (Gonzalez et al., 2016; Müllerová et al., 2017; de Sá et al., 2018; Jiménez López and Mulero-Pázmány, 2019) (Fig. 9). In spite of the enormous power of the tool and new ways to both explore the ecological processes and assist in many fields, including nature conservation, agriculture, forestry, landscape management and planning, and mitigation of negative consequences of global change, it is still underexploited in practice. This is well illustrated by the disbalance between the potential and realization of drone surveys according to the component of heterogeneity addressed (Fig. 9). The green fields in the Recovery wheel (McDonald et al., 2016) at the bottom indicate the current input of drone technology, whereas from the list of possible topics to be addressed and implications of drone surveys for management it implies that the potential for management is not fully capitalized on.

Vegetation complexity is linked to various aspects of biodiversity, including plant functional diversity (as defined by plant functional traits) related to ecosystem processes, such as photosynthesis, and is thus driving various ecosystem services including productivity (Durán et al., 2019; Zhao et al., 2021). Drones are able to support management by assessing and monitoring ecosystem state, such as mapping threatened or alien plant species and habitat types (Baena et al., 2017; Bergamo et al., 2023; Husson et al., 2017; Steenvoorden et al., 2023). The technology is also well suited to describe patterns and changes in vegetation structure (e.g. for forest inventories, Kükenbrink et al., 2022, or forest conservation, Jucker et al., 2023) and its implications for biodiversity and ecosystem functioning (e.g., restoration of Amazon forest, Albuquerque et al., 2022, and floodplain dynamics, Resop et al., 2021), and target some of the processes such as disturbances (fires,

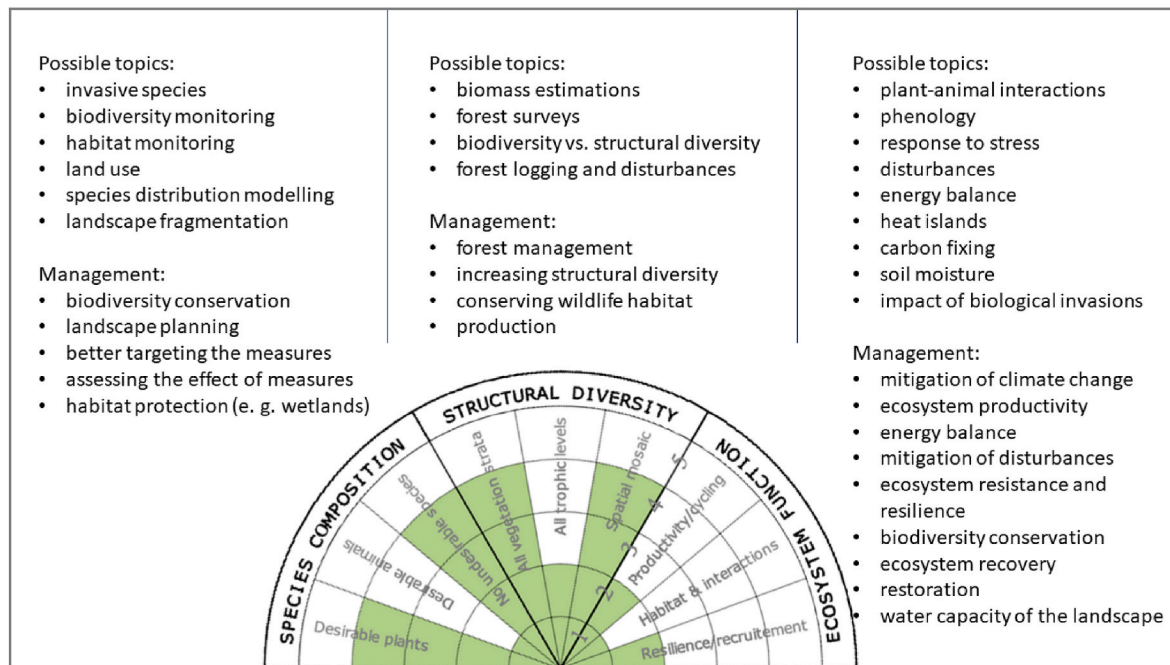


Fig. 9. Potential of drone surveys for practice in relation to the ecosystem complexity. Green fields indicate the current input of drone technology. Based on Recovery wheel (McDonald et al., 2016).

Beltrán-Marcos et al., 2021, Singh et al., 2023; soil erosion, Harris and Baird, 2019; and soil degradation, Krenz et al., 2019), plant stress (Li et al., 2020, Abdollahnejad and Panagiotidis, 2020; Paneque-Gálvez et al., 2014), shifts in phenology (Fawcett et al., 2021, Neumann et al., 2020), impact of invasions (Schulze-Brüninghoff et al., 2021), or interactions between plant complexity and animals (Olsoy et al., 2018; Siewert and Olofsson, 2021; Wagner et al., 2021; Zahawi et al., 2015).

In addition drones can be used in supporting the assessment of ecosystem functions and services that are related to heterogeneity, such as ecosystem productivity (Merrick et al., 2021, Siewert and Olofsson, 2021), carbon stock dynamics (Jayathunga et al., 2018), evapotranspiration (Bulusu et al., 2023), species diversity (Conti et al., 2021, Yang et al., 2021), soil moisture patterns (Zhang et al., 2020), vegetation dynamics (Resop et al., 2021; van Iersel et al., 2018a,b), soil quality and special properties such as biocrusts (Havrilla et al., 2020), ecosystem health (Guerra-Hernández et al., 2021), response to stress (such as drought in Díaz-Delgado et al., 2019), and human impact (Fenger-Nielsen et al., 2019), including climate change effects (Assmann et al., 2020). The use of UAVs can be expanded in capturing functional diversity for estimation of ecosystem services; however, more research is needed to standardize remote sensing protocols across spatial and temporal scales (Cimoli et al., 2024). Such applications help to define and adapt management practices and better target management measures to increase efficiency (Blackburn et al., 2021; Martin et al., 2018; Müllerová et al., 2017; Villoslada Peciña et al., 2021).

As indicated by Müllerová et al. (2023b), we can expect that some technical reasons that hamper the operational use in practice, such as low transferability of algorithms and failure to deliver accurate and timely products, will to certain extent be overcome by improving the sensors, platforms and standardization of processing workflows. Among the promising solutions are leveraging the ability to move across spatial and temporal scales ('rocking'), cloud-based solutions and employment of models based on artificial intelligence. Still, the problem remains in better communicating both advantages and weaknesses of the tool to the potential stakeholders from both practice and other scientific disciplines, and engage public via implementation of drone techniques in citizen science projects (Paneque-Gálvez et al., 2014; Pocock et al., 2018; Ierodiaconou et al., 2022). Interdisciplinary teams and thorough

discussions with possible stakeholders are therefore necessary to better reflect their needs and promote implementation of drone-based solutions into practice.

4.7. Challenges and perspectives

The number of studies using drones in environmental applications is readily increasing. Still, as already mentioned, its power remains underexploited, most studies focus on mapping/monitoring of ecosystem state rather than addressing its dynamics or functions (cf. Müllerová et al., 2023b). Despite the aforementioned challenges, drones represent a powerful tool for environmental studies (Whitehead et al., 2014). To maximize the survey efficiency, the optimal type of drone, sensor, acquisition strategy and processing approach must be chosen according to the purpose and component of complexity addressed (see a framework synthesized by Müllerová et al., 2021).

The temporal resolution (frequency and flexibility of the data acquisition) is still underexploited in terms of vegetation dynamics, phenology and plant ecophysiology and functioning, even though many processes happening at very fine scales are very dynamic and can change markedly on a weekly or daily basis. Sharing drone data on cloud and harmonizing the processing techniques will tremendously increase both the spatial coverage and temporal resolution (i.e., the frequency of the data acquisition), and enable to build continuous drone layers at landscape/regional/country scale and derive products such as ecological variables at relevant scales. Coupled with growing archives of open-access mid to high-resolution satellite imagery (e.g. 10 m for the Sentinel-2, Bhatnagar et al., 2021), drone data reaching sub-centimeter spatial resolution at high frequencies bear potential to revolutionize spatial ecology (Anderson and Gaston, 2013), and provide links to the Earth Observation/Biodiversity Observation Network (Vihervaara et al., 2017).

Up to now, drone research tends to adapt approaches developed using manned airborne and satellite platforms, and, similarly to those, struggles with linking field (often point) data and drone perspective (Gillan et al., 2020). The phenomenon of ecosystem complexity is very complicated, and so is its assessment. At different scales, different parts of complexity are perceived. Although field measurements are called

“ground truth”, their precision and the ways they reflect vegetation complexity are not necessarily much closer to reality compared to distant methods. The differences between field and remote methods can therefore signify either the imprecisions or a change in perspective that reveals new levels and patterns of heterogeneity (c.f. [Anderson, 2018](#); [Roser et al., 2022](#)).

Future research should focus on the development of new original research strategies which leverage specific drone advantages. For example, the ecosystem complexity could be addressed through the development of innovative flight surveys (e.g., below/intra canopy flights or formation flights), and new sensors and flight modes might even open up new perspectives, such as soundscapes, odorscapes or very fine temporal and spatial micro-heterogeneity ([Chen et al., 2019](#); [Hyyppä et al., 2020](#); [Michez et al., 2021](#); [Linchant et al., 2023](#)). Development in drone technology is thus expected to broaden the span of ecosystems studied as well as environmental problems and research questions addressed, and the development of technology and procedures is to be accompanied with a conceptual change of our perception of complexity/heterogeneity in natural ecosystems.

As already mentioned, the potential of drone surveys in ecosystem complexity assessment and management remains to large extent underexploited. Our review, stressing out the importance of careful designing, standardizing and transferability of the drone surveys will hopefully contribute to the transferability, metadata quality, common standards and operational use in management.

5. Conclusions

Spatio-temporal complexity is crucial for understanding ecosystem functioning. Drone technology has the potential to assess dynamic changes in ecosystems at scales that are fine enough to capture underlying ecological processes even though for many purposes, other RS platforms such as manned aircraft and satellites should be considered. Drones are capable of providing unprecedented spatiotemporal resolution; still, many challenges need to be addressed. One key question remains on how to actually measure the ecosystem complexity using drones. Among the most important aspects is to appropriately design the survey considering both the nature of the ecosystem and the focus of the study (i.e. the relevant heterogeneity component). Generally speaking, the optimal setting depends on several factors such as the objective of the study, the characteristics of the ecosystem addressed and the measured trait/pattern/process researched for; there may also be strong dependencies on the spatio-temporal characteristics of the considered ecosystem.

In this context, it is necessary to establish robust, standardized and transferable protocols, and identify a synthetic measure capable of describing both the spatial and temporal structure of an ecosystem. At the moment, the spatial resolution (GSD) of drone surveys is not driven by the actual complexity of the studied ecosystem nor the research questions, but by technical issues. Studies exploring temporal aspects are uncommon even though drones are perfectly suitable for the task thanks to their flexibility. On top of that, the majority of studies focus on describing the state, not the dynamics nor functions and processes of the ecosystem. Despite the fact that very high spatial and temporal resolution provided by drones can be extremely beneficial for ecosystems composed of sparse and/or small individuals, drone studies for such ecosystems (e.g. shrublands) are rare.

Based on our review we believe there are research gaps in drone applications that impede full capitalization on the advantages the drones can provide and hamper their implementation in operational management. To establish the optimal resolution for specific ecosystem types, studies designed to explore the effects of changing spatial and temporal resolution on complexity captured across ecosystem gradients are needed; this is especially true for understudied ecosystem types. This also implies the need to elaborate workflows of drone surveys optimized for addressing various ecosystem properties ([Müllerová et al., 2021](#)).

Where the technology is applied in an appropriate way, drones are found to be both powerful and effective, and can even address new dimensions of ecosystem complexity.

CRedit authorship contribution statement

Jana Müllerová: Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Rafi Kent:** Writing – review & editing, Writing – original draft, Conceptualization. **Josef Brůna:** Writing – review & editing, Writing – original draft, Investigation. **Martynas Bučas:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation. **Joan Estrany:** Writing – review & editing, Writing – original draft, Data curation. **Salvatore Manfreda:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Conceptualization. **Adrien Michez:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Martin Mokroš:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Maria A. Tsiafouli:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Xurxo Gago:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2024.123656>.

Data availability

No data was used for the research described in the article.

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Appendix 5.

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About the link between biodiversity and spectral variation

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Abstract

Aim: The spectral variability hypothesis (SVH) suggests a link between spectral variation and plant biodiversity. The underlying assumptions are that higher spectral variation in canopy reflectance (depending on scale) is caused by either (1) variation in habitats or linked vegetation types or plant communities with their specific optical community traits or (2) variation in the species themselves and their specific optical traits.

Methods: The SVH was examined in several empirical remote-sensing case studies, which often report some correlation between spectral variation and biodiversity-related variables (mostly plant species counts); however, the strength of the observed correlations varies between studies. In contrast, studies focussing on understanding the causal relationship between (plant) species counts and spectral variation remain scarce. Here, we discuss these causal relationships and support our perspectives through simulations and experimental data.

Results: We reveal that in many situations the spectral variation caused by species or functional traits is subtle in comparison to other factors such as seasonality and physiological status. Moreover, the degree of contrast in reflectance has little to do with the number but rather with the identity of the species or communities involved. Hence, spectral variability should not be expressed based on contrast but rather based on metrics expressing manifoldness. While we describe cases where a certain link between spectral variation and plant species diversity can be expected, we believe that as a scientific hypothesis (which suggests a general validity of this assumed relationship) the SVH is flawed and requires refinement.

Conclusions: To this end we call for more research examining the drivers of spectral variation in vegetation canopies and their link to plant species diversity and biodiversity in general. Such research will allow critically assessing under which conditions spectral variation is a useful indicator for biodiversity monitoring and how it could be integrated into monitoring networks.

KEYWORDS

biodiversity, monitoring, remote sensing, spectral variability hypothesis, vegetation

1 | INTRODUCTION

Biodiversity conservation has become a matter of international concern over the last decades. One challenge in the current efforts to conserve the remaining biodiversity is the development of a global biodiversity monitoring and early-warning system. This challenge is being addressed by the activities of, among others, the Group on Earth Observation's Biodiversity Observation Network (GEO BON) (Scholes et al., 2008; Walters & Scholes, 2017). A central task of GEO BON is to develop a set of essential biodiversity variables (EBV) that includes variables describing community composition, ecosystem structure, ecosystem function, genetic composition, species populations and species traits (Pereira et al., 2013). Given the global scale of the task, remote sensing (RS) is expected to make an important contribution to monitor some of these EBVs, particularly those describing species traits and ecosystem structure (Skidmore et al., 2015, 2021).

Besides this globally concerted effort to develop metrics and variables suitable for a global monitoring system, RS has also been invoked to describe and monitor local biodiversity patterns expressed for example by the number of plant species per unit area, also called (plant) species density or species count (Schmidtleein & Fassnacht, 2017). However, studies attempting to establish relationships between RS data and species counts are always of a correlative nature because it is not the taxonomic assignment but rather the traits of the species that affect the RS signal. Additionally, since RS of terrestrial biodiversity is mostly able to capture information about plant traits, most of the studies are uniquely addressing floristic diversity. This is a shortcoming because plant species diversity is not always a good proxy for the diversity of other taxonomic groups (Ritter et al., 2019).

Despite this, recent years have witnessed the emergence of several approaches to assess plant biodiversity via RS. In their review, Wang and Gamon (2019) differentiate between four approaches: (1) habitat mapping; (2) direct species mapping; (3) mapping functional diversity via functional plant traits; and (4) spectral diversity-based approaches. Here, we focus on the spectral diversity-based approaches and discuss conceptual and technical challenges related to the underlying spectral variability hypothesis (SVH) (Palmer et al., 2002). However, to provide some context, we briefly introduce the other approaches as well.

1. Habitat mapping — Inferring species counts from the mapping of habitats or linked vegetation types is a straightforward approach. It assumes that each type can be directly related to a number of species (e.g., Braun & Koch, 2016). For example, the approximate plant species numbers of particularly species-rich or species-poor forest or grassland types are often well known from field surveys. By mapping these types using RS (which essentially is the same task as creating a land-cover map with a quite detailed thematic differentiation) and optionally also considering spatial context (size of habitat patches, and composition of habitats), reasonable estimates of plant species numbers can be obtained. To obtain reliable results, profound knowledge of the plant species richness of the sampled habitats and their precise classification is required. The most important drawback is that this approach is based on categorical types. Hence gradients of species richness within a habitat or vegetation type are difficult to capture. Further, subtle degradations may be missed because only a categorical shift from one type to another would result in a change of the estimated species numbers (see also Schmidtleein & Sassin, 2004 and Feilhauer et al., 2020).
2. Direct species mapping — The feasibility to map individual plant species (particularly the classification of larger trees and shrubs or mono-specific stands) from RS data has been proven (e.g., review by Fassnacht et al., 2016). Particularly high spectral and spatial resolution data (e.g., airborne hyperspectral data or data from unmanned aerial systems) were found to accomplish this task with good accuracy (e.g., Modzelewska et al., 2021; Müllerová et al., 2017). However, the direct mapping of species over wider areas is typically limited by the trade-off between spatial resolution and coverage in most RS systems. Furthermore, the number of species that can be identified within a given data set may also be limited due to the lack of clear species-specific spectral signatures, or other characteristics (shape, texture) enabling distinguishing the species from their surroundings. Currently, most existing RS data sets seem to be unable to reliably separate more than 10–15 dominating species based on their optical traits as mirrored in the amount of target species typically considered (see Figure 3 in Fassnacht et al., 2016). However, given the fast development of methodical advances in the field of deep learning, these numbers may increase in the future, particularly if very high spatial resolution and/or time-series data are available (e.g., review by Kattenborn et al., 2021).
3. Mapping functional diversity — One approach to bypass current limitations of discriminating large numbers of plant species from RS data is to focus on plant functional types instead of individual species. This also takes into account the fact that the occurrence of such types can be of more direct relevance to ecosystem function. It is known that certain biochemical and structural plant traits have a clear effect on the reflected electromagnetic radiation (e.g., Jacquemoud et al., 2009; Kattenborn et al., 2019; Ollinger, 2010). Hence, the range and variation of these traits can be captured and mapped by RS data. Because areas with higher trait diversity tend to harbour more species (Biswas & Mallik, 2011), it is assumed that it is possible to indirectly quantify species counts based on the functional diversity patterns obtained by RS. The suitability of this approach has been demonstrated in a few case studies (e.g., Schweiger et al., 2018) but the verification across ecosystems is still missing. Furthermore, the mapping of trait diversity has a value in itself (and many applications) as functional traits are not only related to biodiversity but also to ecosystem functions and services, which ultimately constitute a conservation priority (Díaz & Cabido, 2001).

4. Spectral diversity-based approaches — Finally, the spectral variability hypothesis (SVH) suggests a more generic relationship between biodiversity and remotely sensed spectral information which can be used to estimate species counts or other biodiversity-related metrics from RS data. The SVH as originally suggested by Palmer et al. (2000, 2002) states that the biodiversity of a given area is positively related to the spectral variation of the same area captured by an RS image. The underlying assumption is that a higher spectral variation can be interpreted as a higher variation in (number of) habitats or linked vegetation types and hence a larger number of species (referred to as 'original SVH' hereafter). In the case of very fine spatial resolution, an increased spectral variation may also directly relate to a higher number of species with a higher diversity in the corresponding species-specific optical traits (hereafter, 'species SVH'). Both are closely related and sometimes difficult to untangle because optical community traits, which allow for differentiating habitats or vegetation types, can be traced back to optical species traits. It is hence rather a matter of scale which of both drives variation across pixels in a place. The intriguing simplicity of the SVH hypothesis may, however, suggest at first glance that this relationship can hold true across ecosystems and scales.

The SVH has been extensively tested in case studies summarized for example in Rocchini et al. (2010), Schmidtlein and Fassnacht (2017) and Wang and Gammon (2019). The strength of the observed correlations between spectral variation and plant species counts (the most frequently applied biodiversity metric) varied strongly in these studies which raises doubts about the general validity of the SVH. Schmidtlein and Fassnacht (2017) pointed out several situations where the original SVH did not hold true and even found areas with the opposite relation, that is, increased plant species counts with lower spectral variation. These inverse relationships between spectral variation and plant species counts could be explained by the landscape composition of the region, proving that the original SVH does not hold true across all spatial scales and ecosystems. In this regard, earlier studies mention several more factors that potentially complicate the relationship between spectral variation and plant species counts, including for example seasonality, spatial resolution and the applied metrics to describe spectral variation (Rocchini et al., 2010, 2018; Schmidtlein & Fassnacht, 2017). Despite the controversy on the validity or applicability of the SVH, it still constitutes an intriguing idea, particularly due to its generic approach which in theory does not require a priori knowledge on the examined area. And even if it is clear by now that the SVH will not hold across all scales and ecosystems, it might still work well in selected environments and under certain pre-conditions (Schmidtlein & Fassnacht, 2017).

The aim of this study is to conceptually discuss and question causal relationships between spectral variation and species diversity (mainly plant species counts) considering the most important factors influencing spectral variation and hence this relationship. These factors include: (1) considered scale; (2) effects of reflectance changes

over time; (3) effects of the method chosen to quantify spectral diversity; and (4) the weak link between habitat or ecosystem numbers and species counts. We support our perspectives by presenting examples including some data simulations and experimental data. With this, we seek to clearly point out the limitations of the SVH but at the same time also carve out the conditions under which spectral variation can make meaningful contributions to the RS-based monitoring of biodiversity.

The paper is structured as follows: we will first discuss scale-, phenology- and habitat-identity-related factors influencing the relationship between spectral diversity and plant species counts. Then we will briefly address some technical aspects related to the calculation of spectral-variation metrics and finally discuss and summarize our findings in a wider context.

2 | SCALE EFFECTS

With 'scale effects' we here refer to effects related to spatial extent (size of the study area) and spatial grain (pixel size, ground sampling distance or spatial resolution) of the spectral (RS) and biodiversity data. In ecology, the species–area relationship is one of the best-established concepts that describes the observation that the larger the extent of a given area is, the more species you can find in it (Rosenzweig, 1995). The exact relationship between species counts and area will depend on the characteristics of the ecosystem under analysis, its history and its surroundings. However, this relationship is always positive if the different-sized areas are nested. We can assume that the coarser the spatial grain of a given RS data set is at a given location, the more species are likely to occur within an individual pixel.

In contrast, we can assume that the coarser the spatial grain of the RS data is, the smaller is the overall spectral variation across all pixels of a given area. This is related to the general rule that aggregating fine-grain data will reduce extreme values (smoothing effect). In other words, RS data with fine spatial grain are more likely to differentiate among the spectral response of individual species, and capture land-cover types or individual objects with extreme spectral behaviour (e.g., at the landscape scale, a narrow bright dust road surrounded by dark forest; or a small dark pond in a bright savannah; and at fine scales, a bright white flower in front of darker green leaves). The coarser the pixels become, the more averaged out (i.e., smoothed) the reflectance values will be (Figure 1). Hence, for a given area, it can be assumed that any spectral-variation metric for a given area will decrease with pixel size (Figure 2). Furthermore, the coarser the grain of the RS data is, the fewer pixels are available for a given plot size to calculate the spectral-variation metric.

Based on these simple and known effects of scale on species counts and spectral-variation metrics, it can be deduced that if a relationship between spectral variation and species counts exists in a given region, the form of this relationship cannot be stable across scales, as seen also in the experimental work by Wang et al. (2018).

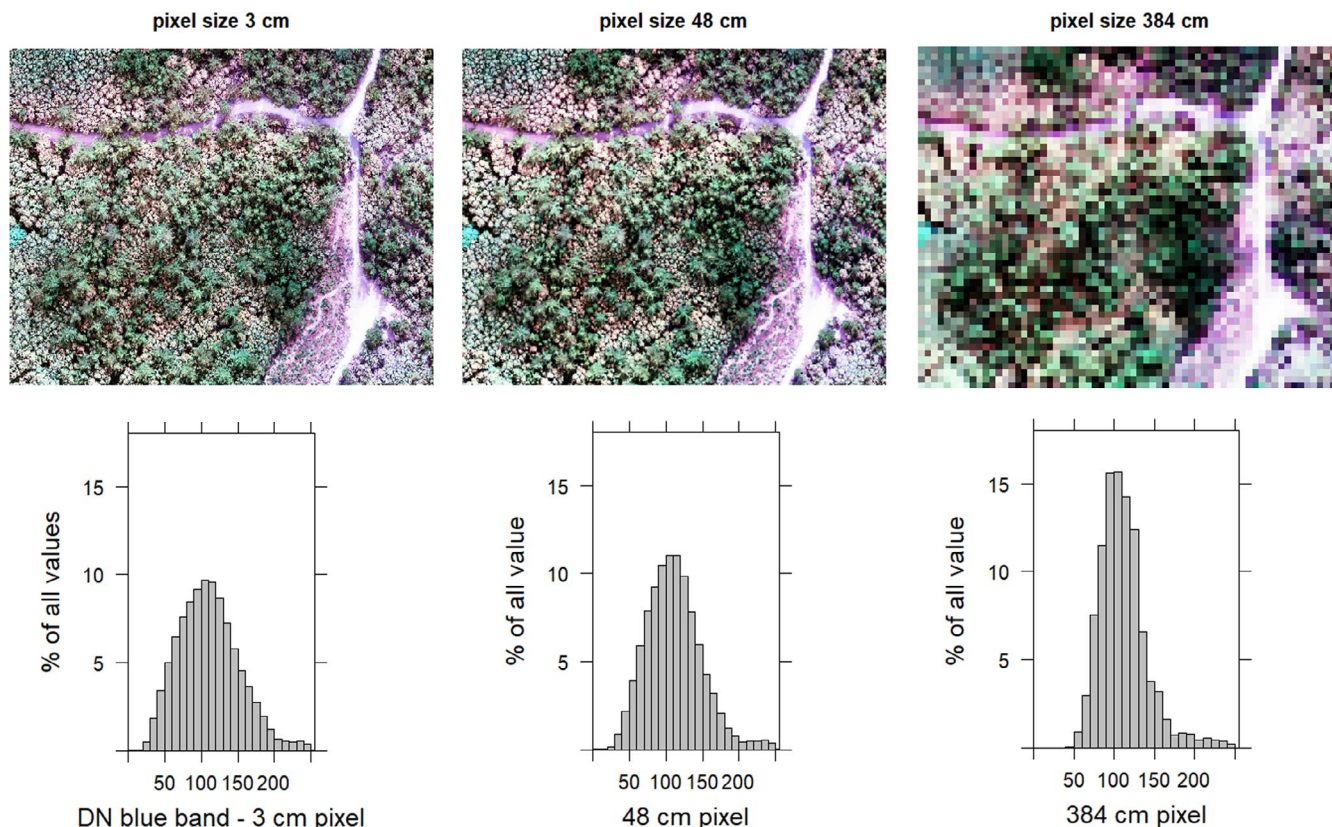


FIGURE 1 Scale effects on the distribution of spectral values. Depicted are histograms of digital number values of the blue band of an RGB-UAS (red–green–blue unmanned aerial system) image at different spatial grains (3-, 48- and 384-cm pixels). The UAS image shows a landscape with a mix of native shrubs, secondary natural forests, and plantation species in south-central Chile in the region of Maule (for exact location see Figure 2). The coarser the spatial resolution of the image, the less extreme the observed values are and the more intermediate values occur

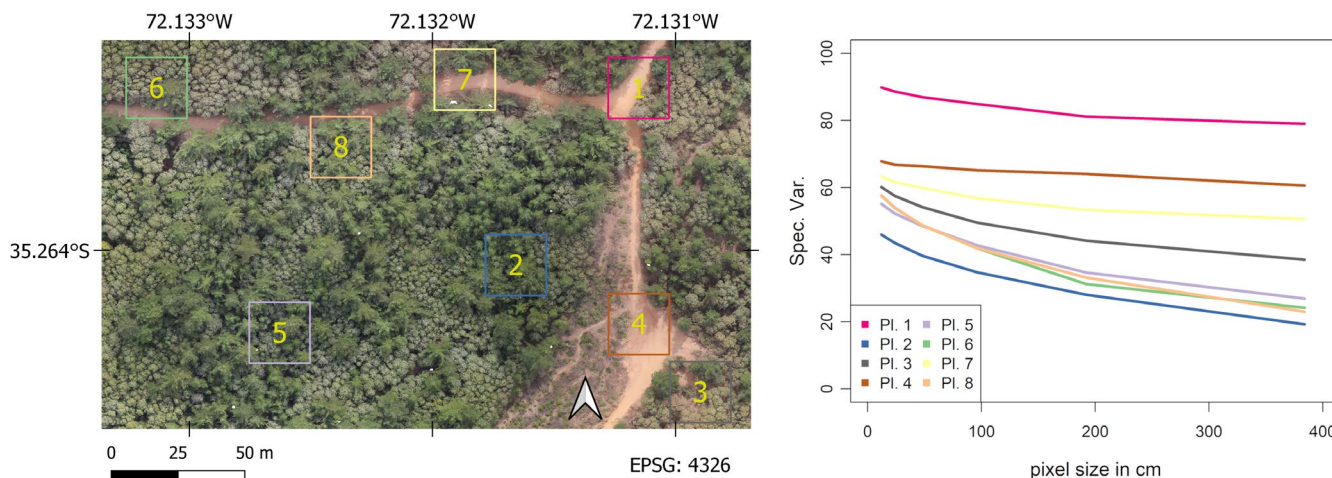


FIGURE 2 The right panel shows the development of spectral variation with changing pixel size (3 to 384 cm) for eight plots sized 630 m² within the area described briefly in Figure 1. The location of the plots is shown in the left panel. The spectral-variation measure for any plot is calculated based on the mean Euclidean distance of all pixels in the plot using the pixel values of the first two components of a Principal Components Analysis applied to the three bands of the red–green–blue imagery collected with the unmanned aerial system. The number of pixels used to calculate the spectral-variation measure decreases with increasing pixel size

A further important aspect related to the topic of scale refers to the visibility of plant individuals or stands, which are relevant to the species SVH. At fine grains, some individual species may be clearly

identifiable in the RS data. However, rare species or species with small individuals might not show or be missed even at fine spatial grains. To provide a chance of capturing the contributions of the

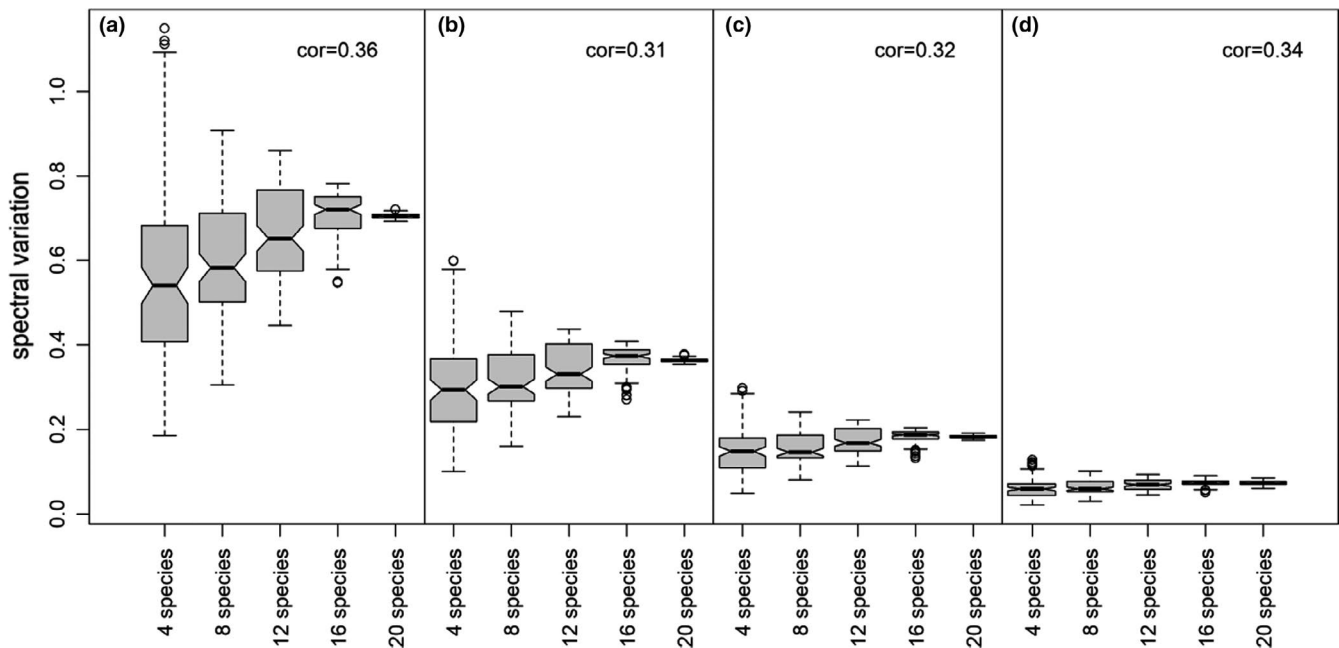


FIGURE 3 Degree of contrast-based spectral variation of simulated grassland plots. One hundred hyperspectral images were simulated, each at four spatial grains: from left to right, the original 100×100 pixels composed of spectra from 4, 8, 12, 16 and 20 species (a), then aggregated to 50×50 pixels (b), 25×25 pixels (c), and 10×10 pixels (d). Images were created by randomly filling up a 100×100 pixel array with spectra from 4–20 species. In total 21 species were available. Spectral variation was calculated in the same way as for Figure 2 (see Appendix S1 for more details). Indicated correlations are Spearman correlations between spectral variation and species counts

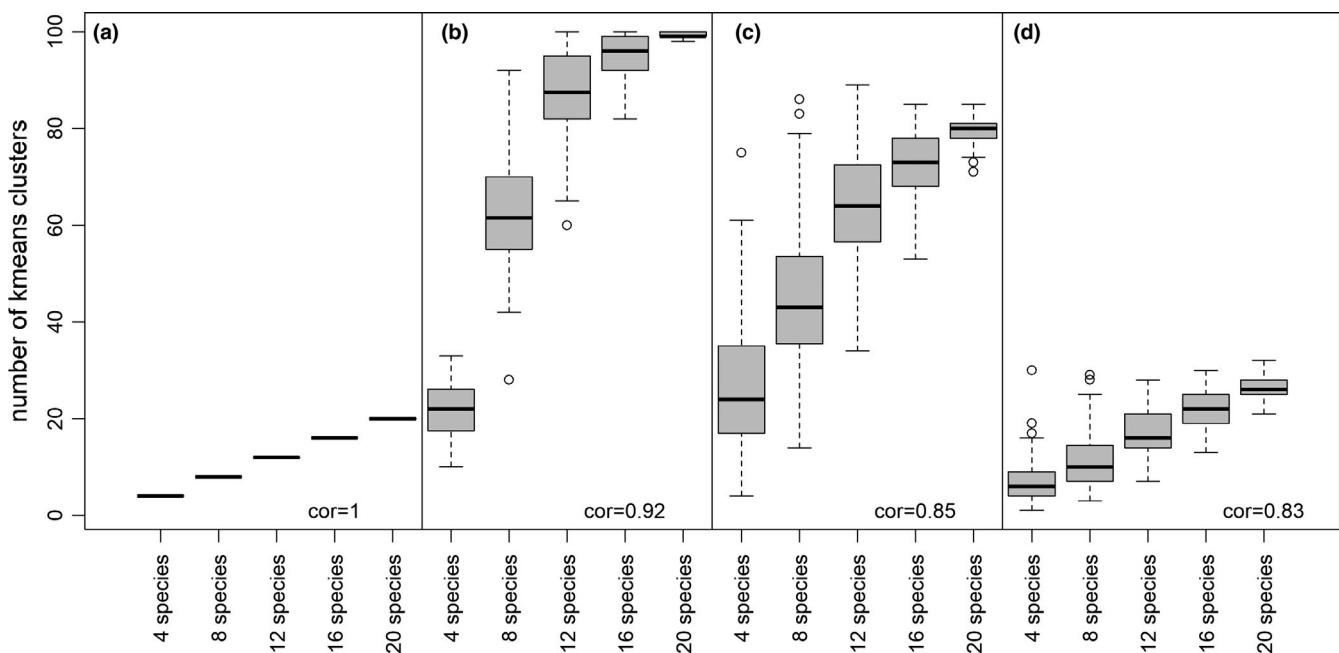


FIGURE 4 Manifoldness-based spectral variation of simulated grassland plots. One hundred hyperspectral images were simulated each at four spatial grains: from left to right, the original 100×100 pixels (a), then aggregated to 50×50 pixels (b), 25×25 pixels (c), and 10×10 pixels (d) and composed of spectra from 4, 8, 12, 16 and 20 species (100 images for each number of species). Images were created by randomly filling up a 100×100 pixel array with spectra from 4–20 species. In total 21 species were available. Spectral variation was calculated by first applying a K-means clustering with 100 clusters to a mosaic including all synthetic images (of a given grain); then the number of unique classes assigned by the unsupervised K-means classification was determined for each individual image

visible species in the framework of the species SVH, the spatial grain of the RS data should be adapted to the size of individuals or species stands occurring in a given ecosystem. For example, grasslands may

require a notably finer spatial grain than forests to capture important patterns in spectral variation (see also section 3 *Phenology and other temporal effects*).



It follows that the choice of spatial scale for capturing species richness has severe consequences for SVH-based counts. Considering that even within the same vegetation type, the size of stands and individuals differs between species, it becomes clear that a single 'correct' or 'ideal' spatial scale for capturing species richness using RS does not exist. Further pitfalls are to be expected when several ecosystems are considered simultaneously.

Another example of how spatial grain influences the relationship between spectral variation and species counts is given in Figures 3 and 4. Here, the spectral variation of synthetic hyperspectral images of grasslands expressed with two different types of spectral-variation metrics is depicted in relation to the number of species and the spatial grain of the images. Each of the synthetic hyperspectral images was created by randomly filling up an array of 100×100 pixels in the x and y dimensions with species-specific spectral signatures. In total, we used 21 spectral signatures corresponding to 21 herb and grass species of Central Europe, thus reducing the real-world complexity by neglecting infra-specific variation. We created 100 of these images for each number of species tested (4, 8, 12, 16, 20, 21), with one species per pixel. Then we calculated two spectral-variation metrics for the original images with 100×100 pixels (Figures 3a,4a) as well as for the same images after they were spatially aggregated to 50×50 pixels, 25×25 pixels, and 10×10 pixels (Figures 3b–d,4b–d). The spatial aggregation was conducted with a simple calculation of means using the 'aggregate'-function of the raster package (Hijmans & van Etten, 2012) in R (R Core Team, 2013) (see Appendix S1 for more details). The first spectral-variation metric (SV_continuous) was calculated based on the mean Euclidean distance of all pixels in the plot using the pixel values of the first two components of Principal Components Analyses applied to the 85 bands of the synthetic hyperspectral images and calculated for a mosaic of the 500 synthetic images of a given aggregation level (see Supplementary material for more details). This metric captures the degree of contrast of the pixels. Following the species SVH, the higher the mean Euclidean distance is, the more species should be present. The second spectral-variation metric (SV_categorical) was derived from an unsupervised K-means clustering with 100 clusters applied to a mosaic of all synthetic images of a given spatial grain. We selected more clusters than species in order to allow for more clusters forming after aggregating pixels with the corresponding increase in reflectance types. In the original image, where each of the species corresponds to a single spectrum, the clustering stops after having derived the number of classes that fits the number of species. After the clustering, the number of unique classes to which the pixels of an individual synthetic image within the mosaic were assigned during the unsupervised K-means classification was determined. This metric captures the manifoldness of the pixels in the image. Following the species SVH, it is assumed that the more unique classes exist in the image, the more species are present. These simulations serve to make three important points: (i) in the results for the original images and SV_continuous metric, we can see that the median spectral variation increases from 4 to 20 species. However, at the same time, numerous (approximately 25%) of the simulated images (even those

composed of only four species) have higher spectral variation than the highest spectral variation observed for 20 species (Figure 3a). The number of K-means clusters in the SV_categorical metric necessarily matches the species numbers perfectly for the original images since no intraspecific spectral variation was considered (Figure 4a). (ii) Both metrics (expectedly) decrease with increasing level of aggregation of the pixels (coarser spatial grain). (iii) Differences in median spectral variation between images with differing numbers of species decreases with increasing level of aggregation (Figures 3a–d, 4b–d).

This example is highly simplified by assuming an approximately equal cover and a random distribution of each species in each image and by assuming that each species individual has exactly the same spectral signature. Nevertheless, the example illustrates a key weakness of spectral-variation metrics capturing the degree of contrast in the visible to shortwave-infrared region (SV_continuous): even if only four species are present, the spectral variation can be very high (higher than the variation of 20 species) in case the amplitudes of the reflectance values of these four species differ a lot.

This problem is closely related to the fact that healthy plant species' spectral signatures all follow a similar typical reflectance curve and hence the overall spectral variation is limited from the start. If even under such simplified and 'close-to-perfect' conditions, the link between spectral variation and plant species counts (within a single ecosystem type) is weak (Spearman correlation of 0.35 in the original data with 100×100 pixels for SV_continuous), it is very unlikely that it will improve under natural conditions with notably increased complexity in species' vertical and horizontal arrangements. On the other hand, the spectral-variation metric based on K-means clustering (SV_categorical) which imitates the spectral-species concept (e.g., Féret & Asner, 2014) will in theory result in a perfect relation between the number of species and the number of clusters if there is just one species per pixel and species feature a unique spectral signature. Although these preconditions are unrealistic, the experiment still proves that the species SVH concept may have its applications if metrics capturing the manifoldness of the pixels in the image are applied.

3 | PHENOLOGY AND OTHER TEMPORAL EFFECTS

The majority of Earth's ecosystems is influenced by daily, seasonal and stochastic dynamics in terms of environmental conditions. Physiological processes such as photosynthetic activity are strongly coupled with these dynamics, and in turn vegetated surfaces also show daily, seasonal or random variation in the related optical traits that shape the electromagnetic signal captured by RS sensors. Species may have more unique spectral signatures at one time but less pronounced differences at another time, meaning that the species SVH will lead to varying results over time. Corresponding processes may affect the original SVH as well. For example, meadow types may be well distinguishable before mowing but lose this separability afterwards.

3.1 | Daily variation

Simple examples of daily variation are changes in leaf orientation to reduce or increase the amount of captured incoming radiation and to thereby regulate evapotranspiration (Chávez et al., 2014). Regular daily variation may be considered less problematic for most polar-orbiting satellite systems with fixed fly-over times. However, there might be related changes in spectral variation in airborne data and in longer time series in the case of orbit shifts of polar-orbiting satellites. For example, vegetation in (semi-)arid regions may adapt its leaf orientation in rather short time periods (Chávez et al., 2014) and a shift in overflight time of one hour as for example reported for Landsat 5 (Zhang & Roy, 2016) may result in notably different spectral signatures and hence spectral variation even though no true change in plant species counts has occurred.

3.2 | Seasonal variation

Seasonal variation is quite well predictable but still poses problems with respect to the SVH because it may be responsible for a notable share of the overall spectral variation at a given location, even if focussing only on the main vegetation period. Furthermore, in many

types of ecosystems, e.g., dryland, grassland and savanna ecosystems as well as in forests' understorey layers, the development of annual herbs and grasses and short-lived species, as well as flowering events and leaf phenology are important. They can lead to a high degree of variation in important optical traits such as leaf area index (LAI), leaf-angle distribution and pigments (colours) (e.g., Landmann et al., 2015; Qi et al., 2014; Spanner et al., 1990). The large influence of flowering events on the spectral signal has been discussed for example in Schiefer et al. (2021).

Figure 5 shows an example of the seasonal variation in spectral signatures of a few common grass and herb species of Central Europe. The spectra were collected during an outdoor cultivation experiment (see Appendix S1). We can see that some of the grassland species strongly differ in their spectral behaviour depending on the phenological state in which their spectral signature is captured.

If we relate this phenological behaviour of herbs and grasses to the species SVH, it becomes clear that all typically used continuous spectral-variation measures would be notably influenced by this phenomenon (corresponding effects on the original SVH can also be assumed). In Figure 5 we can also see that the similarity of the spectra of the six species varies a lot over the year. While at the beginning of the vegetation season (31 May) the six species have widely varying optical traits and corresponding diverse

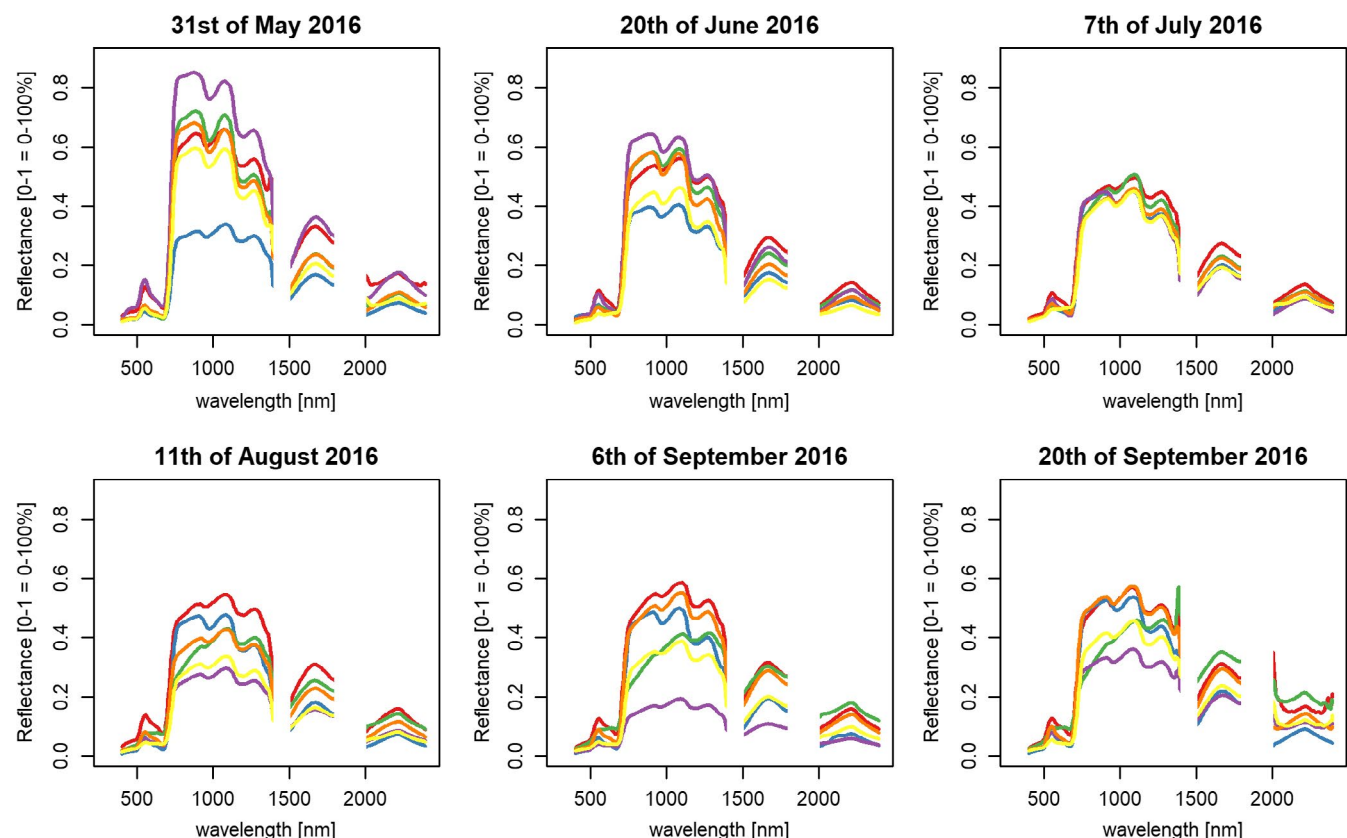


FIGURE 5 Field-collected spectra of six species plotted for different timepoints in the year. Water absorption bands at 1400–1500 nm and 1800–2000 nm were excluded. Different colours represent the different species in this case (red = *Calamagrostis epigejos*; orange = *Geum urbanum*; blue = *Nardus stricta*; green = *Agrostis capillaris*; violet = *Aegopodium podagraria*; yellow = *Festuca ovina*). For explanations of the methodology to create the spectral curves, see Appendix S1



spectra, they have a very comparable spectral behaviour at the peak of the vegetation period (7 July). Assuming an equal fractional cover of the six species for which a continuous spectral-variation (SV_continuous) measure would be derived, the variation measure will change dramatically while the plant species number remains the same. Other spectral-variation metrics based on unsupervised clustering (SV_categorical) may be less influenced, but flowering and co-occurrence of the same species in different phenological stages (e.g., in areas with strong environmental gradients) might also affect the captured manifoldness (as for example represented by the number of classes identified by an unsupervised clustering algorithm in a given area).

Another example for SV_continuous is given in Figure 6. Here it can again be seen that the spectral variation hardly serves as indicator for differing numbers of species. More importantly, it is also apparent that depending on which species were selected in one of the fixed amounts of species examined, the spectral variation can drastically vary over the course of a year. While this is a simplified example, it can still be assumed that the corresponding effects will be visible in real data sets and might be even more complex due to higher intermixture of species canopies. In addition, it should be considered that phenology is only one driver of intraspecific variation in optical traits and hence spectral variation. The health status, growth form due to adaptations to the abiotic and biotic environment and stress events are examples for additional intraspecific variation in optical traits that are likely to occur, particularly when focussing on larger spatial extents.

3.3 | Unpredictable variation

Apart from phenological and daily sources of variation some impacts are more difficult to predict. Such impacts embrace temporary stresses and disturbances including for example droughts in forests (e.g., Asner & Alencar, 2010), mowing of grassland or laying down of plants after rainfall and wind (Feilhauer & Schmidtlein, 2011). Such non-regular variation caused by disturbance or sudden weather conditions is difficult to take into account. An extreme temporal example occurs in arid and semi-arid ecosystems where most of the species are hidden for most of the time, becoming visible only after rare and irregular rainfall events. Similar dynamics may also exist in wetlands where the occurrence of vegetation as well as the optical signal observed by RS data may fluctuate seasonally with the water table which in turn may relate to varying precipitation patterns. Similarly, precipitation-induced rapid vegetation developments can also be observed in other ecosystems and might be hard to describe with spectral-variation measures, particularly if RS data acquisitions are available at a limited temporal resolution.

In summary, seasonal and other temporal differences in optical traits can make up for a notable portion of the overall spectral variation in certain ecosystems and hence have a direct effect on both the original and the species SVH. A relationship between spectral variation and plant species counts (or an alternative biodiversity

metric) found in one part of the year may not exist in another (see also Schmidtlein & Fassnacht, 2017). Hence, establishing a stable link between spectral variation and biodiversity (at least in terms of plant species counts) seems highly challenging in ecosystems with a pronounced temporal dynamic. To use spectral variation as a proxy variable for biodiversity, identifying suitable time windows or including the temporal dimension into the applied spectral-variation measure may hence be important prerequisites. Studies based on repeated RS measurements throughout the season coupled with repeated in-situ sampling of vegetation could help to better understand the influence of phenological changes and other temporal effects. From RS data alone, it is difficult to disentangle the seasonal variation of optical traits of the same species from the seasonal exchange in different species' presence or detectability, and from other unpredictable variation introduced by abiotic and biotic drivers.

4 | HABITAT TYPE MATTERS AT LEAST AS MUCH AS HABITAT NUMBERS

An example for why habitat type (or vegetation type) matters at least as much as habitat numbers are Central European calcareous grasslands. These are very species-rich habitats, but at the spatial resolution of common satellite sensors their spectral variation is low. The area marked in green in Figure 7 shows such a calcareous grassland, the Garchinger Heide, near Munich. This area of 27 ha contains more than 240 species (Bayerisches Landesamt für Umwelt, 2020). However, when visually and numerically (Table 1) comparing the spectral variation within this area (polygon 1 in Figure 7) with the spectral variation of areas of the same size in the surrounding intensively used agricultural landscape (polygons 2–7 in Figure 7), it is obvious that, at the spatial resolution of a Sentinel-2 satellite image, most of the other areas have (in some cases notably) higher spectral variation, despite having a far lower number of species.

The example of the Garchinger Heide relates to the issue of (rare) species-rich habitats that has been already discussed in one of the earliest works on the SVH (Palmer et al., 2002). In the example of the Garchinger Heide, a small habitat with a comparably homogeneous spectral signature contains a high number of plant species. Including or excluding this habitat type from a given area will have a tremendous effect on the plant species count but hardly any effect on the spectral variation. This is a major flaw of the original SVH and strong assumptions have to be made to still enable a general validity of the concept: it is valid to assume that if an additional habitat is added to a given area, the spectral variation of the area will increase, along with the species count (at least it will not diminish). However, comparing for example two areas A and B in which A has two and B has three habitats, B will only have more species than A in the case that B includes all the habitats that are also occurring in A. If this is not the case, it is easily possible that area A has two species-rich habitats and area B has three species-poor habitats and hence, area A could harbour more species than area B while B might still have a higher spectral variation. This problem persists independently

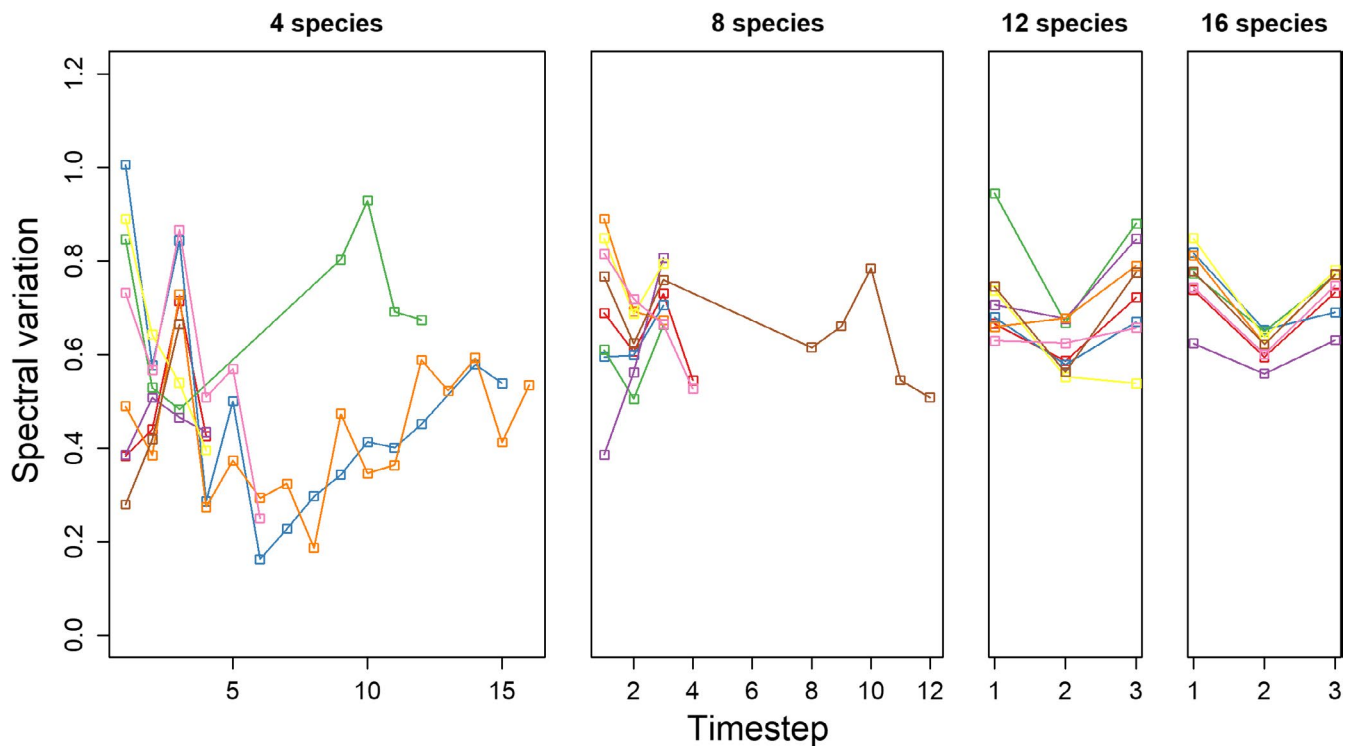


FIGURE 6 Changes of degree of contrast-based spectral variation during the vegetation period (SV_continuous). In the panels, each colour indicates one random composition of species and the line indicates how the spectral-variation value for this composition changes over time. The 'pixels' of each species of the synthetic images were filled with the corresponding field-measured spectra from the corresponding time step. For better visual interpretation we only plotted 8 of the 100 random compositions of 4, 8, 12 and 16 species summarized in Figure 3. Since not for all species spectra were measured at each timepoint, we only plot spectral-variation values of time points where spectra were available for each of the respective species. As can be seen, the higher the number of species is, the less likely it is, that spectra were measured for all species. This is why for 12 and 16 species only spectral-variation values for the first three time steps were available

from the applied type of spectral-variation metric (SV_continuous or SV_categorical).

Following the species SVH, spectral variation would be used to characterize biodiversity patterns only within a single patch (habitat) such as the Garchinger Heide; however, what might be problematic is that there is patchy structure within that area as well. Hence, it would quickly become hard to decide at which scale a between-site approach finishes and at which scale a within-site approach starts. Nevertheless, we can assume that the more we zoom into patches, the more relevance gains the 'species SVH'. The predictive power of the latter has been discussed above and is summarized in Figures 3 and 4.

A further related problem is that habitats that may appear spectrally very similar in the RS data due to shared canopy-dominating species, may still differ widely in species counts. A related example from Central Europe is the various European beech (*Fagus sylvatica*)-dominated forest communities which range from species-poor (Luzulo-Fagetum beech forests) to species-rich (Cephalanthero-Fagetum beech forests) forests. The biodiversity of those habitats is dominated by the herb layer which is hardly visible below the dense canopies of the beech forests and hence cannot be captured by RS.

5 | SPECTRAL-VARIATION METRICS

5.1 | Technical considerations

5.1.1 | Choice of the spectrum/spectral regions – radiometric resolution

Spectral-variation (SV_continuous) metrics calculated based on the variation of the reflectance values of the wavebands in the RS image are affected by the spectral coverage of the bands as well as the radiometric resolution of the bands and sun-sensor geometry (Schaepman-Strub et al., 2006). While differences in radiometric resolution of different sensors can be accounted for by using standardized data or physical units (e.g., surface reflectance values), differing numbers and widths of wavebands are harder to address. Hence, the same metric calculated for different satellite sensors may have notably different meanings and capture different processes leading to the observed spectral variation. This might be a problem with respect to the SVH, especially if data from different sensors are compared and SV_continuous metrics are used.

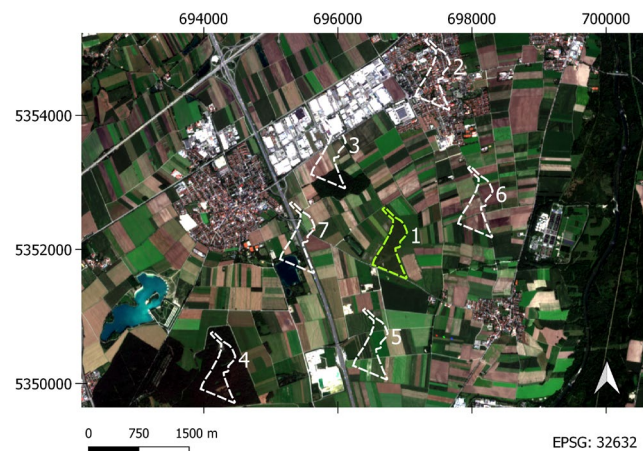


FIGURE 7 The ‘Gachinger Heide’ near Munich, Germany (marked in green with id = 1), a species-rich calcareous grassland embedded in a landscape of intensive agriculture. The spectral diversity of this grassland is compared to other landscape elements of the same size (marked in white with id = 2–7). Area #1 contains many more species than the other areas although only one habitat type is included in this patch. Its spectral variation is accordingly low (Table 1)

TABLE 1 Overview of spectral diversity values calculated with a spectral variation (SV_continuous) metric for landscape patches shown in Figure 7

Landscape element id (Figure 7)	Spectral variation ^a
1 – Species-rich calcareous grassland	319
2 – Urban area	2041
3 – Agricultural/urban interface	1544
4 – Forest	595
5 – Agriculture	1778
6 – Agriculture (bare)	1022
7 – Agriculture/forest/road/water	1557

^aMean Euclidean distance of all Sentinel-2 pixels within the polygons calculated from the first two Principal Components Analysis (PCA) components of the Sentinel-2 raster stack. PCA components were calculated based on digital numbers of the L1C product of Sentinel-2 (nominal value range between 0 and 10000).

5.1.2 | High contrast land surfaces will increase spectral variation

Areas with particularly high or low reflectance values in some wavebands (e.g., bare-soil areas, rocks, sealed surfaces etc.) will have a notable influence on any spectral-variation measure capturing the degree of spectral contrast (SV_continuous). So far, no clear indications were made how this should be considered in the framework of the SVH. An obvious solution could be to exclude all non-vegetated areas by applying a vegetation mask before calculating the spectral-variation metrics. While this is feasible for very fine-grain RS data, it might already become challenging for intermediate spatial resolution

data sets including Sentinel-2 and Landsat which typically contain a large number of mixed pixels. Furthermore, scarcely vegetated patches can also contribute to species numbers. For example, in harsh environments such as coastal dune ecosystems, many focal species are small and occur in a very fine mosaic pattern of bare sand and vegetation (e.g., Ewald et al., 2020). Such areas may face the risk of being masked even though making a notable contribution to the species numbers. This problem may be less prominent for SV_categorical metrics but depending on the number of non-vegetated surface types present in an area, it might still cause some additional unwanted variability.

5.2 | Discrete vs continuous data

The above discussions have demonstrated advantages of SV_categorical over SV_continuous metrics. The continuous approach is the one proposed originally by Palmer et al. (2000) who emphasize continuity in the spatial analysis as a major advantage of the SVH. The SV_categorical approach is closely related to the spectral-species approach originally suggested by Féret and Asner (2014), where class numbers (typically obtained by a spectral clustering approach) are considered proxies of species numbers (thus relating to the ‘species SVH’). Recently, this approach has been scaled up to wider spatial extents and to a higher level of biological organization (e.g., vegetation types or habitats) (Rocchini et al., 2021). The approach has some obvious advantages: (1) consistency over time may increase as even if the optical traits of plant species change over the year, the land-cover patches or landscape elements may be more persistent (e.g., a broad-leaved forest stand may look very different in a satellite scene acquired in summer and winter but may be detectable as a spectrally homogeneous spatial unit/patch in both scenes); (2) spectrally extreme pixels or land-cover types will not have unproportionally large influence on the spectral-variation metric but will rather represent individual discrete classes amongst a plethora of other classes; and (3) the approach is essentially summarizing the continuous spectral values into spatial objects that represent landscape elements or individual species and hence mirror the core assumption of the original SVH or species SVH better. Schmidtlein and Fassnacht (2017) reported persistently higher correlations between species counts and an SV_categorical metric compared to an SV_continuous metric based on Euclidean distances calculated in the spectral feature space of several MODIS bands, but the approach could still not remove the problems of individual habitats with very high (or very low) species numbers discussed in section 4 *Habitat type matters at least as much as habitat numbers*.

6 | FINAL REMARKS

Most of the issues related to the SVH as described in this study pose challenges not only to the SVH but also to other commonly applied RS-based biodiversity assessments outlined in section 1 *Introduction*.

A commonly claimed advantage of RS-based biodiversity monitoring is that repeated and standardized measurements are possible with comparably little effort which enables capturing temporal changes. This is an important requirement for any monitoring. As discussed in this study, establishing a direct and universally valid link between the RS signal and biodiversity information collected in the field is extremely challenging due to the nature of optical RS which does not allow to address the different biodiversity facets equally. Instead of focussing on taxonomic or phylogenetic differences (as typically focused on in field surveys), RS and particularly the spectral-variation approach relies on optical traits that are driven by functional and morphological differences between the species (such as the architecture of leaves and branches, size, width and colour of the leaves, size and colour of inflorescences, etc.). In case a species shows high and spatially differentiated variation in morphology during the life cycle or due to plasticity or disease or pests or disturbance (Feilhauer & Schmidlein, 2011), it can falsely increase or lower the spectral variation and hence the species number predictions.

One question that could be raised, however, is whether searching for this generalized direct link between biodiversity and RS data is useful in the first place. Most RS-based approaches attempt to identify the link between biodiversity and RS signal in the spatial rather than temporal dimension. This is in direct contradiction to the proclaimed most important property of RS data, that is, the option for repeated acquisitions and monitoring over time. Most ecologists and biodiversity experts agree that detailed biodiversity surveys on the ground are the most reliable way to correctly assess biodiversity of a given region. One could assume that once the current biodiversity of a given area is inventoried and well understood (and the best way to do so is going to the field), the main task would be to monitor whether the biodiversity at this location is changing or remaining constant within a certain level of expected natural fluctuations. RS might be a suitable technology for addressing such task, with spectral variation being a key variable.

Adapting to this scenario, the central task of RS would lay in the change detection aspect, that is, in the identification of changes in the spectral and structural properties of the ecosystem rather than describing or mapping the ecosystem/biodiversity state. This type of RS-based monitoring is theoretically possible without support of any field data by simply comparing the current (spectral/structural) state of an area against an expected state derived from earlier observations. It is important that this comparison must occur on multiple spatial and temporal scales to account for the natural dynamics of a given ecosystem (which may widely differ, for example a fire may not have a notable effect on biodiversity in a savanna but may make a huge difference in a temperate ecosystem, natural succession cycles may be fast in one area and very slow in another, etc.). Spectral variation measured at multiple spatial grains and for various extents (window sizes) could be, amongst others, an efficient metric contributing to such a 'real' monitoring scheme.

In this study, we pointed out issues that question a universal, causal direct link between spectral variation and species counts. The

reflective properties and hence the spectral variation of a given area in an RS data set is affected by numerous factors including the landscape composition, spatial grain of the data, the acquisition time and corresponding sun-sensor geometry and the methodical approach to calculate the spectral variation. In some ecosystems, the spatial non-stationarity in the link between spectral variation and species numbers introduced by these factors is likely to be an insurmountable obstacle. Based on the points raised here and considering the results from earlier studies (e.g., Schmidlein & Fassnacht, 2017) we recommend to carefully revise under which condition a link between spectral variation and biodiversity can be assumed. As demonstrated in this study, simple simulation experiments can support this task and are an efficient means to identify conceptual weaknesses of some aspects of the SVH and to compare different methodical approaches to calculate spectral variation. Making valuable field-collected biodiversity data openly available and testing the links between biodiversity and spectral variations in a more systematic way using multiple metrics and approaches could further contribute to an improved understanding of the link between spectral variation and biodiversity.

The need for a more systematic testing of the links between biodiversity and spectral variations applies not only in the context of SVH but also with respect to other RS-based approaches to map and monitor biodiversity as it is likely that the factors influencing spectral variation discussed here do not apply solely for the SVH but also for other commonly discussed approaches to estimate (spatial) biodiversity patterns from RS data. We hence recommend that future studies should focus more on efficiently capturing changes in landscapes over time (and hence a potential change of biodiversity) rather than solely on the direct mapping of biodiversity patterns across space. The latter can be achieved with field surveys at much higher quality but might nevertheless benefit from an indirect integration of RS data. RS data can for example guide and improve the sampling design of biodiversity surveys by providing a pre-stratification of the study area, which also was the original motivation for developing the SVH (Palmer et al., 2002). Similar approaches have successfully been applied in forest inventories for decades and have proven to increase their efficiency.

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AUTHOR CONTRIBUTIONS

All authors contributed to the development of the main messages communicated in the study. Fabian Fassnacht wrote the manuscript with contributions of all authors, and conducted the data analyses. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The spectra used in this study for data simulations are available at <https://ecosis.org/package/canopy-reflectance-plant-functional-gradient-ifgg-kit> (<https://doi.org/10.21232/krt4-6x67>). The corresponding R-codes can be found at: <https://github.com/fabianfassnacht/SVH>. UAV images used in Figures 1 and 2 can be made available upon request. Sentinel-2 data used in Figure 7 are freely available for example on ESA's data hub and can be found with the image ID: S2B_MSIL1C_20190830T102029_N0208_R065_T32UPU_20190830T130621.

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SUPPORTING INFORMATION

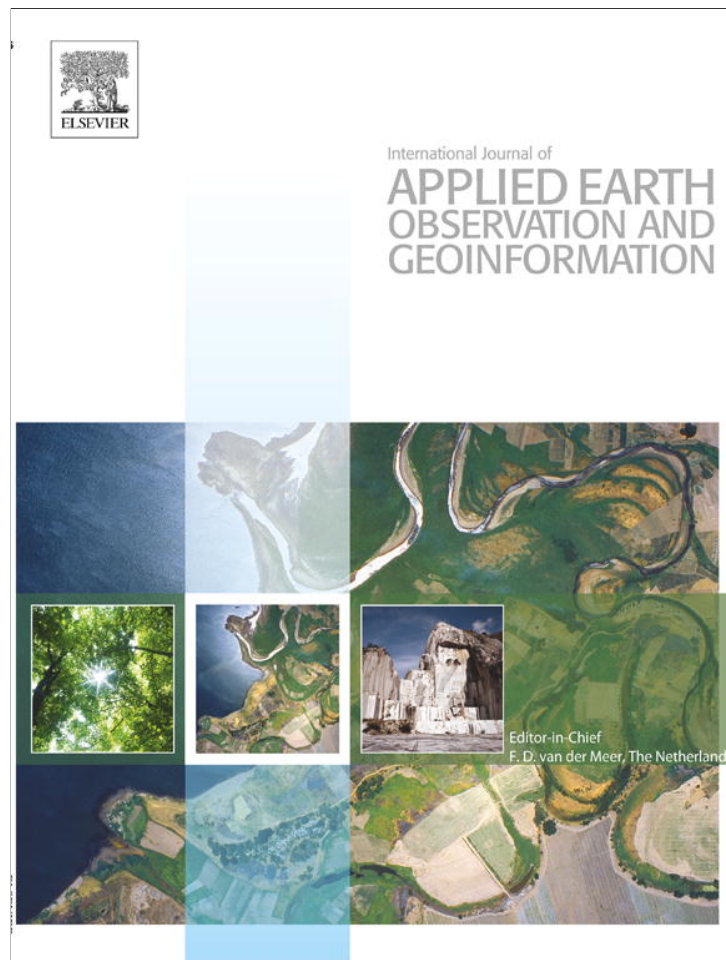
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Appendix S1. Approach to create synthetic images from field spectrometer measurements

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Appendix 6.

PAPER 6. **Müllerová J.**, Pergl J. & Pyšek P. (2013). Remote sensing as a tool for monitoring plant invasions: testing the effects of data resolution and image classification approach on the detection of a model plant species *Heracleum mantegazzianum* (giant hogweed). International Journal of Applied Earth Observation and Geoinformation 25: 55–65. <https://doi.org/10.1016/j.jag.2013.03.004>



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Remote sensing as a tool for monitoring plant invasions: Testing the effects of data resolution and image classification approach on the detection of a model plant species *Heracleum mantegazzianum* (giant hogweed)



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ABSTRACT

Plant invasions represent a threat not only to biodiversity and ecosystem functioning but also to the character of traditional landscapes. Despite the worldwide efforts to control and eradicate invasive species, their menace grows. New techniques enabling fast and precise monitoring and providing information on spatial structure of invasions are needed for efficient management strategies to be implemented. We present remote sensing assessment of a noxious invasive species *Heracleum mantegazzianum* (giant hogweed) that integrates different data sources, spatial and spectral resolutions, and image processing techniques. Panchromatic, multispectral and color very high spatial resolution (VHR) aerial photography (1947–2006, resolution 0.5 m), and medium spatial resolution satellite data (Rapid Eye 2010, resolution 5 m) were analyzed to assess their potential for hogweed monitoring by using pixel- (both supervised and unsupervised) and object-based image analysis (OBIA, automated hierarchical, iterative, and rule-based). Both point and grid based accuracy assessment was carried out. Described methods of object-based image analysis of VHR data enabled monitoring of hogweed at high classification accuracies measured by various means, regardless of the spectral resolution of the data provided that the data came from the species flowering period. Although the proposed automated processing of VHR data is relatively time-effective and standardized, application over large areas would be rather demanding due to the size of datasets, and multispectral satellite data of medium spatial resolution (lower than the size of individuals) was therefore tested. On such imagery, only larger stands could be identified but still the pixel-based supervised classification achieved moderate accuracy. Depending on the size of the area of interest and the detail needed the very high or medium spatial resolution data (acquired at the species flowering period) are to be used. High accuracies achieved for VHR data indicate the possible application of described methodology for monitoring invasions and their long-term dynamics elsewhere, making management measures comparable precise, fast and efficient.

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1. Introduction

Alien plants represent a serious threat to modern changing landscapes that suffer from intensive exploitation by humans, or on the other hand, land abandonment (Millennium Ecosystem Assessment, 2005). They not only have devastating economic impacts, affect human health, and threaten biodiversity and ecosystem functioning (Ehrenfeld, 2010; Pyšek and Richardson, 2010;

Vilà and Ibáñez, 2011; Pyšek et al., 2012b), but also dramatically change the character of traditional landscapes (With, 2002; Chytrý et al., 2012). Regardless of growing eradication and management efforts the abundance of invasive species and their impact on biodiversity worldwide is increasing (Hulme et al., 2010). Invasion is a dynamic process that can be fast, and after the species has spread over the landscape and achieved a high abundance it can be difficult or even impossible to stop or slow down the invasion (Rejmánek and Pitcairn, 2002; Pluess et al., 2012). Early and fast detection is needed to make the management cost-effective (Nielsen et al., 2005; Pyšek and Hulme, 2005; Wittenberg and Cock, 2005; Vilà and Ibáñez, 2011). More information on the invasion process itself, and on the role environmental conditions and landscape structures play in the course of invasion is important for efficient protective

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¹ <http://www.ibot.cas.cz/en/oddeleni.gis>.

measures to be implemented (Andrew and Ustin, 2010; Minor and Gardner, 2011).

To efficiently manage ongoing invasions it is necessary to monitor the species spread regularly, and there is an urgent need for new techniques enabling timely, fast and precise monitoring (European Commission, 2008; Hulme et al., 2009). Semi-automated, computer-assisted approaches of remotely sensed (RS) data are cost-effective and permit fast and frequent mapping (Kokaly et al., 2003; Underwood et al., 2003). RS was successfully used in invasion studies (for reviews see Huang and Asner, 2009), mostly for shrubs and trees (Costello et al., 2000; Fuller, 2005; Hamada et al., 2007; Asner et al., 2008; Lawes and Wallace, 2008; Walsh et al., 2008). RS of herb species is possible only if the data provide enough spectral and/or spatial detail, the species is distinct from surrounding species and background, forms dense and uniform stands, and/or is large enough to be detected (Maheu-Giroux and de Blois, 2004; Müllerová et al., 2005; Peterson, 2005; Bradley and Mustard, 2006; Jones et al., 2011). Due to the difficulties of herb species recognition on RS imagery, hyperspectral data are often used (for reviews see Huang and Asner, 2009; He et al., 2011), and multispectral or even panchromatic data applications focusing on herb species invasions are not common (but see Müllerová et al., 2005; Laba et al., 2010; Jones et al., 2011).

Historical very high spatial resolution (VHR) aerial photography provides an excellent source of information on changing landscapes over time (Laliberte et al., 2004; Brook and Bowman, 2006), and under certain circumstances (appropriate time of acquisition, good recognizability of target, good time series) it can be used for studying invasion process in detail. Due to the low spectral resolution of historical aerial photography, traditional pixel-based approaches of computer-assisted classification are not successful, and in the past, photographs were usually processed manually (Costello et al., 2000; Maheu-Giroux and de Blois, 2004; Müllerová et al., 2005; Morgan et al., 2010). With the development of the object-based image analysis (OBIA) new possibilities of automated or semi-automated processing of such high spatial and low spectral resolution data arose (Laliberte et al., 2004; Pringle et al., 2009). While OBIA is increasingly applied in studies of ecological patterns and processes, few studies have so far used OBIA for herbaceous or invasive species classification (but see Walsh et al., 2008; Jones et al., 2011; Ouyang et al., 2011). In our previous study dealing with RS mapping of giant hogweed, we used manual interpretation, i.e. on-screen digitizing of historical panchromatic VHR aerial imagery (Müllerová et al., 2005). The mapped hogweed invasion history enabled us to assess rates of invasion (Müllerová et al., 2005; Pyšek et al., 2007c, 2008) as well as to address more general ecological questions on the role of long-distance dispersal in population dynamics of plant species (Pergl et al., 2011; Nehrbass et al., 2007). However, manual processing is laborious, time consuming, and not feasible for larger areas. Therefore, it was important to develop automatic or semi-automatic image processing techniques to classify VHR imagery that would enable us to study the patterns at larger scales.

In this paper, we present RS assessment of a noxious invasive species *Heracleum mantegazzianum* (giant hogweed). This well-known invasive herb species introduced from Asia occupies large areas in central and northern Europe and continues to spread. The rate of its invasions is comparable to some of the most dramatic invasions globally (Müllerová et al., 2005; Pyšek and Hulme, 2005). Invading populations not only change the character of ecosystems by forming dense uniform stands (Page et al., 2006; Thiele and Otte, 2006; Hejda et al., 2009) but also pose danger to humans due to toxins that cause skin injuries (Nielsen et al., 2005).

The objectives of our study were to test and evaluate the potential of spectrally and spatially different RS data for automatic detection of giant hogweed, and establish methods that could be

used to monitor invasions at larger spatial scales. Invasions are typically expressed at regional scales as species disperse over long distances, and therefore need to be managed at a landscape level (Lawes and Wallace, 2008). Although recent VHR data are readily available in digital and georeferenced form, their application over large areas is costly and laborious (Chen et al., 2012). Therefore, in addition to the VHR data we also decided to test satellite imagery at a coarser spatial resolution (5 m) in order to address invasions at the landscape scale. Further, we used the results obtained for this particular model invasive species to outline best mapping strategies and management recommendations that can be applied to plant invasions in general.

2. Methods

2.1. Study species

Giant hogweed (*H. mantegazzianum* Sommier and Levier, Apiaceae) is the tallest herbaceous species in Europe, reaching 2–5 m in height during flowering period, with leaves up to 2.5 m long and large white inflorescences of compound umbels up to 80 cm wide (Page et al., 2006; Perglová et al., 2006, Fig. 1). The species is monocarpic, and usually lives 3–5 years, although a 12-year-old individual was recorded (Pergl et al., 2006). It reproduces entirely by seed and can produce enormous numbers of fruits, on average 20,000 per plant (Perglová et al., 2006). In the study area, the species flowers from late June to early August (Perglová et al., 2006).

The species is native to the western Greater Caucasus (Jahodová et al., 2007) where it grows on wet and nutrient-rich soils on mountain slopes, and following its introduction as an ornamental in the beginning of the 19th century it became one of the most serious plant invaders in Europe (DAISIE, 2012), including Czech Republic (Pyšek et al., 2012a). In central Europe, it invades mainly unmanaged semi-natural grassland communities, nutrient-rich sites, forest edges and anthropogenic habitats (Pyšek and Pyšek, 1995; Thiele and Otte, 2006) forming large homogenous populations, although small groups of plants scattered along linear landscape structures such as roadsides and water streams are frequently observed (Thiele et al., 2007). In once invaded sites, it may persist in for a long time, up to many decades (Pergl et al., 2012). Eradication and control of the species is difficult (Pyšek et al., 2007a). On recently infested sites eradication is cheaper and more likely to be successful because it targets small and young populations where the seed bank has not yet established. Early detection of the species and rapid management response is therefore important (Nielsen et al., 2005; Page et al., 2006).

2.2. Study area

The study region is located in the Slavkovský les Protected Landscape Area (PLA), West Bohemia, Czech Republic (Fig. 1). Here, the species was first introduced to the country in 1862 (Pyšek, 1991). After World War II, the region experienced profound changes in settlement and land use. Local German inhabitants were expelled from the country, and the area became a military zone and later uranium mining area with restricted access (until the 1960s). In that time, many villages were destroyed and never restored. After the army and mining industry left, the sparsely inhabited area with extensive agriculture was declared as the PLA in 1973. Natural vegetation of beech and spruce forests, peat bogs and pine forests on serpentine (Neuhäuslová and Moravec, 1997) was largely replaced by spruce plantations (covering 53% of the area), extensive wet grasslands with high species diversity, and pastures. The absence of regular management combined with historical disturbances increased the suitability of the landscape

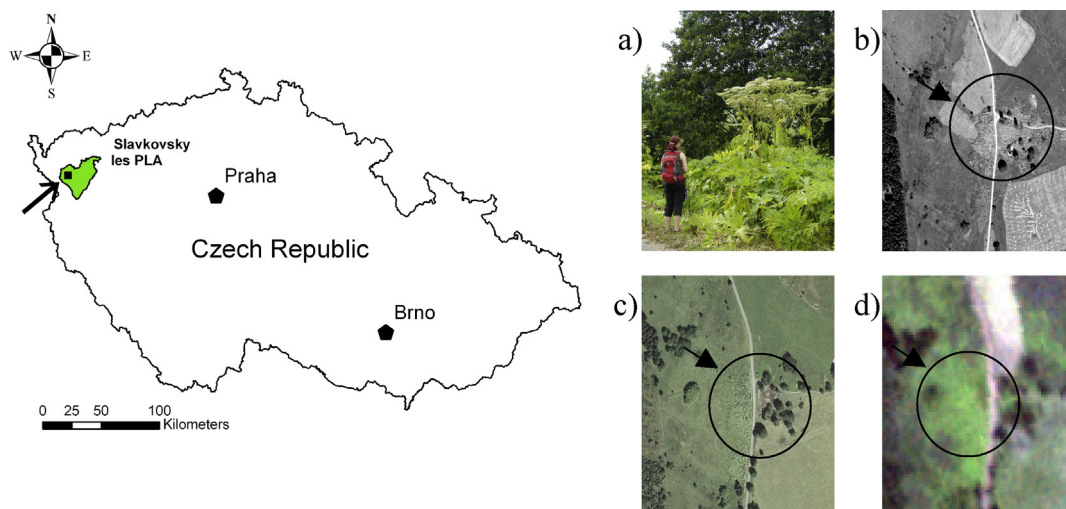


Fig. 1. Location of the study site. *Heracleum mantegazzianum* (giant hogweed) from the ground (a), and from the air: (b) panchromatic photography (1962, Military Topographic Institute, Dobruška); (c) color photography (2006, GEODIS, Prague); (d) multispectral satellite imagery (2010, Rapid Eye AG). Available in color online.

to the invasion (Pyšek, 1991). The invasion started in the 1950s and today the region is heavily infested (Müllerová et al., 2005). The start of the invasion in PLA corresponds to the beginning of the rapid spread of the species over the country, with the Western Bohemian region serving as a source (Pyšek, 1991; Pyšek et al., 2007c). For the purposes of this methodological study we chose a test site of 100 hectares within the study region of PLA (Fig. 1) that has been infested for more than 50 years, and is covered by various RS data sources acquired at the giant hogweed flowering season.

2.3. Data processing

Data of different origin (aerial and satellite, archival and current), spatial (VHR and medium), and spectral (panchromatic, color, and multispectral) resolution (Table 1) were assessed for automatic detection of hogweed. Historical aerial photographs were scanned in 1200 dpi and orthorectified using 2006 orthophotographs with 40–60 ground control points distributed along the whole area of the rectified photograph (2nd order of transformation and nearest neighbor rectification method) at a final pixel size of 0.5 meters. Aerial photographs (panchromatic, color, and multispectral) and satellite imagery (Rapid Eye, resolution 5 m) were analyzed by both pixel- and object-based approaches.

The pixel-based approach classifies individual pixels by similarities in their spectral characteristics. Both unsupervised (ISODATA, *K*-means and Fuzzy *K*-means) and supervised (maximum likelihood and minimum distance) classifications (Jensen, 2004) were tested using software Geomatica 10 (2005). Training areas for supervised classification were selected from visual interpretation of historical data and field observation (2010).

The object-based approach (OBIA) relies on both spectral and spatial information (texture, spatial characteristics, context, and topology; Benz et al., 2004), and is therefore ideal for low spectral resolution imagery such as historical panchromatic photography (Laliberte et al., 2004). In OBIA, the image is segmented into groups of contiguous pixels (image objects) that are then classified according to spectral variables, shape, texture, size, thematic data, and spatial relationship (contiguity) and the distance between objects. In our study, a combination of automated hierarchical, iterative, and ruled-based classification (for description of the terms, see Blaschke et al., 2008) was applied using the software Definiens Developer 8 (Definiens AG, 2009). Only the hogweed objects were classified. Multiresolution segmentation was applied with parameters (scale,

color, and shape) determined using a systematic trial-and-error approach. Various scales were tested and segmentation outputs were visually evaluated to identify the best parameters to extract the targets of interest (i.e. hogweed). Rule-based classification (Fig. 2) was applied on the segmented objects using conditions related to spectrum (brightness, mean layer, maximum pixel values, standard deviation, hue, saturation, intensity transformation for RGB), shape (area, length/width), texture (compactness, GLCM homogeneity, GLCM dissimilarity, and GLCM contrast), and context (existence of thematic layer, relative border, contrast and edge contrast of neighbor pixels, existence of super-object, growth region in certain conditions). To speed up the classification process two hierarchical levels of multiresolution segmentation were performed. Coarser segmentation objects with a high probability of giant hogweed presence (indicated by spectral characteristics and texture) were classified as “Hogweed candidate class”. This candidate class was further segmented by fine segmentation and classified to extract “Hogweed class” (Fig. 3).

Analyzed imagery was acquired at different times during the season, mostly in July, except for the 1973 panchromatic VHR data and 1987 multispectral VHR data (August). Since the species appearance differs markedly in vegetation season (having distinct white rounded umbels in flowering), we considered the timing of the data acquisition as an important factor in the success of the species mapping. Phenophases of hogweed captured on the analyzed RS data were derived from detailed analysis of the course of hogweed phenophases in the study area, carried by Perglová et al. (2006). To eliminate the inter-year differences, the phenological stages in analyzed years were calibrated using long-term phenological observations of summer flowering herbs at nearby phenological stations (Oracle Phenodata database; Czech Hydrometeorological Institute, CHMI; Hájková et al., 2012; Table 2).

2.4. Accuracy assessment

Ground truthing of historical images was obviously impossible, and visual photo-interpretation was therefore used to assess their accuracy. Recent imagery was field verified. In pixel-based assessment (further called “point assessment”), a total of 500 randomly located verification points (distinct from the training areas of supervised classification) were used to create error matrices (Congalton, 1991). To ensure sufficient coverage of hogweed class, the points were stratified (300 points located inside and 200 points outside manually classified hogweed area).

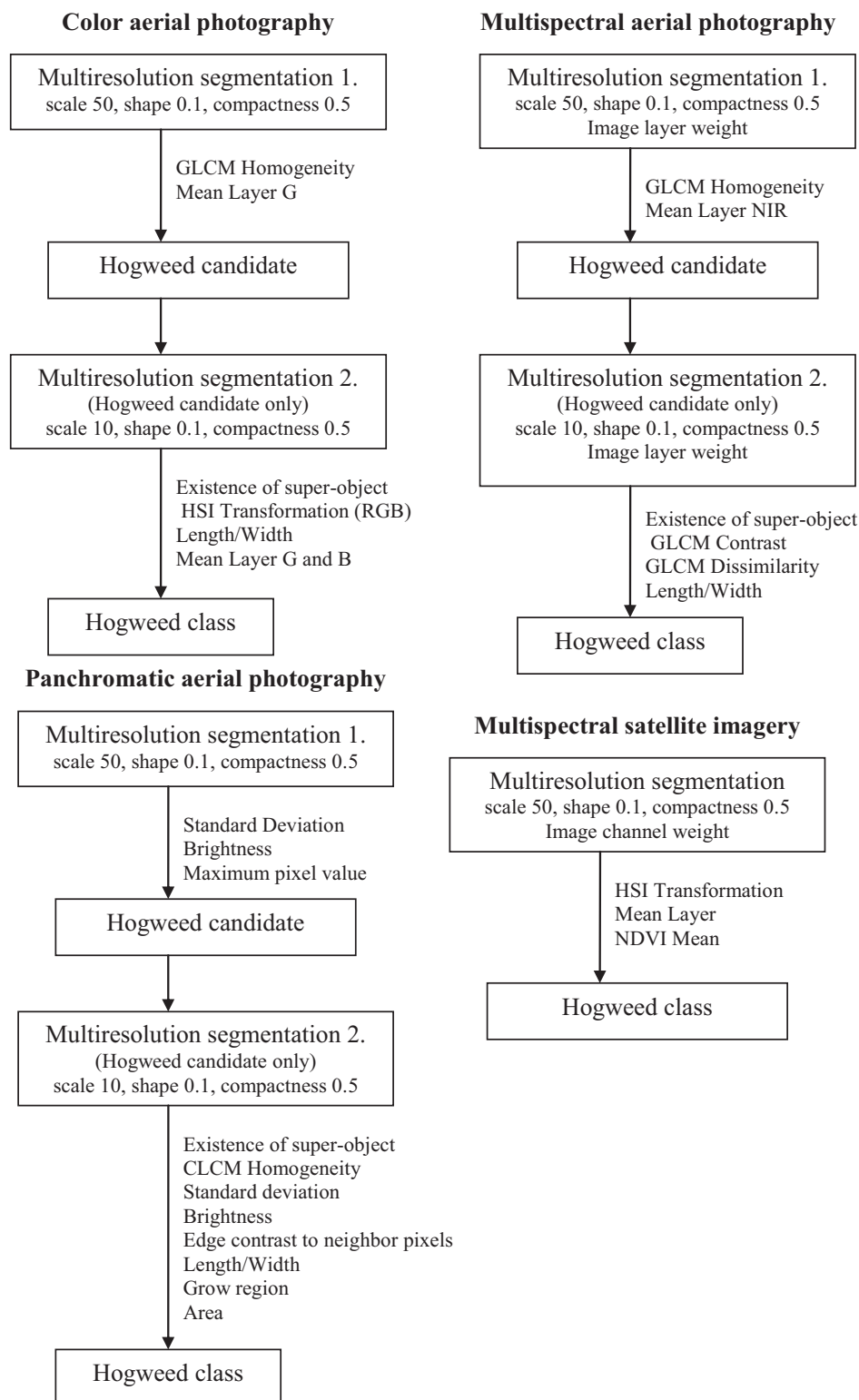


Fig. 2. OBIA classification schemes for the four types of data tested.

Although many authors state that for evaluation and comparison of classification results the accuracy assessment is crucial (Foody, 2010; Chen et al., 2012), there are many methodological uncertainties, especially in object-based approach (Foody, 2002; Morgan et al., 2010). It has been argued that traditional pixel-based accuracy assessment (i.e. points) tends to underestimate object-based image accuracy mainly due to allocation inaccuracies

(Hamada et al., 2007). To verify OBIA classification, some authors used random polygons (Jobin et al., 2008; Mallinis et al., 2008). We rejected this approach because it suffers from several problems: (i) polygon complex borders are difficult to locate exactly in the field and thus verify, especially when working with VHR imagery (in sub-meter resolution it comes to the limits of field GPS instruments); (ii) polygons are not perfectly homogenous

Table 1
Technical parameters of analyzed data.

Year	Date	Scale	Source	Spectral resolution	Channels (in nm)	Camera	Focal length	Film material	Provided by
1962	25 July	1:12,000	Aerial	Panchromatic		WILD 328	209.73	Unknown	Military Topographic Institute, Dobruška
1973	11–16 August	1:27,000	Aerial	Panchromatic		WILD 328	114.36	Unknown	Military Topographic Institute, Dobruška
1987	21–23 August	1:25,000	Aerial	Multispectral	448, 540, 660, 840	MSK-4	125	FOMA (visible), I-840 (NIR)	Nature Conservation Agency of the CR in Prague
1991	23 July	1:13,400	Aerial	Panchromatic		LMK 269152B	152.2	FOMA	Military Topographic Institute, Dobruška
2006	18 July	1:5000	Aerial	Color orthophoto		ZEISS RMK TOP 300	300	AGFA AVICOLOR NP 200	GEODIS s.r.o.
2010	8 July	5 m res.	Satellite	Multispectral	440–510, 520–590, 630–685, 690–730, 760–850	Rapid Eye			RapidEye AG

so it is difficult to evaluate their “correctness” (thus subjective thresholds are needed); and (iii) different sizes of polygons (or segments) make the comparison difficult. Some authors compare OBIA results to manually classified plots (Laliberte et al., 2004; Laba et al., 2010). This approach could work for simple landscapes but for a complex patchy mosaic on VHR data manual delineation is very difficult and subjective (Corcoran and Winstanley, 2008; Hofmann et al., 2008), making the bias caused by inaccuracies in manual classification too great to make relevant assessment (being more manual/digital comparison than the accuracy assessment). After thorough search in the literature, we modified approach from Hamada et al. (2012). We established 20 random quadrates of 40 to 40 m, and to reduce subjectivity of visual photo-interpretation of historical photography overlaid the quadrates by a 1 m² grid assigned onscreen by hogweed presence/absence (further called “grid assessment”; sort of pixelization of the VHR results).

From the error matrices, standard accuracy measures were calculated, such as user's accuracy (UA; ratio of the correctly classified and the number of total classified, evaluating reliability of the results for the user), producer's accuracy (PA; ratio of the number of correctly classified and the number of observed), and Kappa analysis (conditional Kappa index evaluating the statistical significance of the classifications, considers the actual agreement of the class in relation with chance agreement, Congalton and Green, 1999; Foody, 2002). We used the Kappa statistics even though it has recently come under strong criticism due to the randomness used as a baseline (Pontius and Millones, 2011), because it is a widely used mean of the accuracy measure providing an opportunity for comparison with previous studies. Yet, because these classic accuracy measures were developed for pixel-based approach and their application on OBIA results is questioned (Möller et al., 2007; Blaschke, 2010), we also searched the literature for other accuracy indices, tested them for correlation to reduce their number, and finally chose allocation disagreement (AD; Winter, 2000; Pontius and Millones, 2011), calculated as a sum of false positives and false negatives divided by a sum of true positives and all false; and quantity disagreement (QD; Pontius and Millones, 2011), calculated as false positives minus false negatives divided by a sum of true positives and all false. Values of acceptable classification accuracy presented in the literature differ considerably. Pringle et al. (2009) consider accuracy over 70% as adequate, whereas Foody (2002) recommends values over 85%. Landis and Koch (1977) proposed categories for assessment of the classification performance measured by Kappa value as poor (<0.41), moderate (0.41–0.61), good (0.61–0.81), and excellent (>0.81).

We were also interested in comparing the results of manual and computer interpretation of the imagery. Hogweed polygons in 20 randomly located circles of 20 m radius were manually on-screen digitized and fragmentation analysis carried out, counting sets of patch metrics such as class area, number of patches, mean patch size, standard deviation, and coefficient of variance, total length of edge and mean patch edge reflecting the complexity of the polygons. Since we were interested in hogweed class only, other land cover types were not classified in OBIA approach, and the overall accuracy was therefore not relevant. All accuracy values account solely for the hogweed class.

GIS analyses were performed using ArcGIS 9.2 (ESRI, 2006), landscape metrics calculated using Patch Analyst 5.0 for ArcGIS (Rempel et al., 2012) and FRAGSTAT 3.3 (McGarigal et al., 2002), and statistical analysis using Statistica 10 (StatSoft Inc., 2011).

3. Results

The analyses showed rapid invasion of the test site over the 50 years covered (Fig. 4). From the primary dispersal foci in the

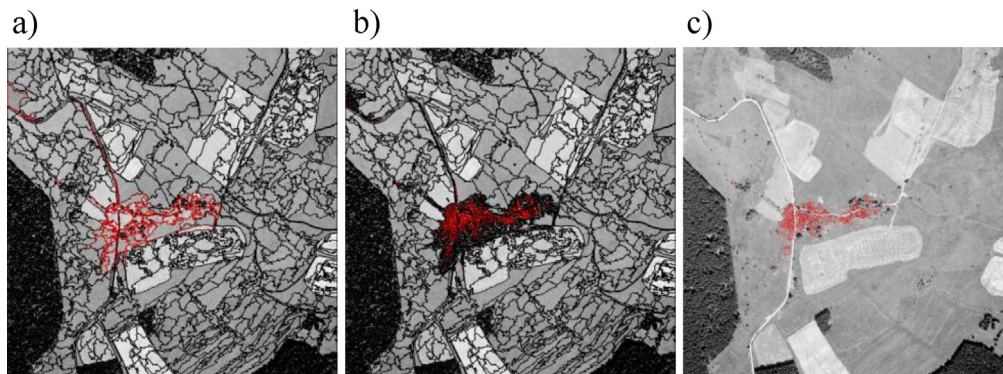


Fig. 3. Example of hierarchical coarse (a) and fine (b) image segmentation, and rule-based classification process (OBIA; c). Panchromatic aerial photography of 1962 (Military Topographic Institute, Dobruška) was analyzed in Definens software. Giant hogweed candidate in segmentation process and resulting hogweed class are marked in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

center of the study site in 1962 the species spread exponentially into the surroundings. For most of the data, good efficiency in hogweed classification was achieved (assessed by both point and grid approach; Table 2). The appropriate classification methods depended on the character of RS data (its spectral and spatial resolution), and on the projection of giant hogweed on different imagery (Tables 3 and 4). For panchromatic as well as color VHR (spatial) imagery, the best results were provided by OBIA approach with average accuracies (by both assessment methods) of UA 81%, PA 87%, conditional Kappa 0.77, QD 0.12, and AD 0.28. Pixel-based methods gave very poor results for such low spectral resolution data and were excluded from further analysis. For multispectral VHR aerial data, acquired at the time of the species fruiting, the OBIA approach yielded better results but the accuracy was still lower compared to the previously mentioned results. Average accuracies (both assessment methods) of multispectral VHR imagery were: UA 71%, PA 65%, conditional Kappa 0.61, QD 0.36, and AD 0.51. The medium resolution satellite data showed comparably higher accuracies for pixel-based methods, with supervised (maximum likelihood) classification achieving the best results (average UA 66%, PA 79%, conditional Kappa 0.5, QD 0.22, and AD 0.45; Tables 2 and 3) but still much lower compared to VHR data.

In our study, we used both grid and point accuracy assessment. Both methods agreed in choosing the best classification methods for the hogweed classification; however, their results differed. The pattern of differences in the two accuracy assessments could be related to the type of classification approach (Table 2). In OBIA,

grid accuracies were usually higher compared to the point assessment, and the opposite was true for the pixel-based classification. This pattern was most pronounced for Kappa coefficient and AD and for other indices the response was more complex. For both types of assessment, UA was significantly positively correlated with the Kappa value and negatively with both disagreement measures whereas PA was only correlated to AD. AD and QD were also significantly correlated, with AD values in all cases higher than QD.

On the imagery, plants were captured in different phenological phases from early flowering to ripe fruiting (Table 2). Classification success was influenced by the phenological stage of the species. The best classification results (VHR imagery – average UA 84%, PA 87%, conditional Kappa 0.8, QD 0.11, and AD 0.26) were obtained during the mid-flowering phase (July) due to the distinct white color of inflorescences, whereas at later stages (end of flowering – early fruiting) hogweed stands were not so distinct, and the detection of stands with ripe fruits was problematic (case of 1973 panchromatic and 1987 multispectral aerial data, Table 2).

The results of automated classification were compared to the manual on-screen digitizing of hogweed polygons (Table 5). The results of manual interpretation were less complex with multiple lower numbers of polygons, significantly higher standard deviation, higher mean size of patches, larger area, lower patch size coefficient of variance, and significantly lower total length of edge compared to the digital classification. This was especially true for the later stages of invasion where a larger area was invaded.

Table 2
Classification results of different data sources and classification approaches. Both point and grid accuracy assessments are included. Accuracy indices were: user's accuracy (UA), producer's accuracy (PA), quantity disagreement (QD), and allocation disagreement (AD). Phenological phases of *H. mantegazzianum* (giant hogweed) on the data were calibrated using detail phenological study of Perglová et al. (2006), and CHMI long-term phenological database (Hájková et al., 2012).

Year	Resolution (in m)	Source	Type of data	Phenological phases (after calibration)	Processing	UA (in %)		PA (in %)		Conditional Kappa		QD		AD	
						Point	Grid	Point	Grid	Point	Grid	Point	Grid	Point	Grid
1962	0.5	Aerial	Panchromatic	Middle flowering	OBIA	80.53	74.29	88.95	98.65	0.70	0.74	0.09	0.24	0.27	0.26
1973	0.5	Aerial	Panchromatic	Final-size/ripe fruiting	OBIA	68.87	78.91	86.39	85.60	0.53	0.78	0.18	0.07	0.38	0.30
1987	0.5	Aerial	Multispectral	Ripe fruiting	OBIA	74.23	67.70	36.55	94.08	0.57	0.65	0.45	0.27	0.68	0.36
1987	0.5	Aerial	Multispectral	Ripe fruiting	MaxLike	57.20	17.43	68.53	64.95	0.29	0.12	0.13	0.67	0.54	0.84
1987	0.5	Aerial	Multispectral	Ripe fruiting	ISO	65.47	26.98	46.19	55.86	0.43	0.22	0.24	0.43	0.63	0.78
1991	0.5	Aerial	Panchromatic	Middle flowering	OBIA	82.39	81.39	82.98	91.13	0.75	0.81	0.01	0.10	0.30	0.25
2006	0.2	Aerial	Color	Middle flowering	OBIA	88.98	95.50	67.26	94.49	0.83	0.95	0.23	0.01	0.38	0.10
2010	5	Satellite	Multispectral	Early flowering	OBIA	39.13	44.07	97.06	87.96	0.24	0.29	0.59	0.47	0.61	0.58
2010	5	Satellite	Multispectral	Early flowering	MaxLike	64.50	67.21	99.50	58.77	0.41	0.58	0.35	0.10	0.36	0.54
2010	5	Satellite	Multispectral	Early flowering	ISO	63.03	39.08	75.38	58.73	0.39	0.26	0.14	0.69	0.48	0.22

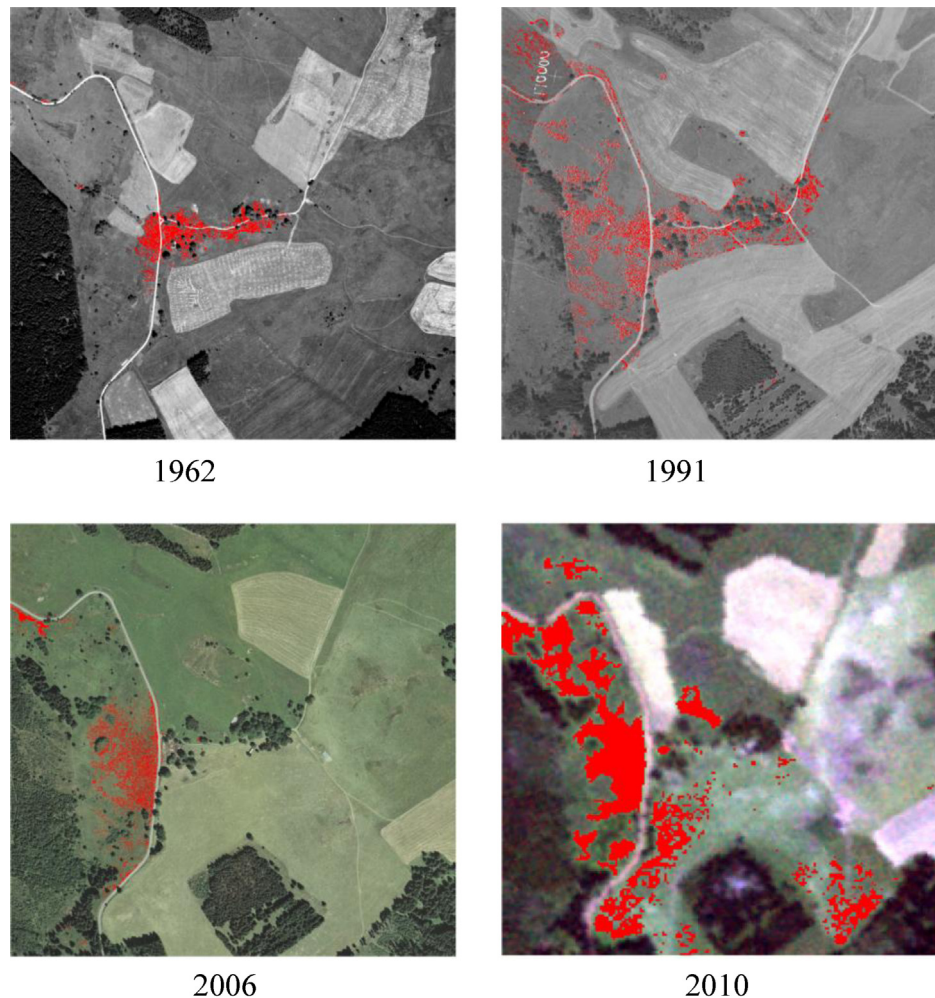


Fig. 4. 50 years of invasion on the study site (giant hogweed class in red). In 2006 protective measures against invasion were implemented, and the area occupied by giant hogweed is therefore temporarily reduced. The imagery comes from Military Topographic Institute, Dobruška (1962, 1991), GEODIS, Prague (2006), and Rapid Eye AG (2010). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Trade-off between accuracy and scale: choosing the most suitable monitoring method

Our study established efficient automatic methods for monitoring of the invasive herb giant hogweed from remote sensing data. VHR (spatial) imagery with pixel size smaller than individual plant enabled reliable detection of individuals with good to excellent results according to Landis and Koch (1977) if classified by object-based methods and acquired at the right phenological stage of the species. The success of classification did not depend on the spectral resolution of data; even historical panchromatic imagery provided good results.

Although at peak flowering hogweed flowers have distinct round shape and white color, they form large compound umbels that flower successively, hence the inflorescences are composed of buds, flowers and ripening seed at the same time (Perglová et al., 2006), and the inflorescences are therefore not spectrally homogeneous on VHR imagery. Such high spectral variability within objects reduced accuracy of pixel-based classification (so called H-resolution problem and salt-and-pepper effect; Yu et al., 2006; Chen et al., 2012) whereas OBIA employing additional information such as shape, texture, and the context of mapped objects (hogweed individuals) reached comparably higher accuracies

(c.f. Cleve et al., 2008; Pringle et al., 2009; and Ouyang et al., 2011).

Mapping of hogweed was generally precise, but under the tree canopy or if grazed or mown, the hogweed could not be detected. On managed sites it could be present in a form of short individuals with few small leaves in ground rosettes, sometimes even manage to flower late in the season producing short stems with and small inflorescences (ca. up to 20 cm in diameter) with a few seeds. Together with a seed bank that persist for up to 3 years (Moravcová et al., 2006; Gioria et al., 2012) this not only ensures regeneration of the populations, but also indicates that such stands are not suitable for giant hogweed in a long-term. However, if the stand is not managed regularly during the whole vegetation season, the species might return quickly to its previous abundance (Pyšek et al., 2007b). Despite such limitations, the overall distribution in the target area could be obtained with a high accuracy.

Even though the proposed automated processing of VHR data is relatively efficient, for large areas it would be rather demanding because of the enormous amount of data to be analyzed and associated high costs (Chen et al., 2012). As shown in our study, satellite data of medium resolution such as Rapid Eye can provide an effective alternative on a coarser level, serving as a useful tool for nature protection to mitigate the large-scale impacts of plant invasions.

Comparing automated and manual interpretation of data, the automated approach captured very small patches as well as gaps

Table 3

Processing approaches for data of different spatial and spectral resolution and their performance illustrated by conditional Kappa coefficient (Congalton and Green, 1999). The measure of classification performance (poor to excellent) follows Landis and Koch (1977).

Low spectral/very high spatial resolution data <i>Our type of data</i> - color/panchromatic aerial data - very high spatial resolution (<0.5 m) - low to very low spectral resolution <i>Pixel-based image processing</i> - not suitable – not enough spectral information <i>Object-based image processing</i> - applied semi-automated hierarchical, iterative, and rule-based classification approach - additional information on shape, texture and context of mapped objects enhance classification considerably - moderate to excellent classification performance (conditional Kappa – 0.53–0.95) High spectral/very high spatial resolution data <i>Our type of data</i> - multispectral aerial photographs - very high spatial resolution (<0.5 m) - high spectral resolution (5 channels including NIR) - wrong timing of the data acquisition (after flowering) ► poor classification results <i>Pixel-based image processing</i> - unsupervised classification – ISODATA: moderate classification accuracy (conditional Kappa – 0.43) - supervised classification – maximum likelihood: poor classification accuracy (conditional Kappa – 0.29) <i>Object-based image processing</i> - semi-automated hierarchical, iterative, and rule-based classification approach - moderate classification accuracy (conditional Kappa – 0.57) High spectral/medium spatial resolution data <i>Our type of data</i> - multispectral satellite imagery (Rapid Eye) - medium/high spatial resolution – lower than the size of individuals but enabling to map homogeneous stands (5 m) - high spectral resolution (5 channels including NIR) <i>Pixel-based image processing</i> - unsupervised classification – ISODATA: poor classification performance (conditional Kappa – 0.39) - supervised classification – maximum likelihood: moderate classification performance (conditional Kappa – 0.41) <i>Object-based image processing</i> - poor classification performance (conditional Kappa – 0.24)	
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in hogweed stands that were often omitted by manual delineation. This was especially true for images from the latter stages of invasion when larger areas were infested. Hogweed structures became more complex and therefore difficult and laborious to delineate manually and so the interpreter tended to omit small patches and generalize (cf. Corcoran and Winstanley, 2008; Morgan et al., 2010). Thus the advantage of automatic classification of RS imagery over the manual one increased with the growing size and complexity of the landscape mapped. The direct use of manually classified maps of hogweed presence as a reference would therefore bring about many inaccuracies.

Overall, there is a trade-off between the accuracy necessary for studies at the ecological scale, and large-scale applicability needed for efficient management. The most suitable method to be applied to monitor a particular plant invasion thus depends on the purpose of the study. As different data types and processing methods can capture different features of plant morphology and structure and different aspects of the ecological dynamics of invasion, follow up studies on monitoring invasive plant species are encouraged to find out the best methods for their purposes by conducting pilot studies.

Table 4

Consequences of different spatial resolution of data for vegetation detection.

Spatial resolution higher than the size of mapped individuals (very high resolution data) <i>Conditions for the species detected</i> - unique spatial (spectral) patterns - recognizable on the images (by eye) <i>Conditions for the RS data</i> - availability of images acquired in the right season <i>Advantages</i> - very high spatial resolution - small patches and individuals can be recognized ► helps in monitoring onset of invasion and dispersal foci - historical datasets enabling reconstruction of invasion progress <i>Disadvantages</i> - spectral resolution often low (panchromatic historical photographs) - data often not standardized (historical datasets) ► difficulties in automatic processing - timing of the data acquisition often not ideal (historical dataset) ► shifts in phenological stage of invasive species - small areal extent of images ► large amount of data ► processing is labor and time intensive <i>Data used in our study</i> Sensor: aerial photography Spatial resolution: <0.5 m Temporal resolution: app. every decade since 1940s Spectral resolution: mostly panchromatic Spatial resolution lower than the size of mapped individuals (high/medium resolution data) <i>Conditions for the species detected</i> - large homogeneous stands - unique spectral characteristics - possibility of ground truth (by field work or aerial imagery with the species clearly visible) <i>Conditions for the RS data</i> - availability of images acquired in the right season - sufficient spectral detail to recognize the species - spatial resolution enabling to capture larger patches <i>Advantages</i> - larger area covered by a single image ► faster processing compared to VHR data - standardized datasets ► possibility to apply automatic processing techniques - repeated temporal coverage for regular monitoring - high spectral resolution <i>Disadvantages</i> - lower spatial resolution compared to VHR data ► impossible to extract small patches or individuals - short temporal resolution compared to aerial photography <i>Data used in our study</i> Sensor: Rapid Eye Spatial resolution: 5 m Temporal resolution: daily (off-nadir)/5.5 days (at nadir) since 2008 Spectral resolution: 5 bands incl. NIR	
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4.2. Accuracy assessment: an important issue

Sources of error in our study were the image mis-registration, and the inability to ground truth historical imagery in the field. At early stages of invasion grid accuracy assessment could be biased by the fact that the extent of hogweed was limited.

Although in our study the results of both pixel and object based accuracy assessment generally agreed (the same methods were selected as the best), the differences in accuracies derived by the two assessment types and different accuracy measures illustrate that the choice of classification accuracy assessment method has a great influence on results (especially true for OBIA). Lower values of AD (as well as conditional Kappa) in grid compared to the point assessment for OBIA (unlike the pixel-one) agree with statement of underestimation of OBIA accuracy by pixel assessment (Hamada et al., 2007). UA and conditional Kappa values derived from the two assessments were strongly correlated. Values of PA were usually higher compared to UA. Although the UA (expressing the commission error) seems important for natural protection applications,

Table 5

Comparison of automated classification (D) and manual on-screen digitizing (M) of hogweed polygons. Significant differences on level $\alpha = 0.05$ are marked by *. Classification approach providing the best results was analyzed, i.e. maximum likelihood in 2010 and OBIA in other cases.

Year	Class area		Number of patches		Mean patch size		Patch size standard deviation [*]		Patch size coefficient of variance		Total length of edge [*]		Mean patch edge	
	D	M	D	M	D	M	D	M	D	M	D	M	D	M
1962	7633.4	9002.3	334	285	22.9	31.6	117.4	131.5	792.0	439.7	10620.2	5810.2	31.8	20.4
1973	17085.7	15242.0	134	47	127.5	324.3	486.6	894.5	381.7	318.2	14063.9	3566.2	105.0	75.9
1987	26642.1	33254.9	204	59	130.6	563.6	582.5	1411.0	774.1	292.7	18766.4	6347.8	92.0	107.6
1991	12679.2	24498.3	3162	823	4.0	29.8	12.0	173.6	800.9	600.9	33825.6	16648.7	10.7	20.2
2006	7811.2	33267.1	3167	50	2.5	665.3	22.3	1941.3	904.4	253.7	32334.0	4454.6	10.2	89.1
2010	24362.9	34474.3	43	14	566.6	2462.4	1626.3	3257.4	287.0	132.3	4318.8	3042.6	100.4	217.3

the PA (omission error) is important for efficient control measures because it reflects the error of omitting of some plants that can later serve as a source of diaspores. An acceptable level of accuracy depends on the map purpose; it should be maximized if the goal is to locate infestation hotspots, but can be lower if all possible locations of the invasive species are to be addressed (Hamada et al., 2007).

4.3. Implications for mapping strategy: the role of phenological stage

We found that timing data acquisition to coincide with flowering and early fruiting was important for successful detection of invading populations because only at these stages were they distinct enough to be accurately distinguished (for other plant species see Huang and Asner, 2009; Somodi et al., 2012). While RS detection of flowering hogweed plants was relatively easy, detection of fruiting or non-flowering plants was limited, and the data capturing the species in fruiting period (1973 panchromatic and 1987 multispectral aerial photography) showed significantly lower recognition success.

In general, the best mapping strategy needs to reflect the morphological and structural features of the plant under study and chose the phenological stage at which individuals are most efficiently captured by monitoring. For invasive plant species with conspicuous flowering appearance it is crucial to collect data at the peak of the flowering period and take the temporal pattern of flowering into account; in case of giant hogweed it is concentrated into relatively short period (Perglová et al., 2006) but other plant species can have the flowering spread over longer periods of time, and for others there can be vegetative features such as the structure of the canopy or spectral signature especially in the NIR part of spectrum that may be effectively used for recognition (Everitt et al., 2005; Laba et al., 2010; Jones et al., 2011; Dorigo et al., 2012; Somodi et al., 2012). Overall, it points again to usefulness of a pilot analysis before a large-scale monitoring is started.

4.4. Lessons learned: implications for management of plant invasions

Our study, using giant hogweed as a model species, established a comparably fast method of detecting and capturing the spread of an invasive plant provided that the imagery is acquired at the time of the species flowering. Medium spatial resolution image analysis gives a fast overview of regional infestation whereas VHR data provide details on invasion progress and serves for early detection at the beginning of invasion. Presented results also underline that RS is important not only for analyses of past invasion dynamics and related issues (e.g. Müllerová et al., 2005; Nehrbass et al., 2007; Pergl et al., 2011) but also for rapid response and eradication of detected invasion foci (Pluess et al., 2012).

The described methodology developed on the test site has been successfully applied over the study region (175 km²) to monitor and manage the hogweed invasion in the PLA Slavkovský les in cooperation with Mariánské Lázně Municipality Office, and to analyze the patterns of invasion process at landscape scale in order to relate the dynamics of hogweed invasion (dispersal foci, maximum infestation, spatial structure, and rate of spread) to the landscape patterns (land cover, land use, fragmentation, connectivity, disturbance, and invisible habitat availability), and study mechanism of the species spread, habitat preferences and driving forces in the landscape. This knowledge helps us to understand why certain habitats are more susceptible to invasions than others and find optimum management strategies (Müllerová et al., 2005).

The high classification accuracies indicate that the method is potentially applicable to other areas and/or other invasive plants, despite the possible biases encountered in managed habitats or under forest canopies where identification by RS is somewhat restricted. For other regions or species with similar characteristics, namely well-recognizable inflorescences, the method is directly transferable; for other species a pilot analysis is advisable to identify features that can be efficiently used in the identification process. If adapted to the purpose of a particular study, the methodology presented here is potentially broadly applicable, enabling (i) early detection, (ii) identification of the foci to be targeted for eradication at the early stages of invasion, and (iii) regular monitoring of the sites. The proposed automated RS detection can make control measures more effective, faster, and less expensive than traditional monitoring methods based on ground mapping of invasive populations.

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Appendix 7.

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8

UAS for Nature Conservation – Monitoring Invasive Species

Jana Müllerová

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8.1 The Problem of Plant Invasions

Plant invasions are considered among the most threatening processes in current landscapes with wide-ranging consequences for socio-economic concerns, biodiversity, ecosystem services, human health, and traditional landscapes (Leishman et al. 2007; Levine et al. 2003; Vilà and Ibáñez 2011; Pyšek et al. 2012). Despite the worldwide efforts to control and eradicate alien plant species, their impact is increasing (Hulme et al. 2009), and may further grow with climate change and global warming. The success of invasion depends largely on habitat and species characteristics (Richardson and Pyšek 2006). However, because of many external and stochastic factors that can contribute to the process, consequences are case specific and difficult to foresee (Levine et al. 2003). The process of invasion comprises of multiple spatio-temporal scales from seed recruitment to long-distance dispersal. Therefore, the data collected at different spatial and temporal scales needs to be integrated into spatially explicit models to better understand the invasion impact and role of individual factors (Andrew and Ustin 2010; Nehrbass et al. 2007). Exploring the spatio-temporal dynamic of invasions including the habitat selection and distribution dynamics ameliorates our ability to understand the drivers of invasion and increases the efficiency of control measures (c.f. Meier et al. 2014; Holden et al. 2016; Pyšek and Hulme 2005).

The invasion process is fast and dynamic, and once established, invasive species are usually difficult or even impossible to reduce/eradicate (Rejmánek and Pitcairn 2002). Control

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of highly infested sites is therefore complicated, and targeting primarily recently infested sites was shown to be efficient and economical. Early monitoring of invasion onsets followed by rapid management measures are therefore crucial (Pluess et al. 2012). Traditional ways of monitoring via fieldwork campaigns are laborious and difficult to organize, and new alternatives of cost-effective techniques are therefore necessary for timely, fast, and precise alien species management (Hulme et al. 2009). It is well known that invasive plants are often easy propagating and fast-growing species with high biomass, fast regeneration, and reproduction rate that tend to dominate the space forming large monospecific stands (Leishman et al. 2007). Such characteristics make invasive plants ideal candidates for remote sensing detection. The method can also be used to study spatio-temporal dynamics of the invasion process at the landscape scale, to model invasion spread, and to plan efficient eradication measures (Müllerová et al. 2005; Nehrbass et al. 2007; Laliberte et al. 2004). Still, to be operational, such methods need to be robust and well defined.

8.2 Remote Sensing Monitoring of Invasions – Temporal, Spatial, and Spectral Aspects

The potential of remote sensing to provide a timely means of invasion monitoring depends on the data resolution and processing approach. The choice for type of remote sensing methodology is specific to the species, and must correspond to its characteristics. Generally speaking, alien plants can be detected by remote sensing means when they represent structure or phenology novel to the neighboring native vegetation (Huang and Asner 2009). For data resolution issues, three components must be considered – temporal, spatial, and spectral (Figure 8.1).

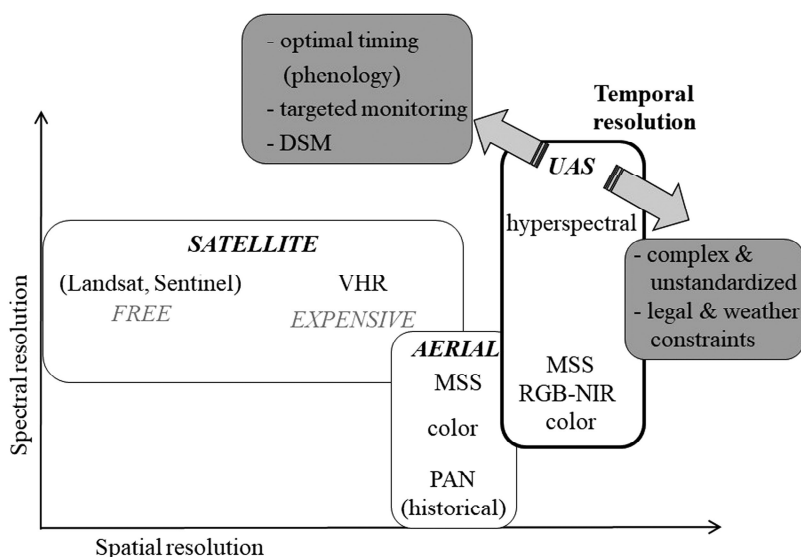


FIGURE 8.1

Different components of resolution related to the remotely sensed data available.

For plant species detection, high temporal resolution covering the plant seasonal variability and/or proper timing of the data acquisition can be very important. Less distinct species might be detected only at particular phenological stage(s) when they differ enough from their surrounding (e.g. in flowering, senescing or early/late start in the season) (Huang and Asner 2009; Müllerová et al. 2017b; Somodi et al. 2012).

Complementary approaches such as change detection (multi-date assessment) ease the species recognition (Diao and Wang 2016; Martin et al. 2018). Specific timing can even enable detection of forest understorey species (Perroy et al. 2017; Müllerová et al. 2017b; Hernandez-Santin et al. 2019).

Over the last decades, we have seen the rapid development of new accurate classifiers for species recognition, and new sensors and data acquisition systems of high spatial and temporal resolution, such as Unmanned Aerial Systems (UAS). Application of UAS enables flexible data acquisition at very high spatial and temporal scales, potentially bridging the gap between small-scale (point) field surveys and air and space-borne Earth observations (Manfreda et al. 2018). Unmanned platforms are currently being adopted by many fields of environmental sciences (Whitehead et al. 2014; Manfreda et al. 2018) and nature conservation (Jiménez López and Mulero-Pázmány 2019), and bear potential to improve environmental monitoring to assist management decisions. Thanks to its flexibility, UAS is able to collect the imagery at the exact date/phenological stage of the target plant species. They can be used to test influence of data acquisition time on the detection accuracy to establish optimal methodological workflow that can be later adopted for larger scale mapping using satellite imagery (Dvořák et al. 2015).

As fast-growing species, invasive plants (especially herbs) can also be detected using a series of Digital Surface Models (DSM) throughout the season, generated as a by-product of the UAS orthophoto mosaicking process of Structure from Motion algorithm (SfM) (Westoby et al. 2012). However, for these purposes, high spatial accuracy in the UAS imagery is necessary to precisely overlay multi-temporal data (Manfreda et al. 2019). DSMs can serve as valuable input to the analysis of plant invasions since such species tend to be large and fast growing, and can therefore be detected using the change detection approach. This is especially true for herb species that show seasonal cycle, such as knotweeds (Martin et al. 2018). If a detailed Digital Elevation Model (DEM) is available (e.g. LIDAR with high density of points per meter), the DSM can be used to both support classification of optical imagery, and analyze the growth of invasion. The lack of detailed DEM can be substituted by a DSM acquired by a UAS flight out of vegetation season. For change detection and canopy height models, precise matching of layers is crucial, and it is often necessary to coarsen the data to avoid possible mismatches and decrease the rate of false change detection (Müllerová et al. 2017a).

Spatial resolution of the data also plays an important role in species recognition. Coarser resolution can prevent the detection of individual plants and small patches, which are particularly important from a management point of view as they can potentially serve as new dispersal foci in the landscape. Some methods are partially able to overcome this problem, such as sub-pixel classification used to estimate vegetation fraction in mixed pixels (Van De Voorde et al. 2008; Tooke et al. 2009). However, sufficient spatial resolution is still crucial and depends again on the target species and the purpose of the study. On the other hand, very high spatial resolution of UAS imagery tremendously increases the data complexity, and can sometimes be counterproductive, as a millimeter pixel size breaks plant individuals into a complex of branches/stems, leaves, inflorescences, insects, and soil background, making classification extremely difficult. In addition, a large amount of data markedly increases the demand for processing time and data storage.

The third component, spectral resolution, can involve data ranging from historical panchromatic, visible RGB, and multispectral (MSS) imagery to hyperspectral imagery. Here again, the suitable spectral range depends on the species characteristics (Mast et al. 1997; Müllerová et al. 2005). There are some examples of very distinct species, which can be distinguished even on panchromatic imagery. These serve as a valuable source of information on long-term landscape change, and in some cases, historical panchromatic aerial photos have been used to reconstruct the invasion process (Mast et al. 1997; Müllerová et al. 2005). Still, most commonly, higher spectral information is needed, with Near-Infrared (NIR) band being the most important to detect plant photosynthetic activity.

As for UAS, commonly used MSS cameras can be substituted to a large extent by consumer cameras modified to be sensitive in the NIR part of the spectrum (exchanging built-in IR-cut filter by Hoya R72 filter, see e.g. Müllerová et al. (2017a)). Such a cheap alternative does not provide perfect spectral information since the filters are not capable of separating the channels completely (Figure 8.2) However, this can still provide valuable information and keep the costs low, making the approach easy to adopt at operational bases. Rasmussen et al. (2016) confirmed the reliability of vegetation indices derived from consumer-grade cameras. On the other hand, hyperspectral sensors represent a comprehensive resource that even enables the separation of similar species and can study plant physiology in detail; yet such sensors are still very costly and not commonly adopted for UAS (Zarco-Tejada et al. 2012; Sankey et al. 2017). In addition, the processing of hyperspectral imagery is very complex and time consuming, and therefore remains reserved for experimental applications; it is not operational in natural conservation efforts.

The large amount of data produced by UAS generates the need for automatic processing that can be complicated especially if the species is not very distinct from the surrounding natural vegetation. To make the detection operational for nature conservation, careful design of the workflow (Figure 8.3) based on testing various data and algorithm settings is extremely important, since the choice of optimal approach is influenced by the data spatial, spectral, and temporal resolution and the target

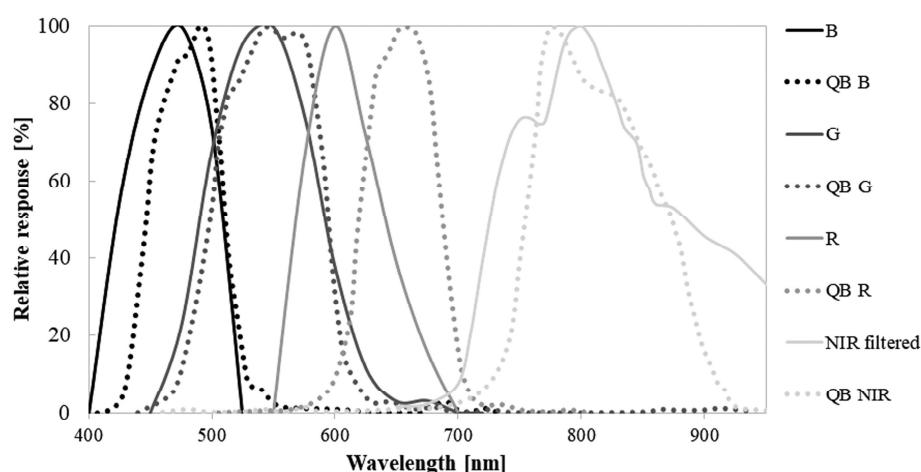
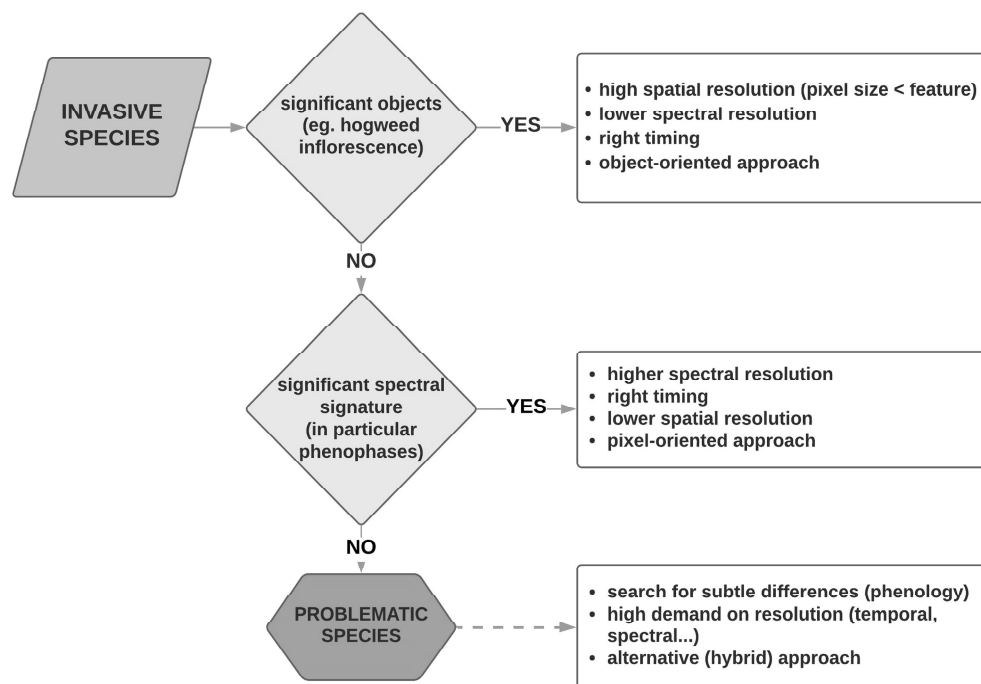


FIGURE 8.2

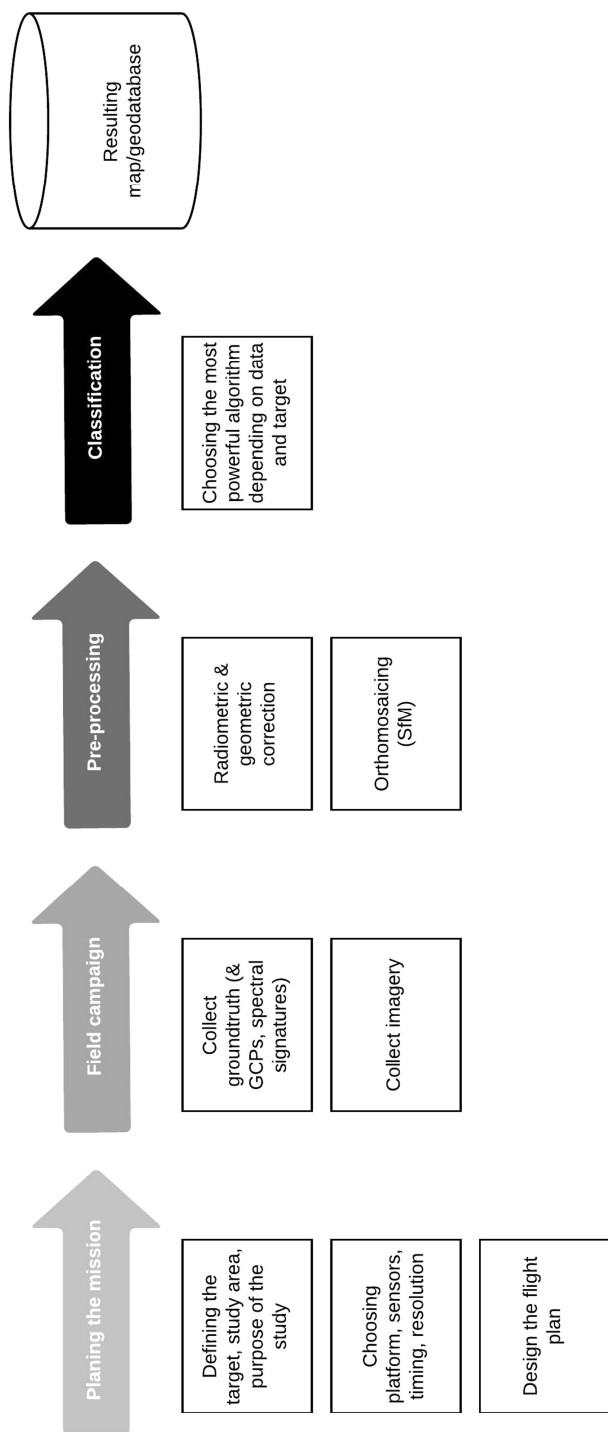
Non-Gaussian relative spectral response of consumer camera modified to be sensitive in NIR part of the spectrum (exchanging built-in IR-cut filter by Hoya R72 filter) compared with standard RGB camera (adapted from (Müllerová, Bartaloš, et al. 2017)).

**FIGURE 8.3**

General workflow of UAS campaign and processing.

species characteristics. Because different aspects of resolution can compensate for each other to a certain degree, e.g. high spatial resolution can partially overcome the spectral handicap of historical panchromatic imagery (Müllerová et al. 2005). A holistic approach for the UAS workflow design that includes the algorithm characteristics should always be considered. The optimal approach is species specific (Müllerová et al. 2017a), and some general rules still apply (Figure 8.4). Machine learning classifiers are particularly promising, showing high classification accuracy either with a limited number of training samples or upon utilizing highly detailed UAS data (Lary et al. 2016). For such imagery, methods that take into account the spatial structure are often applied instead of the pixel-based approach in order to reduce the effects of shadows, within-class spectral variation, mis-registration, and salt-and-pepper effect caused by increased within-patch variability (Zweig et al. 2015; Chen et al. 2018). The type of the object of interest defines the suitable algorithm; object-based classification is suitable if forming distinct objects larger than the pixel size is required, whereas in case of indistinct/small objects, the pixel-based approach would be more effective (Figure 8.4) (Müllerová et al. 2017b; Mafanya et al. 2017). For distinct species, even low spectral resolution data can be sufficient in case of an adequate spatial resolution and processing algorithm, but a combination of high resolution and sophisticated procedure is necessary for effectively mapping problematic species.

As already mentioned, it is important to keep a balance between the data resolution/complexity of algorithms and the aim of the study since high resolution and/or complex algorithms are extremely demanding on computer processing (complexity, time, data storage, and analysis). Higher resolution is not necessarily always the better choice, and the same applies to classification accuracy. Additionally, we should bear in mind both the

**FIGURE 8.4**

Decision tree for choosing optimal data and classification approach depending on the target invasive species.

extent and aim of the study. Regional or country scale mapping would definitely require a different approach compared to the targeted local monitoring. Acceptable accuracy threshold (especially that of omission error) should be adjusted according to the purpose of study, setting it to high in order to locate invasion hotspots and provide information for modeling, and setting it lower for eradication purposes to make sure none of the possible infestations are omitted (Hamada et al. 2007; Martin et al. 2018).

8.3 UAS for Plant Invasions – Advantages and Challenges

UAS are becoming increasingly popular in many environmental applications mainly because of their easy deployment, operation, and extremely high spatio-temporal resolution. The available number of platforms and sensors is growing, and the choice depends largely on the study target, the purpose, and the budget. Specialized sensors such as LIDAR, thermal, or hyperspectral cameras are not yet common because of the high costs and need for larger and more reliable platforms capable of carrying such a payload. Most commonly, UAS are multi-rotors or fixed-wing platforms loaded with optical sensors, such as MSS, modified near-infrared, simple RGB consumer cameras, and GoPro. Even with the simplest settings, a UAS is still able to provide Digital Surface Models (DSM) (Westoby et al. 2012) and orthoimagery at very high temporal and spatial resolution (Colomina and Molina 2014). Still, challenges remain because of geometrical and radiometric distortions, mainly due to the close land surface proximity, and unstandardized processing workflow (Manfreda et al. 2018). Geometrical precision can be enhanced by carefully designed flight configuration, GCP number and distribution, and navigation system onboard the UAS (James et al. 2017; Manfreda et al. 2019). Radiometric distortions are often caused by changing light conditions during the flight. These can be calibrated using onboard radiometer measuring actual incident solar radiation; however, such sensors are usually not part of the low-cost settings. Extremely high spatial resolution of UAS imagery brings new challenges in the training and validation process (GCP and ground-truth data collection) since the centimeter to millimeter resolution reaches the limits of GPS instrument precision. Expensive differential GPS is meant to provide sub-meter precision in ideal conditions. However, in forest growth or complex environments, it reaches meter precision only, and the data collection is time consuming. New ways of collecting the ground data are yet to be deployed; such software applications would support their own very high resolution basemaps (e.g. UAS imagery) to better locate the ground objects of interest. Such applications (e.g. Collector for ArcGIS, NextGIS Mobile, QField, QGIS Mobile, ODK Collect, and CyberTracker) can be installed on smartphones and tablets, supporting larger scale ground-truth campaigns (Müllerová et al. 2017a).

Such limitations must be borne in mind when planning a flight campaign as there is no reason for collecting data in centimeter resolution if we only need or are able to reach meter precision in the final mosaic. If imagery is acquired in ultra-high spatial resolution, individual images cover a very small area, and finding common tie points for the SfM algorithm can be problematic especially in a complex environment such as a forest. In addition, other already mentioned drawbacks of extremely high spatial resolution exist, such as complexity and amount of giga/terra bytes to be processed and stored.

On the other hand, UAS provide considerable benefits over traditionally used satellite and aerial data (Table 8.1). In addition to ultra-high spatial resolution, UAS supports

TABLE 8.1

Benefits and Disadvantages of UAS Imagery Over Traditionally Used Satellite and Aerial Data

	NASA & ESA Satellites	VHR Satellites	Aerial Data
Advantages of UAS	+ spatial resolution + flexibility (timing) + frequency	+ spatial resolution + flexibility (timing) + frequency + lower costs of acquisition	+ spatial resolution + flexibility (timing) + frequency + lower costs of acquisition
Disadvantages of UAS	– higher costs – acquisition constrains – complicated – complex preprocessing – no archival data	– acquisition constrains – complicated – complex preprocessing	– acquisition constrains – complex preprocessing

the exact timing of the mission, providing flexibility in planning and designing the data acquisition, independent from external providers.

UAS are therefore ideal for targeted monitoring, eradication control, and experimental testing to find the best setup of timing, resolution, and classification workflow since they enable regular acquisition at different seasons to account for environmental and context (background vegetation) variability. They are able to provide very high detail, but they are not suitable for covering large areas. Whereas fixed-wing UAS are able to cover larger areas compared to multi-rotors, it is still no more than several square kilometers per flight. UAS operation is also limited by legal constraints, such as visual contact of the pilot with aircraft and restrictions in urban areas (often highly infested by invasive plant species). For regional or country scale monitoring, other data sources such as satellite (ideally) or manned aircraft imagery become viable (Table 8.1). With the growing availability of free or low-cost higher spatial resolution operational satellites such as Sentinel and CubeSats, larger infestations could be monitored; however, small patches and individual plants are still impossible to detect on coarser resolution data. This is especially true for the highly heterogeneous Central European landscape where the occurrence of invasive plant populations is rather patchy. Small patches and individuals, omitted by satellite campaigns, often serve as dispersal foci and new onsets of invasion. However, in fact such early stages of invasion are crucial for eradication, since after the species becomes widespread, it is often difficult or impossible to eradicate it completely from the landscape (Pluess et al. 2012). This implies that UAS hold great potential to reduce the effects of invasions, identify priorities for management, support targeted monitoring, and control eradication efforts.

8.4 UAS-Based Plant Invasion Case Studies

Examples of invasive studies employing UAS imagery are not very common; still, their number has grown considerably over the last number of years, and early results are promising (Table 8.2). They cover different life forms, not only trees, shrubs, grasses, and herbs, but also wetland species, climbing vines, or cacti, and span from tropics through temperate regions to Mediterranean and dry environments (savannas and deserts). UAS data are typically used for (semi)automatic detection, the most common being by OBIA approach (70% of studies) and machine learning algorithms (70%) such as Random Forests. Many studies are benefiting from structural information provided by UAS, including canopy

TABLE 8.2

Plant Invasion Studies Using UAS

Species	Reference
<i>Acacia dealbata</i> , <i>Ulex europaeus</i> , <i>Pinus radiata</i>	Lopatin et al. (2019), Kattenborn et al. (2019)
<i>Acacia longifolia</i>	de Sá et al. (2018)
<i>Asclepias</i> sp., <i>Bromus inermis</i> , <i>Festuca rubra</i> , <i>Solidago canadensis</i>	Lu and He (2017)
<i>Acacia mangium</i>	Lehmann et al. (2017)
<i>Fallopia</i> sp.	Michez et al. (2016), Müllerová et al. (2017b), Martin et al. (2018)
<i>Hakea sericea</i>	Alvarez-Taboada et al. (2017)
<i>Harrisia pomanensis</i>	Mafanya et al. (2017; 2018)
<i>Heracleum mantegazzianum</i>	Michez et al. (2016), Müllerová et al. (2017b)
<i>Impatiens glandulifera</i>	Michez et al. (2016)
<i>Iris pseudacorus</i>	Hill et al. (2017)
<i>Mikania micrantha</i>	Li et al. (2019), Wu et al. (2019)
<i>Miconia calvescens</i>	Perroy et al. (2017)
<i>Pennisetum ciliare</i>	Elkind et al. (2019)
<i>Phragmites australis</i>	Zaman et al. (2011)
<i>Robinia pseudoaccacia</i>	Müllerová et al. (2017a), Carl et al. (2019)
<i>Spartina alterniflora</i>	Wan et al. (2014), Zhou (2018)

height or surface roughness into the classification algorithm. Despite sophisticated classification procedures, the vast majority of studies (70%) use simple low-cost settings of a consumer camera (RGB), often supplemented by a filtered NIR camera sensor. Only five studies work with hyperspectral sensors, and there is no UAS LiDAR deployed. A majority of studies (70%) combine UAS with very high and medium resolution satellite imagery to explore upscaling to the landscape scale, and authors often employ particular phenology and multi-temporal data to support the detection and to explain invasion dynamics.

To demonstrate applicability of the UAS approach for detection of invasive plants, three plant species (taxons) were selected for being invasive and widely naturalized in a number of European countries. They represent different life forms (one tree and two herbs), span along the gradient of sensitivity to the optimal phenological stage, and either form distinct objects or are difficult to distinguish (Table 8.3). Using these model species of different life forms, phenology, and architecture, it will be shown how different aspects of data quality (spatial, spectral, and temporal), costs, and operational issues affect methodology and can have practical implications (Figure 8.4). These examples indicate how important is it to understand the object of interest we want to monitor, and what benefits the UAS brings to invasive species monitoring; most important being the high spatial resolution and the flexible timing of the flight campaign.

8.4.1 Example 1 – Giant Hogweed

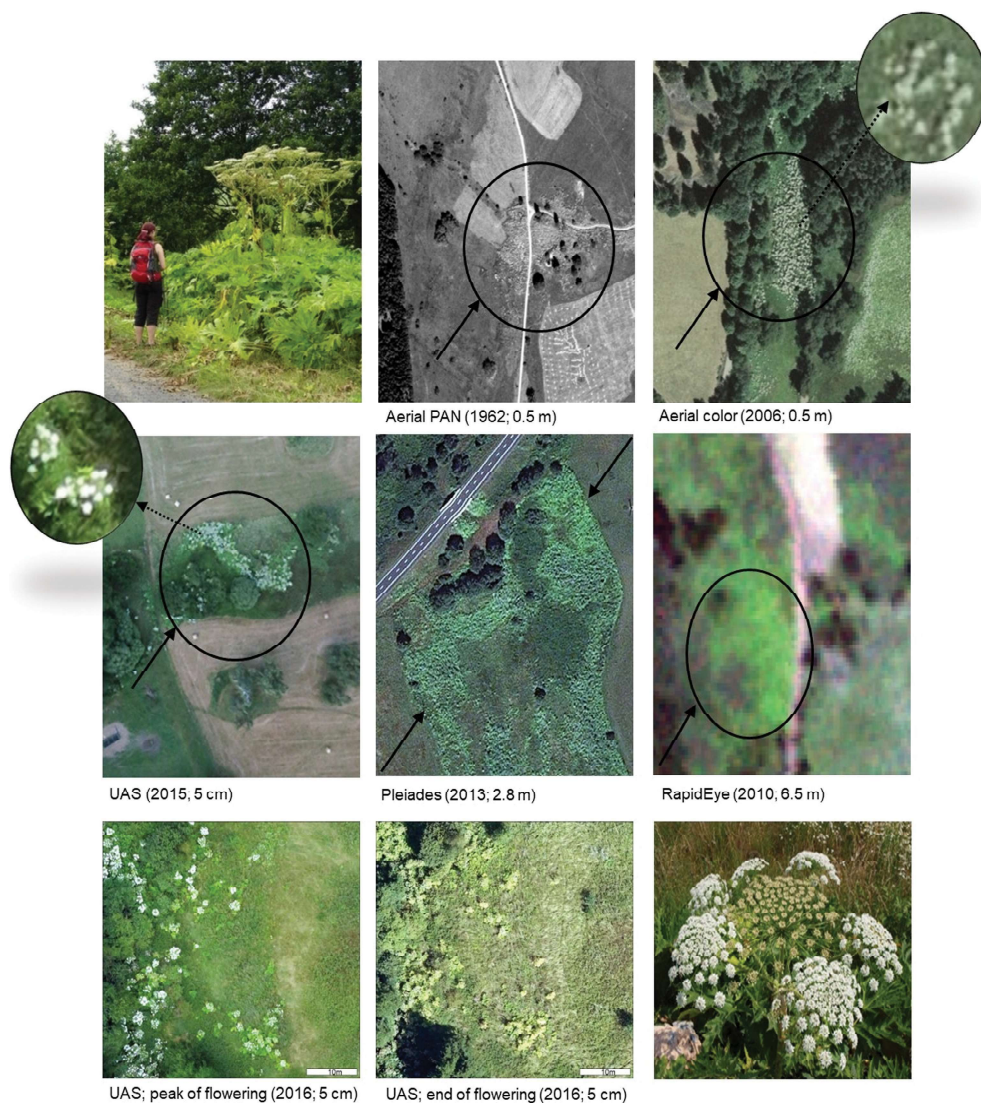
Giant hogweed (*Heracleum mantegazzianum*) is a noxious herb species, native in East Asia, and problematic in colder parts of Europe. It threatens biodiversity and has negative consequences for human health via phototoxins causing contact dermatitis (Drever and Hunter 1970). Certain characteristics, such as a large size of 2 to 5 meters, a large number of seeds (up to 100,000) (Tiley et al. 1996), and a high rate of spread allows the species to be a successful invader, and have significant implications for its management and potential

TABLE 8.3

Detection of Three Target Species – Description, Data Requirements, Optimal Classification Approach

	giant hogweed	exotic knotweeds	black locust
Species	<i>Heracleum mantegazzianum</i>	<i>Fallopia japonica</i> <i>F. sachalinensis</i> <i>F. × bohemica</i>	<i>Robinia pseudoaccacia</i>
Life form	monocarpic herb	perennial herb	deciduous tree
Size	2 to 5 m	2 to 4 m	12 to 30 m
Leaves	large (up to 2.5 m), well structured	medium (10–30 cm), complicated leaf architecture, forming dense stands	small, compound, folding in the summer heat
Inflorescence	large white round compound umbels (1 m), facing upwards, distinct	small white clustered racemes, not distinct	medium white pendant racemes (10–20 cm), rather distinct
Regeneration	generative – up to 20,000 seeds from single plant	vegetative – extensive fragile rhizomes	mostly vegetative – root suckers
Invaded habitats	fallow land, river banks, margins of forests and arable fields, ruderal stands	fallow land, river banks, open forests and forest margins, ruderal stands, disturbed habitats, urban areas	formerly planted, invading step grasslands, disturbed habitats, road and railway corridors and steep slopes
Native range	Caucasus	Japan	South East United States
Impact	human health (skin allergy), biodiversity	biodiversity, economic losses (extensive root system damages construction work and river banks)	biodiversity (but also an important species for wood and honey production, and erosion control)
Optimal phenophases	peak of flowering	senescence (turns reddish)	peak of flowering, but other periods also good
Optimal data timing	2nd half of June – 1st half of July	end of October – beginning of November	vegetation season
Detection accuracy	high	medium	medium
Tested imagery	UAS (5 cm, RGB + modif. NIR), color orthophotos (25 cm, RGB), Pleiades 1B (0.5 m pan sharpened, RGB, NIR)	UAS (5 cm, RGB + modif. NIR), Pleiades 1B (0.5 m pan sharpened, RGB, NIR)	UAS (5 cm, RGB + modif. NIR), WorldView-2 (0.5 m pan sharpened, RGB, NIR)
Spatial resolution	5–50 cm	5–50 cm	5–50 cm
Spectral resolution	low	medium (NIR necessary)	medium (NIR necessary)
Temporal resolution	high (1 month)	high (1 month)	low
Optimal classification	object-oriented (SVM, RF)	pixel-oriented (ML, RF)	pixel-oriented (SVM, ML)
Reference	Müllerová et al. (2017b)	Müllerová et al. (2017b)	Müllerová et al. (2017a)

Abbreviations: SVM – Support Vector Machine, RF – Random Forest, ML – Maximum Likelihood

**FIGURE 8.5**

Giant hogweed at different phenophases and data sources. Effects of spatial resolution and timing of the campaign are clearly visible.

control (Pyšek et al. 2007). Giant hogweed is an example of herb species forming very distinct phenophase in flowering (Figure 8.5). As a perennial monocarpic species it flowers once, mostly in the third year (Pergl et al. 2006), and its huge white round inflorescences (of up to 1 meter) form distinct well defined objects that are easy to distinguish even from low spectral resolution imagery in case its pixel size exceeds the size of individual plants (i.e. 1 meter). Timing of the data acquisition during flowering is crucial, with a time period of about one month in Central Europe (Perglová et al. 2006). At the beginning and end of flowering, the detection rate decreases markedly, and out of flowering, the species is quite difficult to recognize (Müllerová et al. 2013). If captured at the peak of flowering, it can be detected even from historical panchromatic imagery. In our studies, Müllerová et al. (2013)

and Müllerová et al. (2005), we used historical aerial photo time series to reconstruct the process of invasion at the landscape scale, and model the species spread (Nehrbass et al. 2007; Pergl et al. 2011; Pyšek et al. 2008).

Even though manned aerial imagery provides spatial resolution high enough to support the detection, archives are limited and flight campaigns are costly; the same holds true for VHR satellite imagery. This is not the case for UAS which enable the exact timing of the campaign (Müllerová et al. 2017b). They provide a low-cost flexible solution with potential to be widely used in nature conservation. From UAS imagery, hogweed can be detected with very high classification accuracies (Michez et al. 2016; Müllerová et al. 2017b). Since the hogweed inflorescences are well separable from the background forming distinct objects, the object-oriented approach was shown to be the most effective, using either a combination of multiresolution segmentation and Random Forest (RF) classifier (Michez et al. 2016), or that of contrast split segmentation and rule-based classification. Such an approach successfully separated hogweed inflorescences from other white objects, such as artificial surfaces or harvested fields (Müllerová et al. 2017b). Automatic classification was able to detect even individual flowering plants that could potentially serve as dispersal foci in the landscape. Flowering plants were detected with very high accuracy (Table 8.4); still young (not flowering) and mown/grazed plants were difficult to recognize on low-cost RGB + modified NIR imagery. For such an application implemented outside the flowering period, imagery of higher spectral resolution would be necessary. Compared to manual on-screen digitizing, the automatic approach brought more complexity and detail into the analyses. Since manual processing tends to generalize and omit individual plants, the manual approach was more capable of recognizing non-flowering individuals (Müllerová et al. 2013). It is also important to mention that very fine spatial resolution of UAS imagery is not always beneficial – in the case of hogweed, compound inflorescences are visible as white dots on 0.5 m imagery separated into individual umbels at centimeter resolution, creating artificial gaps in hogweed stands (Figure 8.5) (Müllerová et al. 2017b).

TABLE 8.4

Summary of Classification of Giant Hogweed Using Different Data Sources Capturing Different Parts of the Species Vegetation Season. Lower Spectral Resolution can be Compensated by Timing and Spatial Resolution of the Data

Data	Resolution	Phenology	Method	User's Accuracy	Producer's Accuracy	Reference
RapidEye	6.5 m	early flowering	pixel (MaxLike)/OBIA	65/44%	76/65%	Müllerová et al. (2013)
Pleiades	2.8 m	mid flowering	pixel/OBIA (RF)	86/70%	94/99%	Müllerová et al. (2017b)
aerial PAN	0.5 m	mid flowering	OBIA	89%	81%	Müllerová et al. (2013)
aerial color	0.5 m	mid flowering	OBIA	57%	94%	Müllerová et al. (2017b)
UAS RGB+NIR	0.05 m	mid flowering	OBIA	99%	100%	Müllerová et al. (2017b)
aerial PAN	0.5 m	ripe fruiting	OBIA	86%	69%	Müllerová et al. (2013)
aerial MSS	0.5 m	ripe fruiting	OBIA/pixel (MaxLike)	51.6/42%	74.2/28.5%	Müllerová et al. (2013)

Hogweed represents a nice example of species for which timing and spatial resolution is crucial, and can successfully compensate for the lower spectral resolution of the data. UAS can clearly bring the benefit of flexibility; and for nature conservation, even low-cost UAS equipped with a simple RGB sensor would be sufficient. Still, because of small area covered, such an approach is ideal for targeted monitoring and checking of eradication efforts, and not for extensive surveys at the landscape scale, where other means such as satellite mapping come into play (Müllerová et al. 2017b).

8.4.2 Example 2 – Black Locust

Black locust (*Robinia pseudoacacia*) is a North American tree, widely planted in Europe in the past mainly for wood production and soil amelioration (Vítková et al. 2017). This pioneer light-demanding species is extremely resistant to disturbance and therefore difficult to eradicate because trunk damage provokes viable regeneration from root suckers. As a nitrogen fixing tree it is able to completely change the soil properties and understorey species composition, having significant consequences for biodiversity, especially for dry grasslands of high natural value that it frequently invades (Vítková et al. 2015; Lazzaro et al. 2018). Locust has small compound leaves and rather distinct white inflorescences (Figure 8.6).

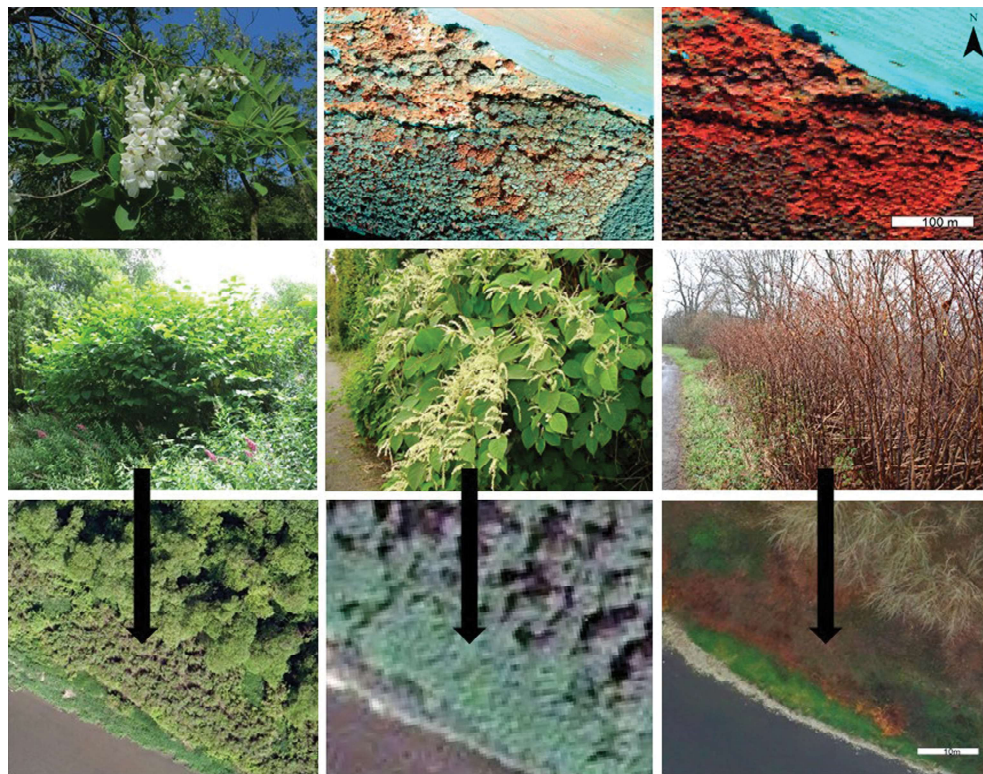


FIGURE 8.6

Black locust (top row) and exotic knotweeds (middle and bottom rows) in the field and on the imagery. NIR-G-B false colour composites of UAS imagery of 0.05 m resolution (top middle), and WV-2 satellite of 2 m resolution (top left). Black locust in bright red. Middle and bottom rows show exotic knotweeds in the spring (UAS imagery of 0.05m), summer (Pleiades satellite, 2.8 m), and autumn (UAS imagery of 0.05m).

According to (Somodi et al. 2012), locust was best separable during flowering. However, its white inflorescences are pendant, and therefore not particularly visible from above. Moreover, the flowering is rather short (one or two weeks), stands usually do not flower exactly simultaneously, and the plant is quite sensitive to the late spring frost that can postpone flowering. This implies that the flowering period is difficult to predict, making this kind of detection rather impractical. Nevertheless, our research showed that locust can also be separated in other parts of the vegetation season based on leaf signature (Figure 8.6) (Müllerová et al. 2017a). It showed good separability in the NIR part of the spectrum, even if assessed using a low-cost modified NIR sensor. Still, precise co-registration of the channels of combined RGB and NIR imagery proved to be an important step in the analysis. Since the tree does not form defined objects but rather heterogeneous stands, the object-based approach was more effective; machine learning algorithms (Support Vector Machine) being less sensitive to the distortion of the orthomosaics, that is an inevitable artefact of UAS data. Deep learning algorithms such as convolutional neural networks represent a powerful option to classify black locust. However, such methods require a high number of labeled training images and are problematic to repeat (Carl et al. 2019).

To improve detection accuracy, ancillary information such as canopy height is often employed in the classification process; however, to create such a canopy height model of forest stand, both detailed Digital Terrain Model (DTM; often unavailable) and accurately located DSM, problematic for ordinary UAS, are needed. To overcome imprecision problems, the vegetation height model can be substituted by surface roughness measure defined as a function of a range of elevation values, i.e. relative elevation differences within a specific subset. In case of black locust, such an approach helped to increase classification accuracy and separate locust from arable fields, which was often misclassified otherwise (Somodi et al. 2012; Müllerová et al. 2017a); still, it did not improve discrimination from other tree species with similar surface heterogeneity values. To detect the species, centimeter resolution of UAS imagery was not necessary and could be substituted by VHR imagery of meter resolution (WV-2 in case of Müllerová et al. 2017a); still, such imagery is very costly, and freely available Landsat imagery seems to be too coarse for the purpose (Somodi et al. 2012).

8.4.3 Example 3 – Invasive Knotweeds

Invasive knotweeds include three taxa expressing subtle morphological differences from the remote sensing perspective. These are *Fallopia* (syn. *Reynoutria*) *japonica*, *F. sachalinensis*, and their hybrid *F. × bohemica*. Originally from Asia, knotweeds are among the most problematic invasive plants in temperate regions of the world since they are extremely difficult to eradicate or manage due to their vigorous growth and regeneration (Child and Wade 2000). Economic losses related to knotweed invasion are vast, with the annual costs estimated to €2.3 billion in Europe (Kettunen et al. 2008). Improving methods for their detection and monitoring would increase the eradication efficiency, especially along their main dispersal axes, i.e. transportation corridors and rivers (Tiébré et al. 2008).

Knotweeds are herbaceous perennials up to 4 m tall with small flowers and highly heterogeneous canopy architecture, forming dense stands with complicated architecture. Knotweeds represent an example of species that do not form distinct objects; however, they can be discriminated capitalizing on phenological dynamics throughout vegetation season since their spectral signature shows strong intra-annual variability (Figure 8.6).

The NIR part of the spectrum seems to be particularly important for the species discrimination. Because of the lack of distinct objects, pixel-based algorithms are generally more beneficial for detection. Such algorithms are also less computationally demanding and therefore easier to operate on the large data volumes UAS provide. Müllerová et al. (2017b) found that VHR satellite data represent a viable option since even with a coarser resolution of 0.5 m, comparable high accuracies can be achieved depending on phenological stage of the knotweed (Table 8.5). However, at coarser spatial resolution, small emerging patches and those growing under the tree canopy tend to be omitted more frequently.

As already mentioned, phenology plays an important role in species detection. Knotweeds usually start to foliate early, but in some stands, the foliage can be postponed. Therefore, during the spring, knotweed stands form a mixture of old reddish stems from the previous year and new emerging stems and leaves, making the detection particularly challenging. During the summer, they are not particularly distinct from the surroundings, and are separable mainly in the NIR part of the spectrum. Although knotweeds are considered as a light-demanding species (Beerling et al. 1994), they can grow under open forest canopy, and particularly along rivers after flooding disturbances. Remote sensing detection under the canopy is generally difficult, although very high spatial resolution was shown to overcome the problem to a certain extent (Perroy et al. 2017; Hernandez-Santin et al. 2019). During late autumn, knotweeds drop leaves and turn senescing stems to brown-red (Figure 8.6), making detection the most effective (Müllerová et al. 2017b). Additionally, at this time of year, overstorey deciduous trees drop their leaves, exposing understorey knotweeds. Unlike earlier remote sensing studies (Dorigo et al. 2012; Michez et al. 2016; Jones et al. 2011; Müllerová et al. 2017b) achieved operational classification accuracies that are meaningful for practical application of the technology. This part of the season therefore seems ideal for the task; however, unstable weather, cloudiness, strong winds, and long shadows can make UAS data acquisition at this period particularly challenging. Martin et al. (2018) showed an alternative option capitalizing on the knotweeds fast growth. They used the summer imagery supported with canopy height models and multi-date band ratios derived from UAS imagery acquired at different parts of the vegetation season that were entering the classification process. Machine learning algorithms (Random Forests) were the most powerful; still this cannot be taken as a rule of thumb as they can in some cases be outcompeted by traditional algorithms such as Maximum Likelihood. For object-based

TABLE 8.5

Classification of Exotic Knotweeds from UAS and Pleiades Satellite Data Acquired in the Summer and Late Autumn During the Senescence. Summary of Accuracies Achieved Using Different Approaches, Data, and Phenological Stages

Data	Resolution	Phenology	Method	User's Accuracy	Producer's Accuracy	Reference
Pleiades 1B	0.5/2 m	green	pixel (RF)	44%	95%	Müllerová et al. (2017b)
UAS RGB/NIR	0.05 m	green	pixel (SVM)	60%	92%	Müllerová et al. (2017b)
UAS RGB/NIR + BTBR/CHM	0.05 m	green	OBIA (RF)	80/78%	83/86%	Martin et al. (2018)
UAS RGB/NIR	0.05 m	senescence	pixel (MaxLike/SVM)	80/54%	78/95%	Müllerová et al. (2017b)

classification, rule-based algorithms are often more successful compared to machine learning; still, the method is based on expert knowledge and is therefore more subjective and case-specific.

8.5 Implications for Management and Future Research

As demonstrated here by several examples, remote sensing represents an important tool supporting active management of invasions. Remote sensing tools provide precise information on extent of invasion, and supplemented with ancillary data such as environmental variables, land cover/land use, and plant characteristics (means of dispersal, plant traits, population characteristics), it can be used to study the process of invasion. This includes an assessment of the species impact, the susceptibility to invasion of different habitats, and potential of the species to invade the landscape. This is followed by modeling different scenarios of eradication to define the most effective management strategy. This information supports eradication efforts, identifies management priorities, and establishes management protocols (Figure 8.7).

UAS as an easily accessible tool can be used not only for detection of problematic species, but also to study the invasion process and check eradication efficiency. Still, since its areal extent is limited, it is meant for testing the best monitoring approach and targeted monitoring, and to map invasions at landscape scale; other means such as satellites assume importance. UAS can provide unbeatable high spatial resolution and flexibility of the data acquisition at relatively low costs. However, to make UAS mapping operational, there is still a long way to go for standardization of the methods, especially in sense of data acquisition, geometric, and radiometric pre-processing, ground-truthing, and validation.

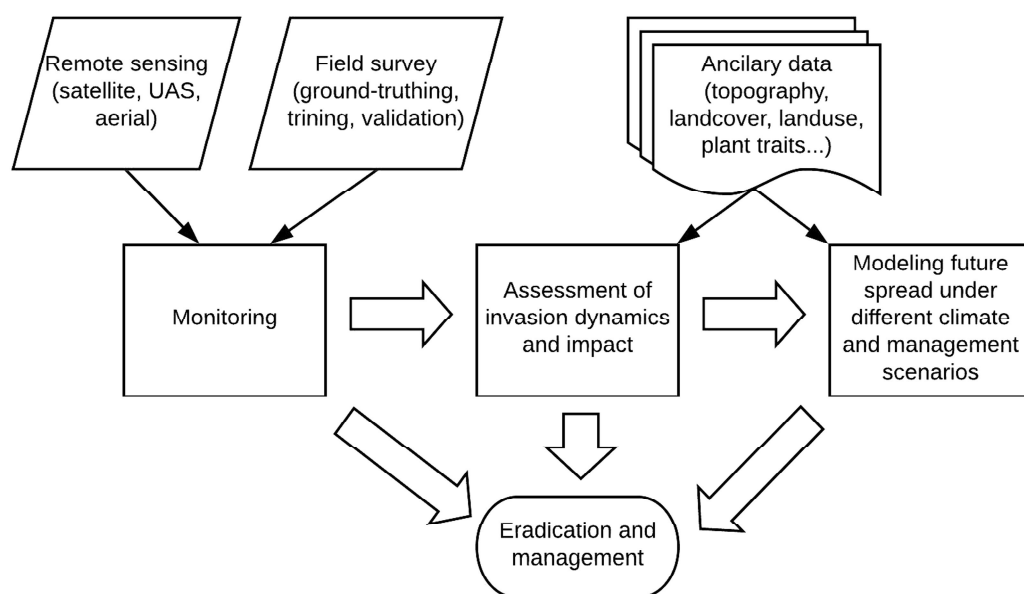


FIGURE 8.7

How can the remote sensing help to tackle the invasions?

8.6 Conclusions

The chapter summarizes the potential and limitations of detection of relevant invasive species in terms of (i) the effect of the spatial/spectral resolution of the RS images, and (ii) the detection rate as a function of the phenological stage of the vegetation. Efficient and cost-effective methods for fast and timely monitoring of plant invasions must be selected based on accuracy of the species detection, data acquisition costs, and labor demands; whereas the selection of methods largely depends on the needed accuracy driven by the purpose of the study, flexibility, and economic efficiency. This holds true for all aspects of the flight mission: (i) selecting the appropriate UAS platform (fixed-wing for mapping larger areas, and multi-rotor for better maneuverability, with size of platform according to the payload), and sensors, ranging from simple GoPro to the most sophisticated hyperspectral cameras and LIDAR; (ii) selecting appropriate spatial resolution according to the study; and (iii) right timing of the mission/temporal coverage (frequency) that often plays a fundamental role in invasive species detection and analysis of invasion dynamics. Still, the trade-offs between detection accuracy and the spatial and spectral resolutions must be borne in mind.

Describing the phenology and species variability at invaded sites at fine spatial and temporal scales not only allows identification of the target alien species, but also the ability to assess species habitat requirements and their impact on soil properties and biodiversity. Evaluation of the negative impact posed to invaded communities and susceptibility of the site to invasion enables the prioritization and focusing of the eradication efforts to the most affected sites and sites important for nature conservation (such as Natura 2000 sites).

Precise detection and monitoring of the invasion process provides knowledge on the mechanisms and spatial patterns of plant invasions and their amelioration. This improves the scientific knowledge on environmental and human-induced factors driving their spread, in order to make the protective measures more effective, and thereby minimize their negative impact on the society, economy, environment, and biodiversity.

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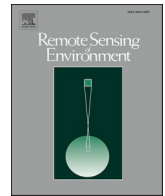
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Appendix 8.

PAPER 8. Kupková, L., Červená, L., Potůčková, M., Lysák, J., Roubalová, M., Hrázský, Z., Březina, S. & **Müllerová, J.** (2023). Towards reliable monitoring of grass species in nature conservation practice: evaluation of the potential of UAV and PlanetScope multi-temporal data in the Central European tundra. *Remote Sensing of Environment* 294: 113645. <https://doi.org/10.1016/j.rse.2023.113645>



Towards reliable monitoring of grass species in nature conservation: Evaluation of the potential of UAV and PlanetScope multi-temporal data in the Central European tundra

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ABSTRACT

The reliability of remote sensing technology is essential for its efficient operational applications in nature conservation practices. In our study, multi-temporal, multispectral, and hyperspectral data from an Unoccupied Aerial Vehicle (UAV) with a ground sampling distance (GSD) of 3 cm were applied to a permanent research plot (1 ha), while spaceborne PlanetScope multi-temporal data with GSD of 3 m were used for a wider area of 250 ha. The main aim of the study was to evaluate the potential of these data for monitoring vegetation at the species level in the Central European relict arcto-alpine tundra (in the Krkonoše Mountains, Czech Republic). We evaluated both types of data and their performance for various classifiers, and the benefits of adding multi-temporal aspects to the classification and robustness of remote sensing for monitoring grass species. This study addresses the requirements of nature conservation practices in the Krkonoše Mts. National Park to find a suitable method for monitoring changes in dominant and expanding grass species in response to global warming. The object-based Support Vector Machine, pixel-based Random Forest and Maximum Likelihood classifiers were evaluated. We confirmed that the UAV multispectral and hyperspectral data with GSD of 3 cm can monitor dominant grass species (*Nardus stricta*, *Calamagrostis villosa*, *Molinia caerulea*, *Deschampsia cespitosa*) in tundra with excellent accuracy (95.9% and 94.0% overall accuracy for multi-temporal and mono-temporal composites, respectively). The best F1-scores for these species ranged from 94.7 to 99.4%. However, the accuracies were substantially lower for small and sparse growing species (*Avenella flexuosa* and *Carex bigelowii*). Unexpectedly, the UAV multispectral and hyperspectral data yielded comparable results. The multi-temporal approach improved the accuracy of all types of data. Overall, we confirmed the robustness of the remote sensing approach for grass monitoring at the species level given the high spatial match between various classification outputs. Our study established a workflow for reliable monitoring of tundra grass vegetation according to the requirements of nature conservation and proposed innovative measures for the spatial accuracy assessment of classification outputs.

1. Introduction

Central European relict arcto-alpine tundra (alpine treeless) is a rare ecosystem, an ancient reminder of Arctic times in several European mountain ranges, such as the Krkonoše Mountains, Hrubý Jeseník, Králický Sněžník, Harz and Schwarzwald (Jeník, 1961). It is a unique

and valuable ecosystem formed by a combination of Arctic-subarctic and high-mountain landforms and biota (Soukupová et al., 1995). It is characterized by severe climatic conditions, pedological, geological and geomorphological variety, and high species diversity, including endemic species and glacial relicts (Grace et al., 2002; Holtmeier and Broll, 2017; Soukupová et al., 1995). Given its unique features, alpine tundra is

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among the most valuable natural phenomena (Grace et al., 2002; Holtmeier and Broll, 2017; Soukupová et al., 1995; Verrall and Pickering, 2020). However, biotopes above the treeline are adapted to specific conditions and are therefore very sensitive to disturbances and environmental changes such as warming, atmospheric pollution, drought and anthropogenic disturbances (Grabherr et al., 2010; Verrall and Pickering, 2020; WRI, 2005; Hejman et al., 2009; Johnson et al., 2011; Müllerová et al., 2011). Changes in biodiversity may also be accelerated by the expansion of certain species, such as native grasses and shrubs (Beamish et al., 2020; Hejman et al., 2009, 2010; McDougall et al., 2005; Štursa and Wild, 2014).

To efficiently protect arcto-alpine tundra, accurate and robust monitoring methods are essential for detecting changes in biodiversity and for tailoring ecosystem management plans. Besides the traditional methods of field monitoring (Díaz-Varela et al., 2010; Elmendorf et al., 2012; Hejman et al., 2009; Henry and Molau, 1997; Matějka and Málková, 2010; Zeidler et al., 2012), remote sensing (RS) technology presents a promising alternative. RS is advantageous for its capability to monitor large areas at different spatial and temporal scales, in a repeatable manner (Atkinson and Treitz, 2012; Beamish et al., 2020; Bolton et al., 2018; Kupková et al., 2017; Müllerová, 2005; Rees et al., 2014; Stow et al., 2004; Suchá et al., 2016; Wakulińska and Marcinkowska-Ochtyra, 2020; Zagajewski et al., 2005). To distinguish individual species, spatial resolution is crucial (Beamish et al., 2020; Bradter et al., 2020; Melville et al., 2019; Suchá et al., 2016). Moreover, high temporal resolution allows for the monitoring of phenological changes that exhibit different spectral responses, which can contribute to increasing the classification accuracy (Beamish et al., 2020; Bradley, 2014; Dudley et al., 2015; Marcinkowska-Ochtyra et al., 2019; Weisberg et al., 2021). One option for RS is time series of free-access data. Multispectral Landsat data (GSD 30 m) have been extensively used for both mono- and multi-temporal vegetation monitoring since the 1970s at the level of ecosystems, habitats and plant communities (Bolton et al., 2018; Cingolani et al., 2004; Ochtyra et al., 2020; Suchá et al., 2016; Ullmann et al., 2014; Virtanen and Ek, 2014), and, in some cases, even individual species (mainly trees or shrubs) (Frost and Epstein, 2014; Chen et al., 2015; R. Suchá et al., 2016). Sentinel-2 data, with higher spatial (GSD 20 m) and temporal resolutions enable more detailed classification of various habitats and plant communities, including alpine vegetation (Bayle et al., 2019; Belcore et al., 2020; Jędrych et al., 2017; Kupková et al., 2017; Macintyre et al., 2020; Rossi et al., 2019; Wakulińska and Marcinkowska-Ochtyra, 2020). Classification can be potentially improved by the fusion of Sentinel-1 and 2 data (Beamish et al., 2020; Crabbe et al., 2020; Mngadi et al., 2021). Still, given their relatively coarse spatial resolution, such data are not suitable for classification of most species and mixed stands, such as the Krkonoše tundra grasslands (Kupková et al., 2017). In recent decades, very high resolution (VHR) data from different commercial satellites (e.g., WorldView-2 and 3, RapidEye, QuickBird, IKONOS etc.) have been utilized for detailed vegetation monitoring at the community or species level (e.g., Dobrowski et al., 2008; Fenske et al., 2020; Immitzer et al., 2012; Suchá et al., 2016). However, their use is limited due to their high price and irregular data acquisition. The insufficient temporal resolution of VHR satellite data was alleviated by the PlanetScope satellites (Doves) that provide optical imagery on a daily basis (GSD 3 m). Despite limited spectral resolution, the importance of PlanetScope data in detailed vegetation monitoring is increasing (Minallah et al., 2020; Liu et al., 2019; Francini et al., 2020). However, studies using PlanetScope data for species classification of heterogeneous vegetation habitats/communities are rare (Räsänen and Virtanen, 2019).

Another option is aerial data that have flexibility in acquisition timing, use of various sensors and relatively large measurement footprints (tens of km²). However, due to the high cost, multi-temporal aerial observations are relatively rare. Although GSD (usually tens of centimeters) is fine, producing species-level accurate classifications may still require higher resolution. Marcinkowska-Ochtyra et al. (2017)

reported an overall accuracy (OA) of 74% for the classification of sub-alpine and alpine vegetation at the species level using mono-temporal aerial APEX data (GSD 3 m) and a support vector machine classifier. The accuracy was further increased by using a multi-temporal composite (Marcinkowska-Ochtyra et al., 2019).

In recent years, Unoccupied Aerial Vehicles (UAVs) have been extensively applied for detailed vegetation monitoring given the extremely high spatial resolution of UAV observations (Müllerová et al., 2021). Vegetation classifications derived from UAV data often include community and species levels of organization in the same classification legend (Komárek et al., 2018; Lu and He, 2017; Miranda et al., 2020; Senthilnath et al., 2017; Woellner and Wagner, 2019; Yan et al., 2019). For increased spectral resolution, hyperspectral sensors are also utilized but such applications are still rare (Cao et al., 2018; Sankey et al., 2018; Yan et al., 2019). Despite the importance of phenology for vegetation classification at the community/species level and the notable flexibility of UAV sensing, there is a lack of studies using multi-temporal UAV data (however see van Iersel et al., 2018; Weil et al., 2017), especially with regard to the use of hyperspectral sensors (see Miyoshi et al., 2020) or phenology based classification (Vega et al., 2015; Weisberg et al., 2021).

Some studies have successfully deployed UAVs (Fraser et al., 2016; Palace et al., 2018; Qin et al., 2020; Räsänen et al., 2019) to classify alpine/(sub)arctic/mountain/tundra vegetation, but no studies have yet applied them specifically for arcto-alpine tundra in European mountain ranges. However, there are several studies that have already used other types of RS data to monitor vegetation in the Krkonoše Mts., such as spaceborne multispectral data (Kupková et al., 2017; Suchá et al., 2016; Wakulińska and Marcinkowska-Ochtyra, 2020), aerial hyperspectral imagery (Kupková et al., 2017; Marcinkowska-Ochtyra et al., 2017, 2018b), and aerial orthoimagery (Müllerová, 2005; Suchá et al., 2016; Potůčková et al., 2021). These studies were mainly based on mono-temporal data with GSD of decimeters to meters and yielded OA of 60 to 85% depending on the classified categories.

Our study reflects the needs of the Krkonoše National Park to establish protocols for monitoring the vegetation of relict arcto-alpine tundra using remote sensing, specially UAVs. We evaluated the potential of UAV multispectral and hyperspectral and satellite PlanetScope multi-temporal (intra-seasonal) data for monitoring tundra grass vegetation at the species level. More specifically, our objectives were:

- 1) To determine the capability, reliability, and accuracy of UAV multispectral/hyperspectral data with 3 cm GSD for monitoring tundra grassland vegetation at the species level. Intercomparison of accuracy between the UAV multispectral and hyperspectral data was performed.
- 2) To compare the potential of UAV and satellite PlanetScope data for grassland vegetation monitoring at the species level. Despite the clear advantages of very high spatial resolution, UAVs have limited spatial coverage compared to PlanetScope data. It is also nearly impossible (economically and practically) to ensure a temporal resolution with UAVs comparable to that of PlanetScope data.
- 3) To evaluate and quantify a potential improvement in classification accuracy of the multi-temporal time series compared to mono-temporal imagery.
- 4) To compare the performances of different pixel and object-based classifiers for grass species classification and to establish a workflow for reliable and operational monitoring of Central European tundra grasslands at the species level.
- 5) To assess the robustness and reliability of the RS technology for monitoring plants, specifically grass species, in nature conservation practice.

2. Study area, data, and methods

2.1. Study area

Central European relict arcto-alpine tundra of the Krkonoše/Karkonosze Mountains National Park is distributed across the highest parts of the mountain range, above the treeline (1300 m a. s. l.), with average elevation 1452 m a. s. l., average annual temperature 0 °C to +1 °C and annual precipitation of 1400 mm (Soukupová et al., 1995). It covers 7.4% of the National Park (32 km² and 15 km² in Czechia and Poland, respectively). Due to the Scandinavian ice sheet expansion during the Holocene, tundra was present in this area (Margold et al., 2011; Tremblé et al., 2012). As a result of this paleogeographic history, the mountains virtually form the “biodiversity crossroads”, with the coexistence of Nordic and alpine flora and fauna (Jeník and Jan Štursa, 2003). In addition to mosses, lichens, and alpine heathlands, the prevailing vegetation above the treeline is represented by alpine grasslands dominated by a high proportion of *Nardus stricta*, subalpine tall grasslands, and *Pinus mugo* scrub (Chytrý et al., 2010).

Along with natural disturbances, such as snow avalanches and debris flows, the area has been significantly affected by anthropogenic activities since the Early Middle Ages. Prior to the beginning of the 19th century, anthropogenic activities mainly included deforestation, grazing, and grass mowing (Lokvenc, 1995). During the 19th and 20th centuries, tourism (and later, winter sports) became a more important source of income compared to farming, which rapidly declined. Since the 1960s, when an area was converted into a strictly protected nature reserve, almost no direct human management (e.g. farming, logging) was practiced in the tundra zone. At the same time, however, tourist pressure has intensified, severely disturbing tundra vegetation (Müllerová et al., 2011).

Recently, a spread of three native grass species *Molinia caerulea*, *Calamagrostis villosa* and *Deschampsia cespitosa* at the expense of a common, less competitive dominant grass *Nardus stricta* has been recorded in the area (Hejcman et al., 2009, 2010). Furthermore, the native dwarf pine (*Pinus mugo*) has also expanded in the area formerly dominated by *Nardus stricta* (Harčarik, 2007; Štursa and Wild, 2014;

Potůčková et al., 2021). However, these changes and developments were neither explicitly documented, nor systematically monitored at broader scales.

The study area is located in the eastern part of the Krkonoše Mountains in a strictly protected zone of the National Park (Figs. 1 and 2). A permanent research plot of 100 × 100 m was established at the Bílá louka meadow (yellow square in Fig. 1). The plot covers the representative stands of all grass species of interest. The UAV hyperspectral and multispectral data were acquired and analyzed within this plot. Additionally, we analyzed the PlanetScope satellite data in a wider area of interest of 352 ha, which is mostly covered by grasslands (marked in red in Fig. 1).

2.2. Image data and their preprocessing

Data of different spectral and spatial resolutions from 2018 (PlanetScope satellite data) and 2019 (UAV data) were used in this study (see Table 1 and Fig. 3). The reason for using consecutive years was the lack of cloud-free satellite imagery in 2019. Vegetation changes in this area are very slow; the use of data from two consecutive years is therefore appropriate.

Seven cloud-free PlanetScope satellite (PS) images from different dates during the growing season in 2018 that cover the wider area of interest were downloaded for free (in the framework of Planet Education and Research Program) from <https://www.planet.com/explorer/> as 3B level products (Analytic Surface Reflectance Ortho Scene Product) and clipped by the border of the wider area of interest. Products of this level are geometrically, radiometrically and atmospherically corrected and transformed into a WGS84 coordinate reference system (Planet Labs, 2020).

The UAV sensing was performed in June, July, and August 2019. The hyperspectral (HS) UAV images were collected using a Headwall NanoHyperspec® camera mounted on a DJI M600 Pro UAV. The multispectral (MS) UAV images were acquired by an MS camera (MicaSense RedEdge M) in combination with an RGB camera (Sony A7 ILCE-7) mounted on a DJI M600 Pro UAV. The basic characteristics of all the data are summarized in Table 1.

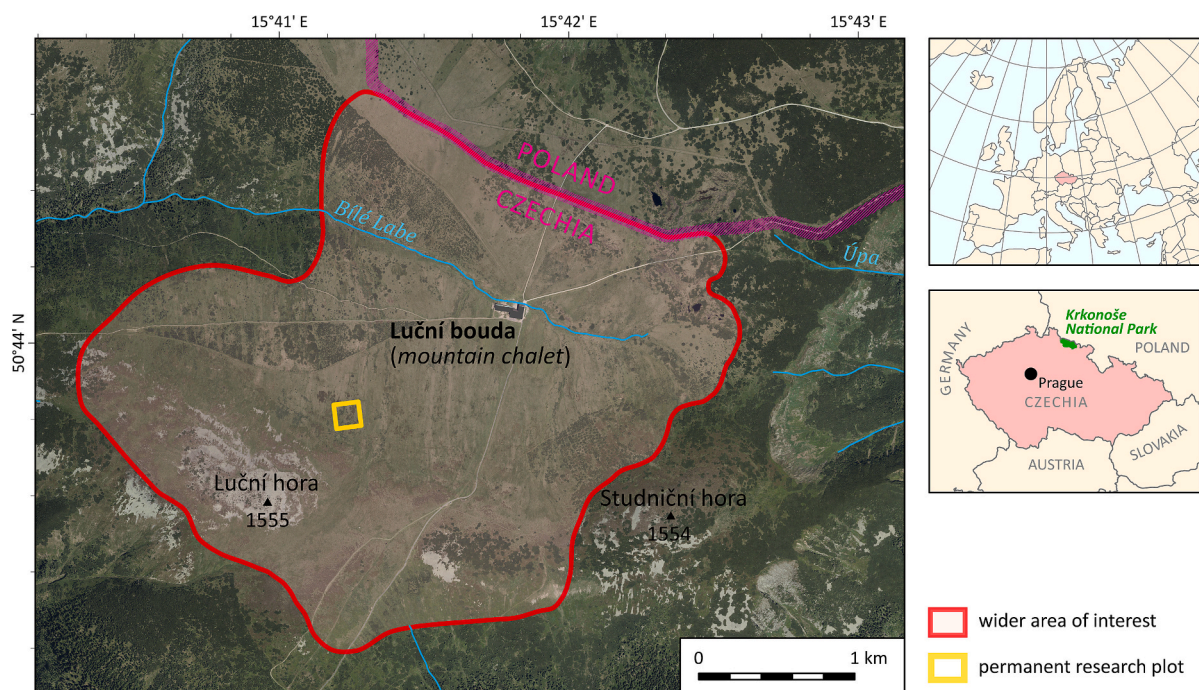


Fig. 1. Location of study areas in the Krkonoše Mts, Czechia. Within the wider area of interest analysis of PlanetScope data was performed, while for permanent research plot UAV data were acquired and analyzed. Source of orthophoto: ČÚZK (<https://1url.cz/YKUzd>).



Fig. 2. The overall view of the eastern tundra of the Krkonoše Mts. (left – red dot shows location of Bílá louka meadow), and detailed view of Bílá louka permanent research plot (right). Source: Martin Lukeš (left), Lucie Kupková (right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Parameters of used imagery.

Data type	Platform and sensor	Dates of acquisition	Spectral resolution	GSD
PlanetScope MS data (PS)	Dove satellites Bayer-masked CCD camera	2018 June 7 July 7 and 22 August 7, 20 and 27 September 10	4 bands	3 m
UAV hyperspectral data (UAV HS)	UAV DJI M600 Pro Headwall Nano-Hyperspec® camera	2019 June 14 July 11 August 15	270 bands	3 cm
UAV multispectral data (UAV MS)	UAV DJI M600 Pro MicaSense RedEdge M and RGB camera Sony A7 ILCE-7	2019 June 14 July 10 August 14	8 bands	3 cm

The hyperspectral data cube consisted of 270 bands with wavelengths ranging from 400 to 1000 nm and a GSD of 3 cm. Radiometric and geometric preprocessing was performed in SpectralView - Hyperspec (version 3.1.0. Headwall Photonics®). A portable 3 m × 3 m fabric target placed in the scanned area (Group 8 Technology, Inc., Provo, UT, USA) was used for radiometric corrections.

As for geometric correction, the cubes were merged into flight lines based on GNSS and IMU records collected during the flight. A 1 m raster digital terrain model derived from airborne laser scanning data acquired in 2012, and supplied by the Krkonoše National Park Administration, was used for orthorectification. Nevertheless, the positional accuracy of the flight lines orthorectified in SpectralView – Hyperspec software was unsatisfactory due to the low accuracy of GNSS and IMU (the RMSE on the check points was 1.74 m). Further processing was therefore carried out in ArcGIS for Desktop software (version 10.7.1 (c)1999–2019 Esri Inc.) and included the following steps. First, adjustment of each flight line was performed using 10–12 control points manually selected in the orthophoto taken from the drone by Sony A7 ILCE-7 camera on a date close to the hyperspectral data acquisition (± 1 day). Control points well recognizable in both reference (Sony) and hyperspectral orthoimages were used. Considering the irregularity of geometric distortions in orthoimages obtained from the SpectralView software, a spline transformation was applied. Second, a conversion of the 32-bit data to 16-bit data was applied to reduce the size of the resulting file. In this step, reflectance values from the interval (0,1) were converted to an integer

value with the interval (0,10,000) by multiplying by 10,000 and rounding. Finally, the orthorectified flight lines were mosaicked in ArcGIS for Desktop using a script that we developed. The script used the standard Mosaic To New Raster function, which was applied to individual flight lines. The order of the mosaicking for the lines was determined by the order in which they were flown, or determined while manually collecting the control points so that the resulting raster value was based on the line with the better radiometry. In order to preserve maximum radiometry, we resampled the data using the nearest-neighbor method without color balancing. The final horizontal accuracy (quantified as Root Mean Square Error) on nine check points measured with an RTK-GNSS receiver varied from 6 to 14 cm. For further details see Červená et al. (2020a).

As for spectral resolution to mitigate the problem of multicollinearity, we tested three methods to evaluate the potential for elimination of redundant information and noise in the hyperspectral data. First, we analyzed the spectrum using spectral resampling based on calculating inter-band correlation (Adjorlolo et al., 2013). According to the results of the spectrum analysis (for further details see Appendix A1), each five neighboring bands were aggregated resulting in 54 bands. The spectral resampling was performed in ENVI software (version 5.5 (c) 2018 Harris Geospatial Solutions, Inc.). Using band center wavelengths, ENVI assumes critical sampling and uses a Gaussian model with a full width at half maximum (FWHM) equal to the band spacings for the resampling (L3HarrisGeospatial, 2022).

Further, Minimum Noise Fraction (MNF) transformation was performed. According to the recommendation from Kupková et al. (2017), different numbers of MNF bands were classified and evaluated and, finally, the best performing MNF transformations were used, as shown in Fig. 7. Also, Principal Component Analysis (PCA) was tested, but classification results of PCA outputs (using various numbers of principal components) were not good (in most cases the overall accuracy was about 10 percentage points lower than when MNF was applied). Therefore, we ultimately did not use PCA outputs for classifications.

The UAV MS data comprised a combination of MicaSense RedEdge M camera (blue, green, red, red edge and near-infrared bands, 3 cm GSD) and Sony A7 ILCE –7 camera (red, green and blue bands, 2 cm GSD). The data preprocessing was performed in Agisoft Metashape Professional (© Agisoft). Radiometric calibration was performed based on the calibration panels (automatic detection of the panel captured in the image). Ground control points (GCPs) were used for georeferencing of the RGBMS images. Four GCPs (black and white chessboard-like signals 30 × 30 cm placed in the corners of the area) were measured with the geodetic RTK-GNSS receiver (mean position error = 0.008 m). The GCPs were marked on all RGB images, and the parameters of the interior and

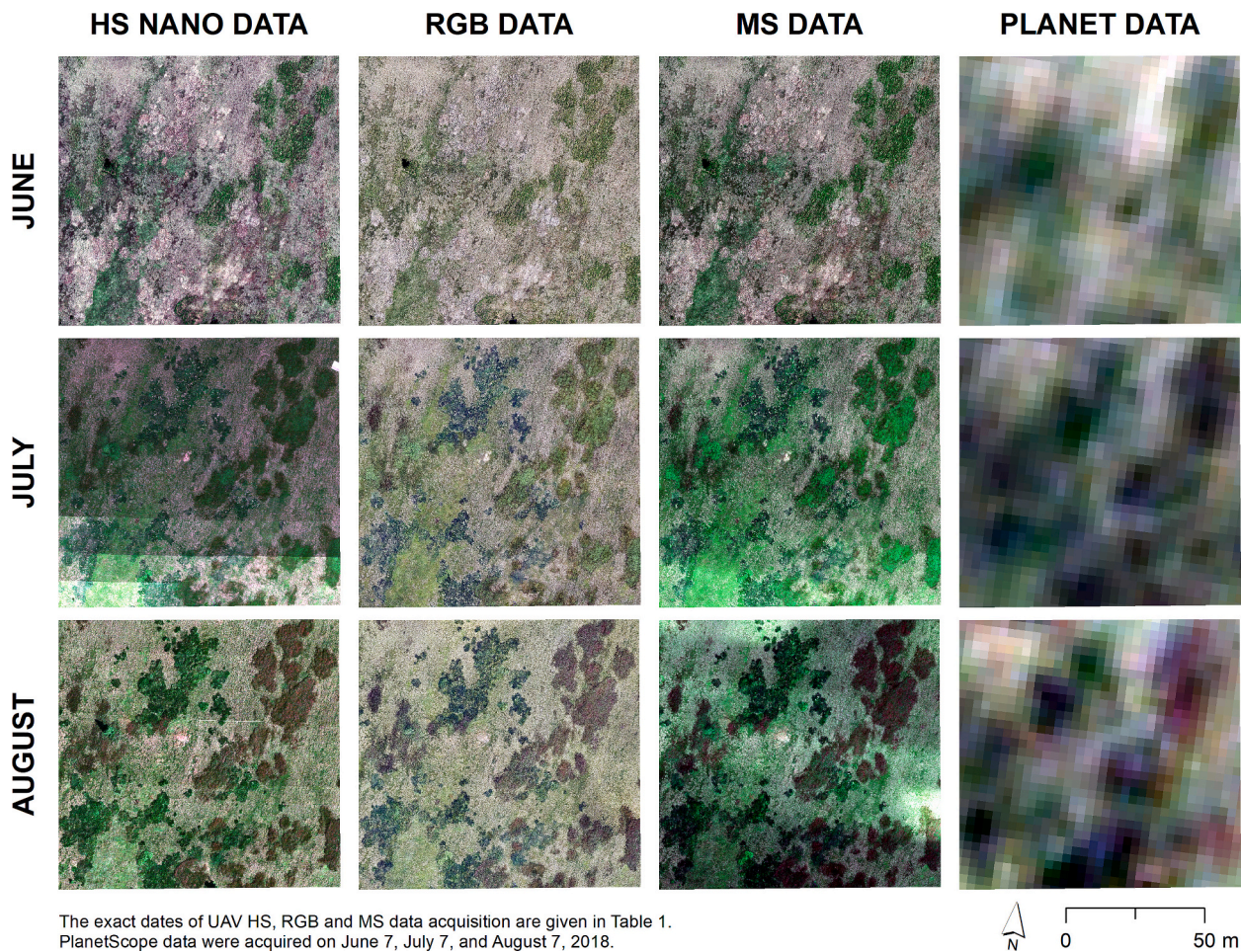


Fig. 3. Image data of Bělá louka meadow from RGB composites of hyperspectral camera Headwall Nano-Hyperspec®, RGB camera Sony A7 ILCE-7, multispectral camera MicaSense RedEdge M and PS satellite data.

exterior orientations were derived by bundle adjustment. The average position error of the GCPs was <5 cm. The final mosaics with GSD of 3 cm comprised both the RGB data (from the Sony camera) and MS data (from the MicaSense camera).

The classifications were performed for mono-temporal images (for all individual dates of PS, UAV MS, and HS data - see Table 1). Then, multi-temporal composites were created in ENVI (version 5.5 (c) 2018 Harris Geospatial Solutions, Inc.) using the *layer-stacking* function, and classifications were performed for multi-temporal composites listed in Fig. 7.

2.3. Classification scheme

The classification scheme for PS data includes four categories of dominant grass species, one originally common species (*Nardus stricta*, NS), and three currently expanding grasses: *Calamagrostis villosa* (CV), *Molinia caerulea* (MC) and *Deschampsia cespitosa* (DC) (Fig. 4). For UAV data with substantially higher spatial resolution, additional species with sparse growth on the permanent research plot - *Avenella flexuosa* (AF), *Carex bigelowii* (CB) and *Picea abies* (PAb) - were classified (Fig. 5). From Figs. 3 and 4, the phenological changes during the season are clearly observed. For example, CV starts to grow rather early in the season, while MC is at full biomass only in the second half of the summer. Some species (particularly CV) have distinct leaf color during senescence.

2.4. Reference data

The field data for the PS classifications (wider area of interest, Fig. 1)

were collected during the summers of 2015, 2016, and 2017 by using a Trimble GeoExplorer 3000 GeoXT GNSS system (position accuracy ~10 cm). The botanical data were selected in the field by botanists to representatively (spatial distribution, abundance) cover the whole wider area of interest. A set of 97 polygons was overlaid on the orthophoto from 2018 and edited to ensure that all polygons reliably represent the predetermined categories (clean pixels in the centers of reliably identified patches of the species were selected). We used 43 randomly selected polygons distributed within the study area for the training, while 54 polygons were used for validation. For the specific numbers of training and validation data, see Table 2.

For the UAV data classification, 226 polygons were collected in 2019 within the permanent research plot using GPS (with positional accuracy on the order of centimeters). The polygons were collected in the center of homogeneous patches of individual species to avoid a collection of mixed pixels at the edges. Furthermore, 76 polygons were applied for the training, and 150 polygons were utilized for the validation. The proportion of training and validation data was determined based on our previous research, which had demonstrated that the best classification results can be achieved by using <50% of the field data for training and > 50% of the data for validation purposes (Potočná, 2019). Table 3 shows the number of training and validation data used for the UAV imagery. A limited reference dataset was collected for CB and AF due to their sparse occurrence in the permanent research plot. But it was important to classify these species because the classification tests showed that the accuracy would decrease, if we excluded them from the classification scheme.

Prior to classification, we evaluated the separability of the training

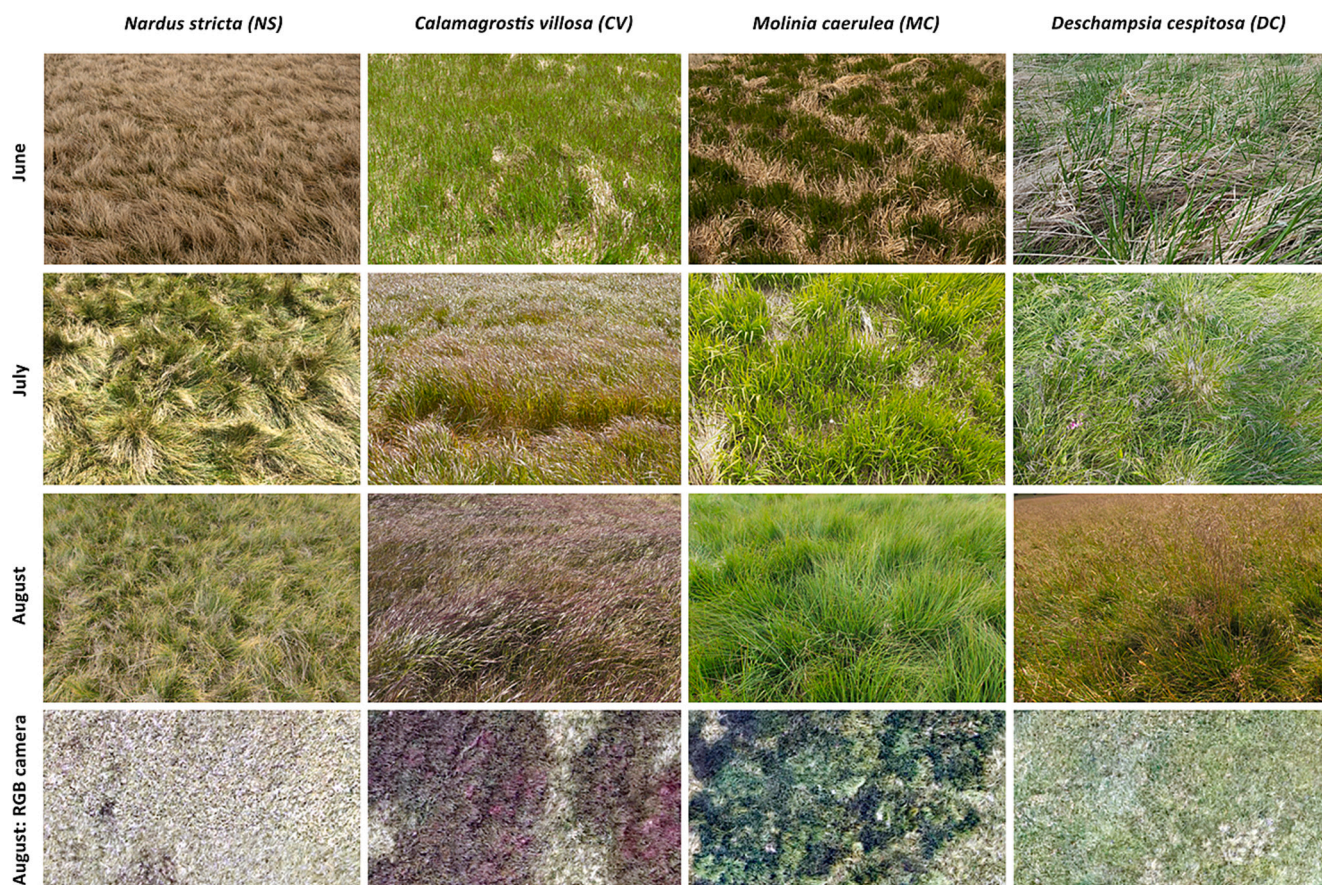


Fig. 4. Dominant grass species (*Nardus stricta*, *Calamagrostis villosa*, *Molinia caerulea* and *Deschampsia cespitosa*) classified from PS and UAV data and their phenological changes during the growing season (in the dates of acquisition in June, July, and August).



Fig. 5. Additional species classified from UAV data (*Avenella flexuosa*, *Carex bigelowii* and *Picea abies*).

samples for all types of data in ENVI (version 5.5 (c) 2018 Harris Geospatial Solutions, Inc.) using the Jeffries-Matusita distance and transformed divergence. The analysis confirmed that classification at the species level was possible, though some classes were more difficult to

separate than others. The main results of this evaluation can be found in the Appendix A2.

Table 2

Training and validation dataset – PS data (wider area of interest).

Classified species	Number of polygons		Area of polygons (m ²)	
	Training	Validation	Training	Validation
<i>Nardus stricta</i>	15	16	4752	6237
<i>Calamagrostis villosa</i>	7	13	2691	2673
<i>Molinia caerulea</i>	11	14	2754	3609
<i>Deschampsia cespitosa</i>	10	11	2403	2439

Table 3

Training and validation dataset – UAV data (permanent research plot).

Classified species	Number of polygons		Area of polygons (m ²)	
	Training	Validation	Training	Validation
<i>Nardus stricta</i>	13	25	60.4	85.4
<i>Calamagrostis villosa</i>	15	30	156.8	148.2
<i>Molinia caerulea</i>	17	33	142.3	184.8
<i>Deschampsia cespitosa</i>	13	27	84.4	113.5
<i>Avenella flexuosa</i>	8	15	13.3	15.8
<i>Carex bigelowii</i>	7	14	3.7	3.5
<i>Picea abies</i>	3	6	2.9	1.1

2.5. Creation of mask for PS images

As we focused on the mutual discrimination of the four dominant grass categories in PS imagery (wider area of interest), a mask was created to mask out other vegetation and non-vegetation categories (see Fig. 6). After several unsuccessful tests for creating the mask by using unsupervised classification and/or vegetation indices, the area covered by target grass categories was extracted by using the classification output of the APEX image developed in our previous work (with OA 82.6%) (Kupková et al., 2017) for a larger study area. The mask was further improved by manual editing, based on NDVI (Normalized Difference Vegetation Index), retrieved from the PS images on August 7, 2018, and the aerial orthoimagery from 2018 (residual pixels of water areas, other vegetation categories, block fields, and anthropogenic areas were masked out). The final area remaining for classification after applying the mask was 250 ha.

2.6. Methods used for the data analysis

Based on the existing literature (Pande-Chhetri et al., 2017; van Iersel et al., 2018; Marcinkowska-Ochtyra et al., 2018a; Liu et al., 2021) and our own experiences (Kupková et al., 2017; Suchá et al., 2016) we tested a wide range of classification methods. Those yielding low accuracies (e.g. pixel-based classifiers Support Vector Machine, Random Trees in ArcMap) were excluded. We present and compare results of three best performing supervised classification algorithms - Maximum Likelihood (MLC) and Random Forest (RF) classifiers (both pixel-based), and object-based image analysis (OBIA) combined with a Support Vector Machine (SVM) classifier (Fig. 7). The MLC and OBIA SVM were performed in ENVI (version 5.5 (c) 2018 Harris Geospatial Solutions, Inc.), while RF classification was performed in the R software (version 3.5.3 (c) 2020; The R Foundation for Statistical Computing). For the PS and UAV data, the classifications were performed separately for all the dates of mono-temporal image data acquisition, as well as for multi-temporal composites (see Fig. 7).

In the case of the MLC classifier (Richards and Jia, 2006), the only parameter that can be modified is the probability threshold. The default zero value for the probability threshold was used, as we intended to classify all the image pixels and to have continuous classification output.

For RF classification (Belgiu and Drăgut, 2016; Breiman, 2001; Gao et al., 2015) in R software, we used the ‘randomForest’ package (Liaw and Wiener, 2002). The RF classifier was evaluated by using different combinations of two input parameters: the number of trees (*ntree*) and

the number of input variables (features) randomly sampled at each split (*mtry*). We tested various values of *ntree*, and the best results were achieved for the *ntree* value of 1000. The performed tests of *mtry* values showed that the default *mtry* value worked best for the PS and UAV HS data, as we achieved the lowest Out-of-Bag (OOB) error rates for the default *mtry* values. In the case of UAV MS data (multitemporal composite from July and August), the OOB error rate was slightly higher for a different *mtry* value than for the default value (specifically, for the default *mtry* value of 11, OOB error rate was 1.43, while for *mtry* = 13, the OOB error rate was 1.38). However, the overall classification accuracy differed just slightly (in favour of *mtry* = 13) and, after rounding, was the same for the classification outputs obtained for both (i.e. 11 and 13) *mtry* values.

Besides the spectral features (retrieved from the original/transformed bands), other input variables were examined as well (textural features, NDVI, topographic variables). The finally used input variables were the spectral features retrieved for all classified bands. Further, we used also standard textural features (mean texture, variance, homogeneity, contrast, dissimilarity, entropy, second moment) (Haralick et al., 1973) calculated by using the Gray-Level-Co-Occurrence Matrix (GLCM) in ‘glcm’ R package (Zvoleff, 2020) with window size of 3 × 3 pixels and default settings of other parameters. These variables were selected based on the values of importance score.

Many studies have applied OBIA to classify vegetation using VHR imagery (Blaschke, 2010; Kupková et al., 2017; Salas et al., 2016). In this study, we implemented the segmentation algorithm, which calculates a gradient map for the digital image in ENVI (L3HarrisGeospatial, 2021). The segmentation was performed using all available spectral bands. The SVM classification algorithm with a Kernel-type radial basis function (RBF) was used. The SVM algorithm was selected based on a comparison of classification accuracies gained from all available classifiers in ENVI Feature Extraction module. The other classifiers (i.e. K Nearest Neighbor and PCA) provided significantly lower overall classification accuracies (over 5 percentage points). We also tested all available Kernels for the SVM classifier in ENVI. Linear and Sigmoid Kernels performed worse in comparison with polynomial and RBF Kernels. Differences between polynomial and RBF Kernels were small. In accordance with L3HarrisGeospatial (2022) and Marcinkowska-Ochtyra et al. (2017) who elaborated detailed tests of SVM Kernel-types, we found that the RBF Kernel works well, in our case best.

Spectral and also textural parameters, based on the GLCM were applied in OBIA for effective delineation of the spectrally similar grass categories. The experiments indicated the best Scale Level, Merge Level and Texture Kernel parameters for individual data types, as shown in Table 4.

2.7. Evaluation of classification accuracy

The evaluation of the classification accuracy for PS was based on all pixels within the collected validation polygons (Table 7). For the validation of UAV data classifications, 3393 points were randomly generated within the 150 validation polygons and were stratified according to the area of the collected field data for each category. This approximately corresponds to the proportion of the individual categories in the permanent research plot. The number of validation points was calculated based on the equation from Foody (2009):

$$n = \frac{Z_{\alpha/2}^2 P(1 - P)}{h^2} \quad (1)$$

with the two-tailed significance level $\alpha = 0.02$, the critical value of the normal distribution for the given two-tailed significance level $Z = 2.33$, the planning value for the population proportion $P = 0.5$, and the half width of the desired confidence interval $h = 0.02$. The minimal count of points for the least abundant categories was set to 50. The points were generated as pixel centroids with a minimal distance between points of

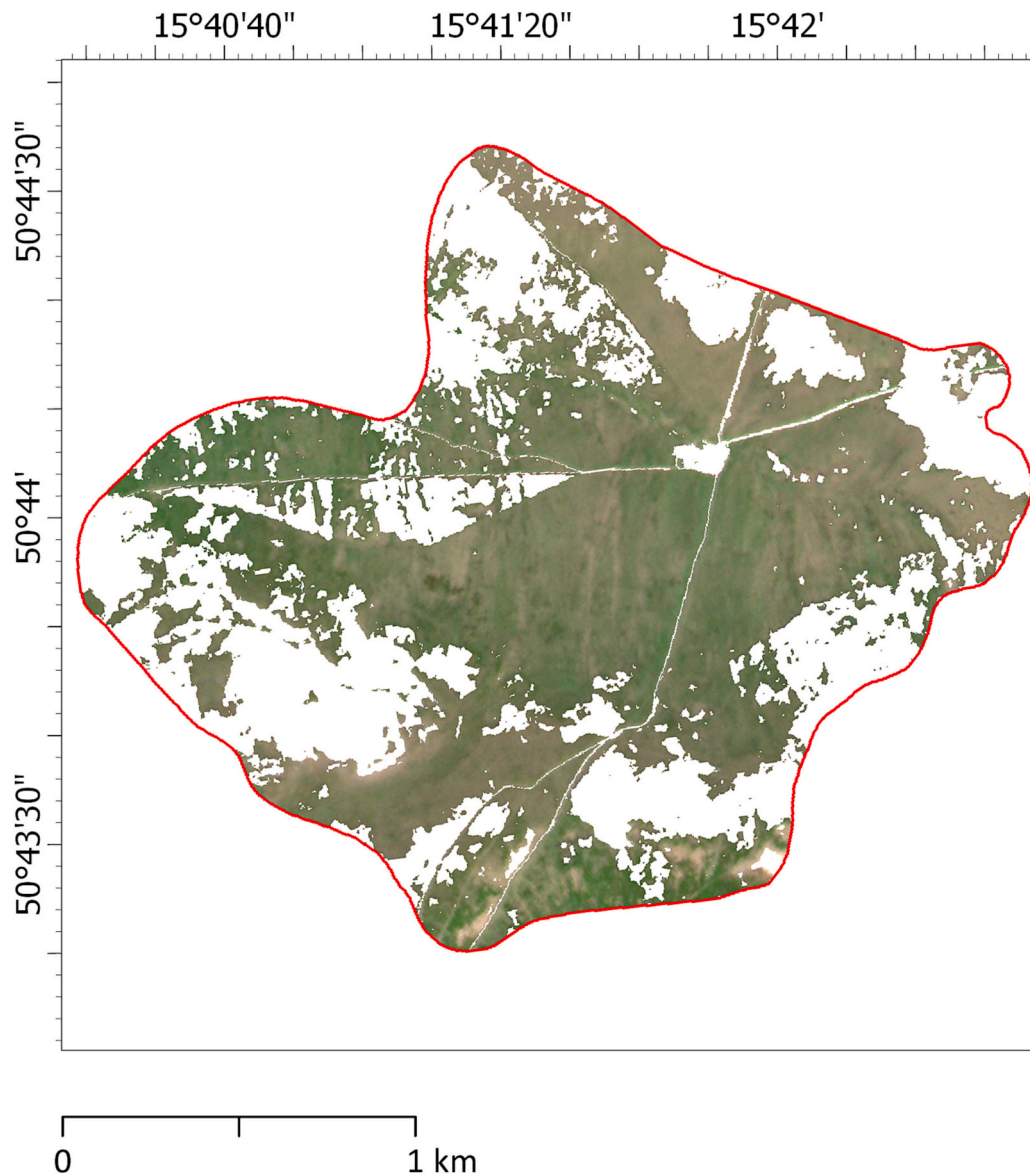


Fig. 6. Wider area of interest overlaid with a mask (in white).

13 cm. To ensure that the two approaches were comparable, we evaluated both validation methods on UAV data, and the results were similar. The number of validation pixels for each category is shown in Table 5.

The classification accuracy was evaluated in ENVI (version 5.5 (c) 2018 Harris Geospatial Solutions, Inc.) by using a confusion matrix, based on ground truth, and the overall accuracy (OA), Producer's (PA) and User's accuracy (UA) for different categories were derived (Jensen, 2005). Since the two components of accuracy (PA and UA), often markedly differ for the same species and approach, we also used the F1-score (Goutte and Gaussier, 2005), which is the harmonic mean of Producer's accuracy and User's accuracy.

2.8. Assessment of the spatial consistency of UAV classification outputs

We propose two measures that can be used for spatial accuracy assessment of thematic classification outputs. The assessment is based on the assumption that the classification reliability of a given category increases if it is detected/classified at the same location by more than one classifier. The total spatial accuracy is then greater with a larger area of all classified categories detected/classified at the same location by a larger number of classifiers.

In our case, we compare the spatial distribution of classified categories in various classification outputs of the UAV MS and UAV HS data for the permanent research plot. The first step of the assessment is a spatial overlay of two or three different classifications outputs. We overlaid and compared outputs from different classifiers for MS and HS data respectively, and also outputs of MS data with outputs of HS data classifications. Maps of overlaps were created, and the following measures were calculated:

1) *The matching area of the given category* (MA_C, in %) in the two different classification outputs was calculated as follows:

$$MA_C = M_{12} / (A_1 + A_2 - M_{12}) \cdot 100 \quad (2)$$

where MA_C: matching area of the category in both classification outputs, M₁₂: area of spatial match in both classification outputs, A₁: area of category classified in first classification, A₂: area of category classified in the second classification (overlaid classification outputs must have the same spatial extent).

2) *The total matching area* (TMA) of all categories in two (or more) different classification outputs.

(in %) was calculated as follows:

Area of interest	Meadows of eastern tundra (250 ha) wider area of interest	Bílá louka meadow (1 ha) in eastern tundra permanent research plot	
Legend	<i>Molinia caerulea</i> , <i>Calamagrostis villosa</i> , <i>Nardus stricta</i> , <i>Deschampsia cespitosa</i>	<i>Molinia caerulea</i> , <i>Calamagrostis villosa</i> , <i>Nardus stricta</i> , <i>Deschampsia cespitosa</i> , <i>Avenella flexuosa</i> , <i>Carex bigelowii</i> , <i>Picea abies</i>	
Training data	43 polygons collected in the field 2014-2017 edited based on orthophoto from 2018	76 polygons collected in the field in 2019	
Image data	Satellite MS PlanetScope	UAV HS Headwall Nano-Hyperspec	UAV MS MicaSense RedEdge M and Sony A7 ILCE-7
Mono-temporal (1-date) images used for classification	7 images from 2018 (4 bands each image) 6/7, 7/7, 7/22, 8/7, 8/20, 8/27, 9/10	3 images from 2019 (54 bands each image) 6/14, 7/11, 8/15 3 MNF images (9 bands each image) 6/14, 7/11, 8/15	3 images from 2019 (8 bands each image) 6/14, 7/10, 8/14
Multi-temporal composites used for classification	2-date 7/7, 8/7 3-date 6/7, 7/7, 8/7 4-date 6/7, 7/7, 7/22, 8/7 5-date 6/7, 7/7, 7/22, 8/7, 8/20 7-date 6/7, 7/7, 7/22, 8/7, 8/20, 8/27, 9/10	2-date 7/11, 8/15 2-date MNF 7/11, 8/15 3-date 6/14, 7/11, 8/15 3-date MNF 6/14, 7/11, 8/15	2-date 7/10, 8/14 3-date 6/14, 7/10, 8/14
Pixel-based classification	MLC, RF		
Object-based classification	SVM		
Validation data	54 polygons collected in the field 2015-2017 edited based on orthophoto from 2018	3393 points generated from 150 polygons collected in the field in 2019	

Fig. 7. Data processing chart.

Table 4

Best performing parameters used for OBIA classification.

	PS*	UAV HS data**	UAV MS data
Scale Level	15	50	20
Merge Level	30	90	60
Texture Kernel	3	5	5

* For all temporal composites except for 2-date composite, in this case, combination 10, 20, 3 performed best.

** Except for composite July/August - in this case, combination 20, 60, 5 performed best.

$$TMA = (MA/TA) \cdot 100 \quad (3)$$

where TMA: total matching area; MA: matching area of all categories in all evaluated classification outputs; TA: total area of classification outputs (the overlaid classification outputs must have the same spatial extent).

Table 5

Number of validation points/pixels.

Classified species	Number of validation pixels	
	UAV data	PS data
<i>Nardus stricta</i>	475	693
<i>Calamagrostis villosa</i>	1005	297
<i>Molinia caerulea</i>	1071	401
<i>Deschampsia cespitosa</i>	646	271
<i>Avenella flexuosa</i>	96	
<i>Carex bigelowii</i>	50	
<i>Picea abies</i>	50	

3. Results

3.1. Overall accuracy

The study considered three different data types with various spatial, temporal, and spectral resolutions, and therefore, the results varied. Despite these differences, general trends were discerned for both the data type and the classifiers. The accuracy increased with increasing spatial resolution, and the ultra-high spatial resolution data of the UAV brought very good OA > 90% (Table 6). The coarser satellite data of PS

Table 6

Best overall accuracies (OA, in %) for UAV MS and HS data (permanent research plot). The best results for HS and MS data are highlighted in bold.

Temporal resolution	Parameters	UAV HS data			UAV MS data		
		MLC	RF	OBIA SVM	MLC	RF	OBIA SVM
Mono-temporal	OA	87.4**	<u>90.1</u>	<u>91.5</u>	83.6	<u>90.4</u>	<u>94.0</u>
	month	July	July	August	July	July	July
	OBIA parameters*			50, 90, 5			20, 60, 5
July, August	OA	91.1	93.7	94.6	92.6	<u>92.7</u>	<u>95.9</u>
	OBIA parameters*			20, 60, 5			20, 60, 5
June, July, August	OA	<u>92.7**</u>	<u>93.7</u>	<u>95.6</u>	<u>93.8</u>	92.6	95.3
	OBIA parameters*			50, 90, 5			20, 60, 5

Notes for Table 6:

1) * OBIA classification parameters: first value: scale level, second value: merge level, and third value: texture kernel size.

2) ** All best OAs for UAV HS data except those marked by ** were obtained for data transformed by MNF.

3) Underlined are best classification outputs that were further used for the assessment of spatial consistency (refer to the chapter 3.3).

performed with maximum OA = 82.1% (Table 7). As for the temporal resolution, the multi-temporal composites outperformed the mono-temporal data in all cases. We also identified the best time window during the peak of the growing season - the best OAs were recorded in most cases for images from July. As for the algorithms, the results strongly depend on the spatial resolution of the data. We found that the OBIA approach, coupled with the SVM classifier was the most powerful for the ultra-high spatial resolution UAV data, whereas for the coarser PS satellite imagery, both pixel-based classifiers remarkably outperformed OBIA.

More specifically, the highest OA (95.9%) was achieved for the July/August composite of the UAV MS data, followed by the June/July/August composite of the UAV HS data (95.6%), where the OBIA SVM was used in both cases (Table 6). For the PS data, the highest OA (82.1%) was found for the June/July/August composite using the RF classifier (Table 7). As for individual months, July was the most successful followed by August.

The benefit of adding the temporal dimension (second date) into the classification was apparent in the case of both UAV data types, but adding the third date did not yield such a large additional increase in OA (Fig. 8). Moreover, for the UAV MS data, we achieved relatively good results for the mono-temporal OBIA SVM classification (OA only 2 percentage points lower compared to the multi-temporal composite). For the PS the best results were shown for the June/July/August composite irrespective of the classifier, adding more dates did not improve the accuracy (Fig. 9).

Figs. 10 and 11 show the best classification outputs for each data type. Fig. 10 directly compares the results of UAV HS (composite of June/July/August) and MS (composite of July/August) classification using the OBIA SVM. Although the spatial distribution of the species with high density (*NS*, *CV*, *MC*, and *DC*) is very similar, some differences are visible for the species of low density (*AF* and *CB*). Fig. 11 presents the best classification output for the PS data obtained using the RF classifier.

Table 7

Best overall accuracies (in %) for PS data (wider area of interest). The best result is highlighted in bold.

Temporal resolution*	OA	OA	OA OBIA	OBIA SVM
	MLC	RF	SVM	Parameters**
1-date	71.7	71.2	69.5	15, 30, 3
2-date	72.1	75.6	66.5	10, 20, 3
3-date	77.0	82.1	70.4	15, 30, 3
4-date	67.0	74.3	66.9	15, 30, 3
5-date	66.4	75.3	63.5	15, 30, 3
7-date	74.6	80.8	68.0	15, 30, 3

* For exact dates and their combinations refer to Fig. 7. ** OBIA classification parameters: first value: scale level, second value: merge level, and third value: texture kernel size.

3.2. Individual species

The results show high accuracies for most species, >95% for the UAV data, and above 80% for the coarser PS data. The UAV data analysis (Table 8 and Fig. 12) exhibited excellent results. In particular, the values of >99% were reported for UA or PA and > 96% for F1-score, for the following species: *CV* (both PA and UA of composites July/August for both MS and HS UAV data, June/July/August composite of MS data), *DC* (PA of June/July/August composite for HS data); *MC* (UA of mono-temporal and both multi-temporal composites for MS data, and June/July/August composite for HS data). Slightly lower, but still very good, values were found for *NS*.

Considering best PAs and UAs of the four dominant grass species, there was only a slight difference between the MS and HS UAV data (Fig. 12). Larger differences were found for the two remaining species, classified with considerably lower accuracies of ~60% for *AF* and as low as 48.0% UA for *CB*. For the F1-score, the MS multi-temporal composites generally had better results, but the differences for the dominant species were not significant, compared with the HS multi-temporal composites.

For the PS data (Table 9), the accuracies of the four dominant grass species were lower than for the UAV data. However, with respect to the differences in spatial resolution (3 cm for UAV and 3 m for PS), they can be deemed satisfactory. The highest values were identified for *NS* (UA 90.2%, F1-score 85.1) and *CV* (UA 88.9%, F1-score 84.8%). *MC* exhibited slightly lower F1-score but best PA was rather high (89.2%). *DC* had lower value of best individual PA and markedly lower value of the F1-score (71.8%).

For UAV data, OBIA was found to be the best classifier and temporal composites consisting of images from July and August (7, 8) and June, July, and August (6, 7, 8) brought best results. For PS, OBIA yielded the lowest accuracy, with RF being the best performing classifier. 3-date and in several cases also 7-date composites provided best results.

As for the most suitable month for individual species classification, the best average F1-score (average across all classifiers) for UAV data was achieved for all species in July. In comparison with other months, *NS* was classified significantly worse in June and August (F1-score of >10 percentage points lower than in July), for *CV* August was the second-best month (F1-score of 5 percentage points lower than in July). We obtained similar results in case of *MC*, *DC*, *AF* and *CB* for June and August. The best results for individual species classified from PS data were also achieved for the data from July. However, for individual species, the multi-temporal composites outperformed in general the mono-temporal data. The benefit of the multi-temporal dimension is apparent in case of the poorly classified species of *AF* and *CB* (UAV data). For further detailed comparison of the results for mono-temporal and all multi-temporal composites for individual species see Appendix A3.

3.3. Spatial consistency/reliability of the UAV classification outputs

Our assessment of the consistency/reliability of the UAV MS and HS

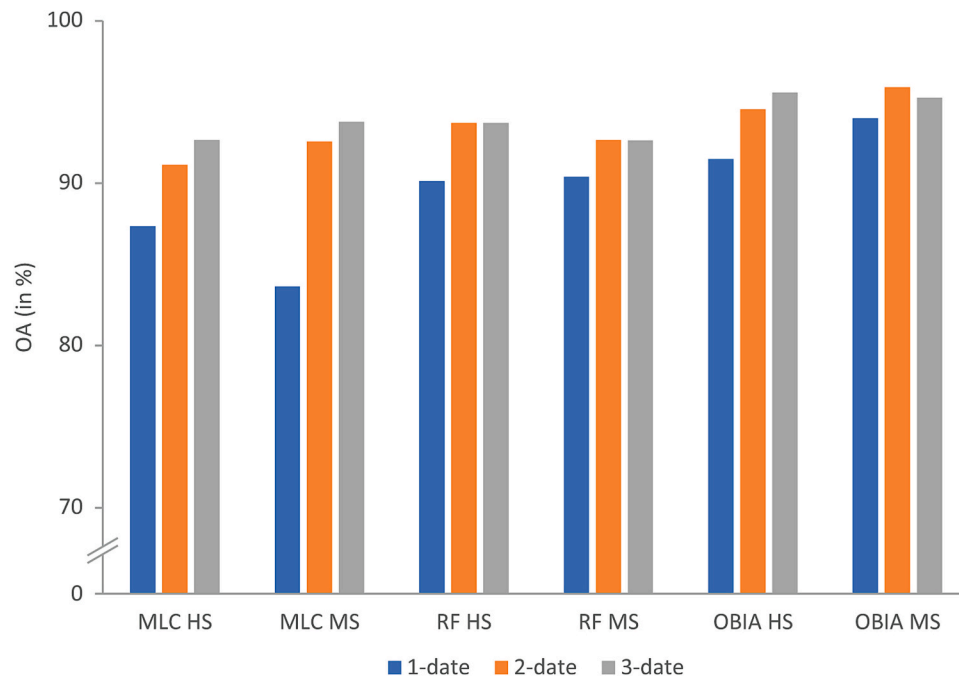


Fig. 8. Comparison of OAs for UAV mono-temporal and multi-temporal data using MLC, RF, and OBIA SVM classifiers (permanent research plot). Note: For the exact dates of images that create multi-temporal composite refer to Fig. 7.

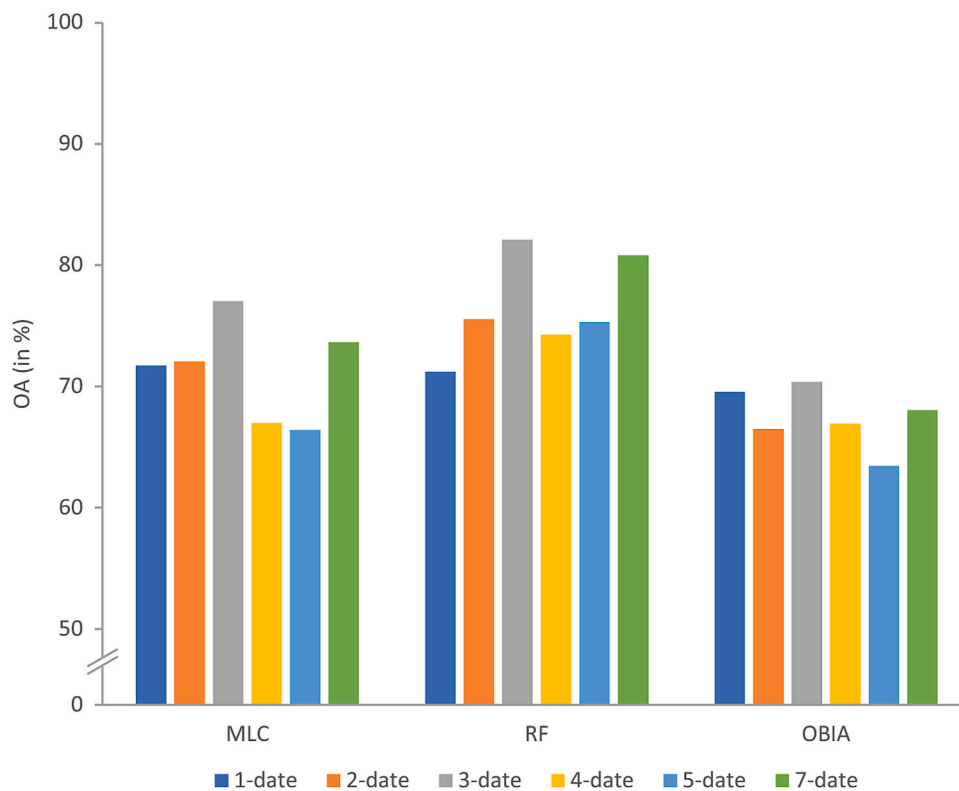


Fig. 9. Comparison of OAs reached for PS mono-temporal data and multi-temporal composites using MLC, RF, and OBIA SVM classifiers (wider area of interest). Note: For the exact dates of images that create multi-temporal composite refer to Fig. 7.

data classification outputs was based on spatial overlays. We analyzed the spatial match of the classified categories for various (two or three) classification outputs with high OAs (those underlined in Table 6). The consistency in the classified area of all the categories, expressed by total matching area (TMA) – Eq. (3) – for the selected outputs is shown in

Fig. 13.

The best agreement between the multi-temporal MS and HS data was discerned when both data types were classified using the OBIA SVM (TMA 82.9%) and RF (TMA 82.8%) (Figs. 13 and 14). The results were also highly consistent for the same type of multi-temporal data and

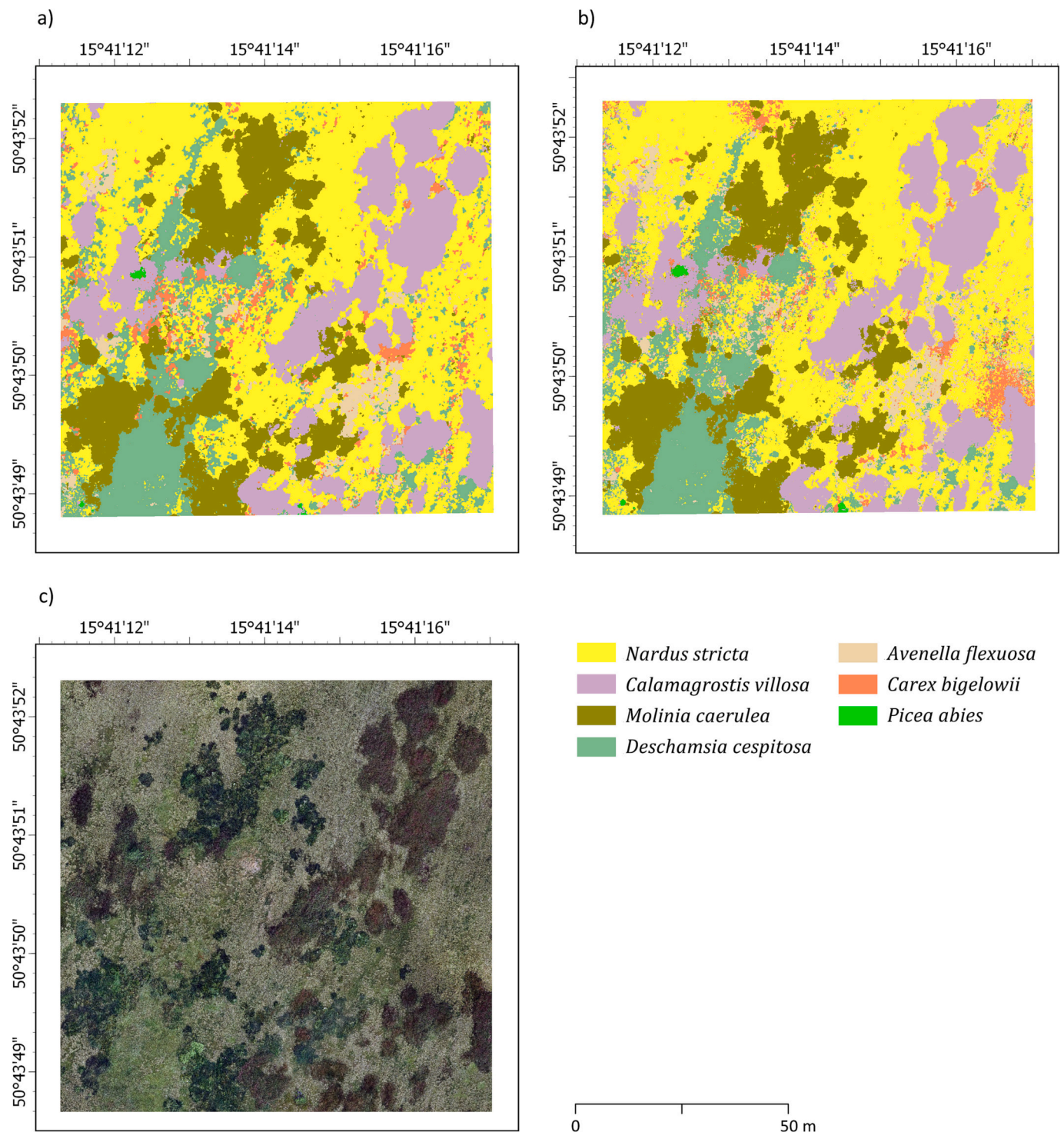


Fig. 10. Best classification for (a) UAV HS data – multi-temporal composite June/July/August (27 MNF bands), OBIA SVM classifier, (b) MS data – multi-temporal composite July/August (16 bands), OBIA SVM classifier (permanent research plot). Fig. (c) - an example of an original image (August 14, 2019). For the spatial context refer to Fig. 1.

different classifiers. For HS data, the best agreement was discerned for OBIA and RF (TMA = 82.1%), while for MS data, OBIA and MLC were in best agreement (TMA = 81.7%). The three best multi-temporal classification outputs (MS OBIA, HS OBIA, and HS RF) yielded TMA of 77.5% (see Fig. A4 in Appendix A4). As for the mono-temporal data, the MS classification output overlay of RF and OBIA outputs exhibited 80% agreement, while HS data had only 69.5% agreement.

We also examined the spatial agreement of individual species – Eq.

(2) – in best matching classification outputs (for the detailed results see Table A4 in Appendix A4). We found that the best spatial agreement of categories (Mac > 80%) was discerned for MC and CV (in overlay of multi-temporal MS and HS OBIA SVM classifications), and relatively good results (Mac > 70%) were also obtained for NS (overlay of multi-temporal MS and HS RF and OBIA SVM).

The inter-comparison of the three best multi-temporal classification outputs (MS OBIA, HS OBIA, HS RF) indicates that the matching area

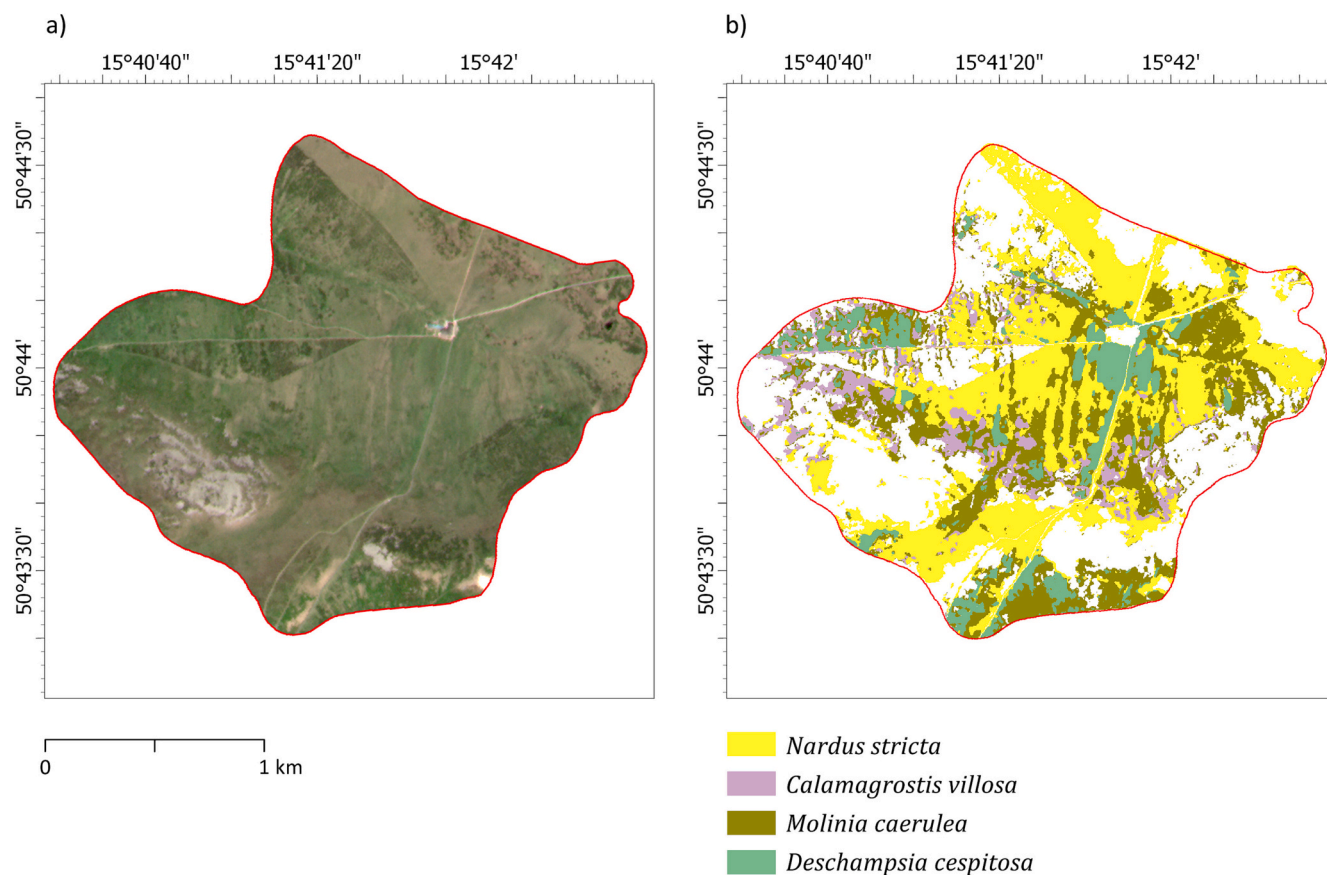


Fig. 11. Best classification for PS (b) – multi-temporal composite June/July/August, RF classifier (wider area of interest); in white other categories than studied grass species. Fig. (a) - an example of an original image (July 7, 2018). For the spatial context refer to Fig. 1.

Table 8

Best Producer's accuracy (PA), User's accuracy (UA), and the F1-score achieved for species classified from UAV data (permanent research plot).

Species	Best PA (in %)				Best UA (in %)				Best F1-score (in %)			
	PA (corresponding UA)	Data	Composite (month/s)	Classifier	UA (corresponding PA)	Data	Composite (month/s)	Classifier	F1- score	Data	Composite (month/s)	Classifier
NS	95.8 (UA = 91.6)	MS	7	OBIA	93.8 (PA = 95.6)	MS	7,8	OBIA	94.7	MS	7,8	OBIA
CV	99.6 (UA = 99.2)	MS	6,7,8	OBIA	99.6 (PA = 99.2)	HS	7,8	OBIA	99.4	MS	6,7,8	OBIA
MC	98.6 (UA = 99.7)	MS	7,8	OBIA	99.8 (PA = 97.6)	HS	6,7,8	OBIA	99.2	MS	7,8	OBIA
DC	99.7 (UA = 93.2)	HS	6,7,8	OBIA	96.6 (PA = 90.4)	HS	6,7,8	MLC	96.3	HS	6,7,8	OBIA
AF	61.5 (UA = 56.7)	MS	7,8	OBIA	68.9 (PA = 43.8)	HS	6,7,8	OBIA	59.0	MS	7,8	OBIA
CB	48.0 (UA = 18.5)	HS	7,8	MLC	66.7 (PA = 12.0)	HS	6,7,8	RF	45.6	HS	6,7,8	OBIA

Species abbreviations: NS - *Nardus stricta*, CV - *Calamagrostis villosa*, MC - *Molinia caerulea*, DC - *Deschampsia cespitosa*, AF - *Avenella flexuosa*, CB - *Carex bigelowii*; *Picea abies* was not entered into the table as it is not a grass species.

was negligibly reduced for MC and CV (by 2.5% and 3.7%, respectively). Regardless of the classification approach, the total areas of NS were very similar, but the overlapping area was lower (reduced by 6%). DC exhibited rather low overlaps and large differences in the classified areas, while CB and AF exhibited high classification inconsistency.

4. Discussion

The reliability of RS data is essential for its effective operational use in nature conservation practice. In our study, we evaluated the potential

of RS for mapping/monitoring of individual grass species, applied to relict arcto-alpine tundra. To evaluate the effects of changing spatial, spectral, and temporal resolutions on the efficiency of species classification, we used three different data types: UAV data from multispectral and hyperspectral sensors (GSD 3 cm) and satellite data from a multi-spectral sensor (PS, GSD 3 m). We evaluated mono-temporal and multi-temporal approaches by using a variety of classification methods. The four dominant native grass species - one originally widespread (NS) and three expanding (CV, MC, DC) - were classified in a wider area of interest using the PS data. We studied the same species and two additional

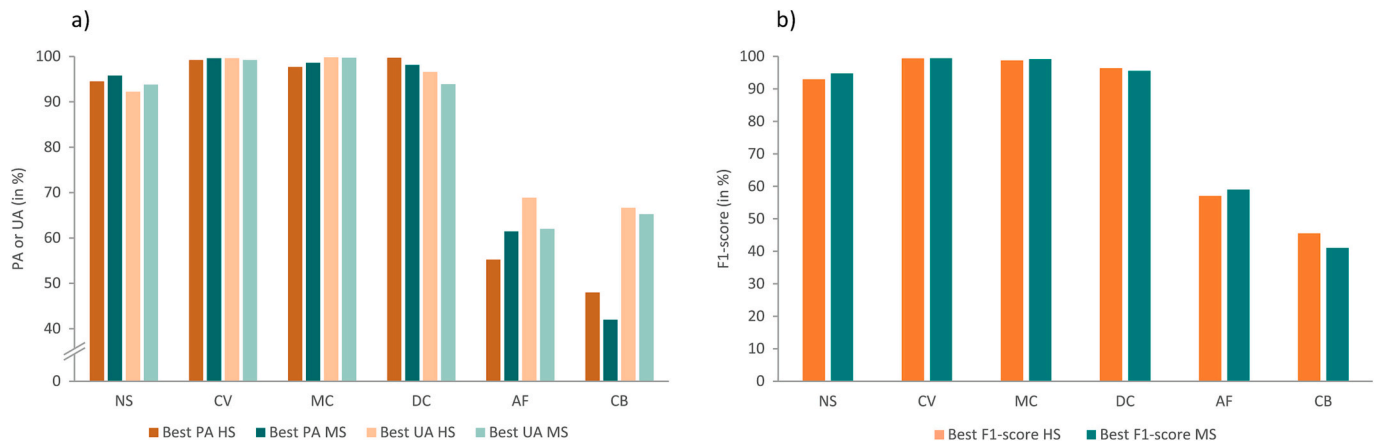


Fig. 12. Best Producer's accuracy (PA), User's accuracy (UA) (a), and the F1-score (b) for UAV HS and MS data (permanent research plot). Species abbreviations: NS - *Nardus stricta*, CV - *Calamagrostis villosa*, MC - *Molinia caerulea*, DC - *Deschampsia cespitosa*, AF - *Avenella flexuosa*, CB - *Carex bigelowii*.

Table 9

Best Producer's accuracy (PA), User's accuracy (UA), and the F1-score achieved for species classified from PS data (wider area of interest).

Species	Best PA (in %)			Best UA (in %)			Best F1-score (in %)		
	PA (corresponding UA)	Temporal composite	Classifier	UA (corresponding PA)	Temporal composite	Classifier	F1-score	Temporal composite	Classifier
NS	81.7 (UA = 88.9)	3 dates	RF	90.2 (PA = 77.2)	7 dates	RF	85.1	3 dates	RF
CV	81.8 (UA = 84.7)	5 dates	MLC	88.9 (PA = 81.1)	7 dates	RF	84.8	7 dates	RF
MC	89.2 (UA = 77.1)	7 dates	RF	81.9 (PA = 85.2)	3 dates	RF	83.5	3 dates	RF
DC	79.0 (UA = 56.5)	1 date	RF	82.3 (PA = 61.6)	7 dates	MLC	71.8	3 dates	RF

Species abbreviations: NS - *Nardus stricta*, CV - *Calamagrostis villosa*, MC - *Molinia caerulea*, DC - *Deschampsia cespitosa*.

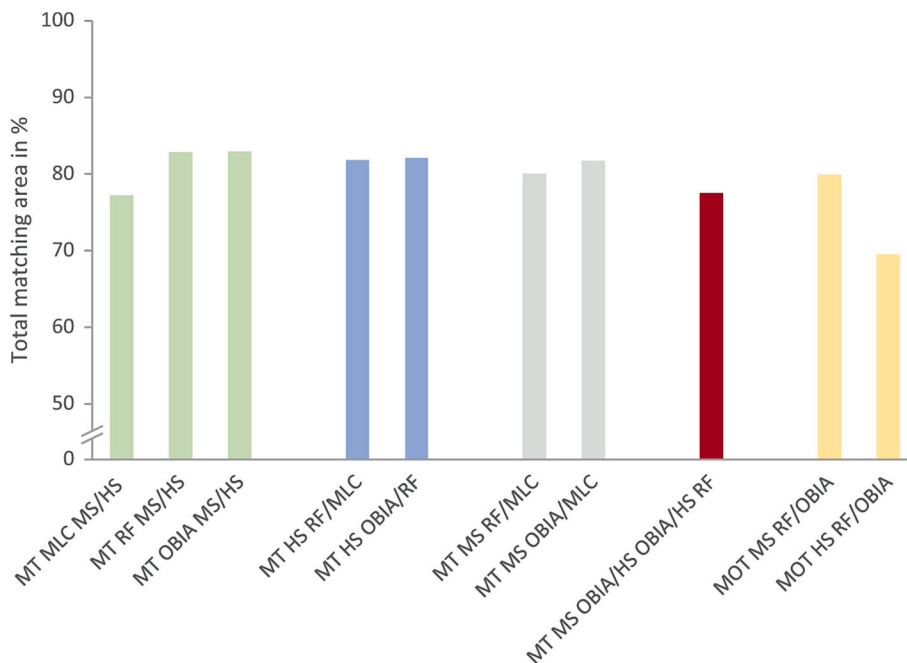


Fig. 13. Total matching area for the selected best classification outputs of the UAV MS and HS data (permanent research plot). Overlaid were the following classification outputs: green bars - comparison between MS and HS multi-temporal (MT) outputs for different algorithms, blue bars - comparison between different classification methods applied on MT HS data, gray bars - comparison between different classification methods applied on MT MS data, in red - overlay for three best MT outputs, yellow bars - comparison between two methods applied on MS and HS mono-temporal (MOT) data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

grasses (AF and CV) in detail on a 1 ha permanent research plot within the wider area of interest using the UAV MS and HS data.

4.1. Impact of spatial and spectral resolution

As anticipated, the best classification results, i.e. OA of over 95%, were achieved by using UAV data with an extremely high GSD of 3 cm.

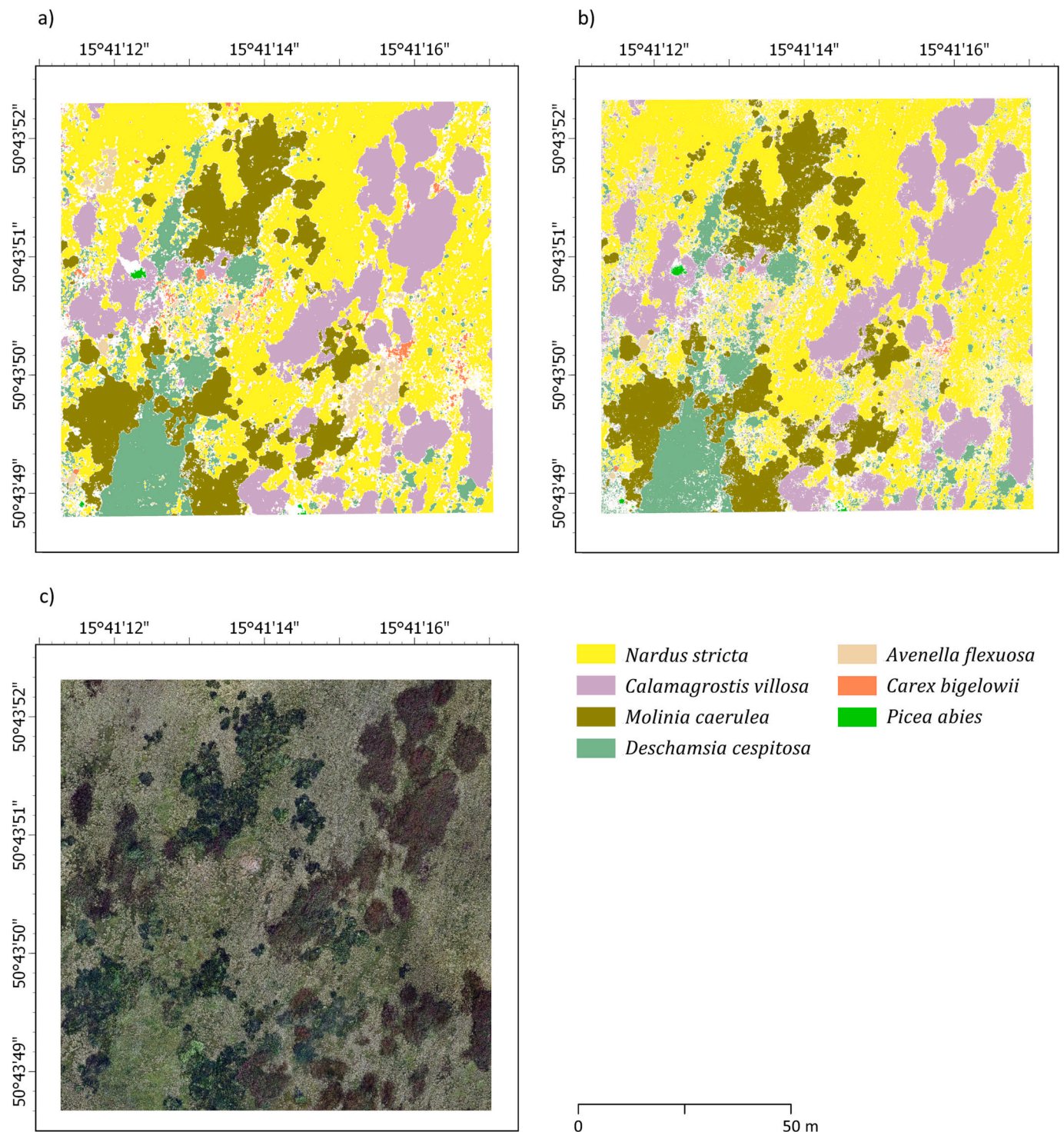


Fig. 14. Spatial match between the best classification outputs of UAV MS and HS multi-temporal composites (permanent research plot) using OBIA SVM (a) and RF (b) classifiers. Disagreement is marked in white. Fig. (c) - an example of an original image (August 14, 2019). For the spatial context refer to Fig. 1.

Accordingly, the final accuracies retrieved through the coarser data of PS were considerably lower with the best OA for PS (June/July/August composite) being 14 percentage points lower than the UAV data. This difference resulted in further significant differences in the classification reliability. As for individual species, the accuracies of PS were also substantially lower than those of UAV, despite the PS data having higher temporal resolution with seven applied dates compared to three for the UAV imagery). Overall, spatial resolution was identified as the most important factor for classification accuracy.

Unexpectedly, there were no significant differences between the UAV MS and HS data. The best OA estimates from the two different sensors were similar (95.9% for MS and 95.6% for HS imagery). Moreover, values of the F1-score for individual species were also very similar. The small difference between HS and MS data could emerge due to the inconsistent illumination of the HS imagery from July and potentially larger georeferencing errors. Alternatively, MS data can be deemed as “satisfactory” for accurate classification results at this level of spatial resolution, as any higher spectral resolution did not improve the results.

This finding resonates with those of Weisberg et al. (2021), where multi-temporal classification of invasive grass species was conducted using UAV MS data (GSD = 2 cm); it was concluded that multi-temporal information can be an alternative for richer spectral information. This premise should be examined more in future studies.

Notably, our results varied depending on the species. While the four dominant grass species (*MC*, *NA*, *DC*, and *CV*) were classified with high accuracy, the classification results for *AF* and, especially, *CB* (the two additional species with low abundances monitored only on the permanent plot) were rather poor. Both species were often under-classified (i. e., not detected). Moreover, the classified areas and spatial distributions from different methods significantly varied. These results are in line with the low separability of *AF* and *CB* in the UAV data (Jeffries-Matusita distance $AF - CB = 1.44$) and rather sparse growth. Additional training data might improve the results, but it is challenging, because the two species are rather small and do not typically form large or uniform stands. Possibility of discriminating and monitoring small and sparse growing species, such as *AF* and *CB*, is thus limited even from imagery with very high spatial and spectral resolution.

One of our objectives was to assess the robustness and reliability of the RS technology as important features for operational use in nature conservation. Within this objective we proposed an innovative approach/measures for the assessment of the spatial consistency of classification outputs. This approach, which is relatively simple but not commonly used, evaluates the spatial match of identical categories detected in different classification outputs (using different classifiers) with high OA. The spatial match among the products was rather high, reaching 80% for both mono-temporal and multi-temporal classification outputs, with the best results for *MC* and *CV* species, and 77.5% in total if three classification outputs were overlaid. Such a high spatial match confirms the high spatial reliability of the classification outputs. These results are promising for dependable long-term monitoring of changes in dominant grass species distribution. On the other hand, the spatial match was very low for low-frequency species (30% for *AF* and 15% for *CB*), and not satisfactory for *DC* (57%).

So far, only a few studies have used data with such high spatial and spectral resolution for analyzing grasslands at the species level; thus, the comparison of results is limited. Bing and Yuhong (2017) classified vegetation including two grass species (Awnless brome and *Fescue*) using MS imagery with GSD of 5 cm and OBIA, with the best OA 86%, UA 86%, and PA 97% for dense stands of Awnless brome, whereas for sparse stands, these dropped to UA 74% and PA 93%. Their results support our conclusion that the abundance/density of vegetation is important for classification accuracy. Liu et al. (2021) used close-range HS imagery (images from Rikola HS camera were taken from 1 m above the ground with GSD of 0.65 mm) to evaluate alpine vegetation, including one graminoid species (*Kobresia humilis*) in Nagqu Tibet. They applied various classification methods and spectral indices, where the best method yielded OA of 95.1%. This OA is slightly lower compared with our results, despite the extremely detailed spatial resolution. Bing and Yuhong (2018) evaluated the influence of spatial resolution on species (including two grass species) on the classification accuracy, by resampling UAV MS data from 5 cm to 10, 15, and 20 cm. They concluded that OAs were the lowest for 20 cm data but were still comparable to other resolutions. However, the response was more complicated for UAs and PAs, as they varied depending on the individual resolutions. More often, aerial HS data have been used for grass species classification (Kupková et al., 2017; Marcinkowska-Ochtyra et al., 2018a), but accuracies are markedly lower (UAs and PAs 60%–80%).

4.2. Impact of temporal resolution

The augmented classification accuracy driven by the additional multi-temporal dimension has been previously demonstrated with the use of various types of VHR imagery at both the species and community levels (Marcinkowska-Ochtyra et al., 2019; Miyoshi et al., 2020; van

Iersel et al., 2018; Vega et al., 2015). However, the multi-temporal approach has been rarely used.

In this study, July and August were the best months for the data acquisition in the context of mountain grassland vegetation; June was considered unsuitable, as it marks the onset of mountain vegetation development, and abundant senesced grass was still present. For instance, the *NS* and *MC* stands retain abundant dry matter from the previous season until June, beginning regrowth in July. Given the significance of phenological changes for spectral response (thus, for increasing the accuracy of multi-temporal composites), the largest changes can be identified for *CV* and *DC*, especially those in color, but also in grass height and structure. This pattern was clear when comparing images taken from July and August. *CV* exhibited the best results for the multi-temporal composites of both HS and MS UAV data. These conclusions are supported by our previous research findings on the seasonal spectral separability of the analyzed species (Červená et al., 2020b). We found that the most suitable month for differentiating the individual species on the levels of leaf, canopy, and image was in general July.

In our study, the benefit of the multi-temporal approach, over the mono-temporal approach, was confirmed for all types of data. In fact, the easily accessible UAV MS data (in comparison with UAV HS data) were sufficient for the analyses, and the number of the temporal acquisitions could be limited to just two dates. This is promising for conservation applications. For the PS data, the multi-temporal approach also markedly increased the accuracy, where the highest increase was registered for the composite created from three images (June, July, and August). Other combinations of dates or adding more dates into the analysis did not result in significant improvement.

Weisberg et al. (2021) reported that differences in species phenology may aid accurate classification with only three of their eight dates necessary to capture species-specific differences. Müllerová et al. (2017) found out that selecting data with specific timing can improve the classification accuracy. Most likely, the composites created for just two or three dates during the season with good timing can yield the best results in general. Future studies should include similar research, as it is currently challenging to support this assumption.

High temporal resolution of PS imagery can be advantageously used for more frequent coarser community level monitoring. This can be especially important in cloudless areas, where the temporal resolution of PS data is very high (theoretically daily). However, for mountain areas (such as the tundra in the Krkonoše Mountains), the availability of cloudless images is very limited (usually 5–10 images for one vegetation season). Regardless, the relatively long time series of the data from PS satellites (already six years) can be advantageous for the evaluation of middle-date vegetation changes, since the data from UAVs for such a long period are hardly available.

4.3. Evaluation of data types, procedure, and methods: Advantages and possible drawbacks

The workflow of the analysis consists of several inputs and processing steps that influence the final results and their accuracy. For the input, we used three types of image data. A schematic evaluation and comparison of their potential, reliability for monitoring, advantages, and drawbacks is provided in Table 10. Comparison of performance for the three types of the data was based on the best achieved values of the relevant parameters (resolutions, reliability, spatial coverage, and availability). Scores of individual parameters are expert-assigned weights based on a comparison of the differences of the best values achieved for each data type. Overall score is calculated as an average from all evaluated parameters (average from the columns 2–9). This table reflects results in our study and the results for different image data, species, and classification methods can be different.

Each type of data naturally has some advantages and can be used to answer certain questions and monitor certain ecosystem types/habitats

Table 10

Usefulness of the used data types in terms of reliability, advantages and disadvantages for tundra grass species monitoring practice in the Krkonoše Mts. National Park. Scores of individual parameters in columns 2–9 were awarded based on the best values of the given parameters; overall score is calculated as an average from the columns 2–9. Higher numbers mean a better score.

Data	Resolution			Reliability Multi-/mono-temporal			Spatial Coverage	Availability / costs	Overall score	Main advantages	Main drawbacks
	Spatial	Spectral	Temporal	OA	PA/UA	Overlay					
UAV MS	5	3	3	5/4	5/5	4/3	3	5	4.1	- extremely high spatial resolution - operability	- weather constraints (clouds, wind) - small coverage - weather constraints (clouds, wind)
UAV HS	5	5	3	4/4	4/5	5/2	1	1	3.5	- extremely high spatial and spectral resolution - operability	- small coverage - high cost - complex pre/processing - low spatial resolution
PS	2	2	5	2/1	2/2	N/A	5	4	2.8	extensive spatial and temporal coverage	weather constraints (clouds)

at particular levels of reliability (Beamish et al., 2020; Hennessy et al., 2020; Librán-Embid et al., 2020; López and Mulero-Pázmány, 2019; Xie et al., 2008). From this standpoint, it is essential to decide which type of data should be used, considering the goals of monitoring and the “cost-benefit” trade-off. In this study, the main goal was to propose RS-driven methods for robust monitoring of tundra grass vegetation at the species level. Considering the performance, cost, and complexity of processing, UAV MS data with spatial resolution in the order of single centimeters were shown to be the optimal solution. Indeed, other methods can be further tested to improve the results, such as CNN classifiers, subpixel classification, improvement of preprocessing and calibration of the data, or separability of the reference dataset. Despite (a) the significant weather-driven (cloud/wind) constraints of UAV technology that are particularly pronounced in mountainous areas and (b) the limited spatio-temporal coverage of UAVs, compared to PS, outstanding spatial resolution, operational use, and reasonable costs are advantageous; all these factors boldly emphasize the efficiency and applicability of the UAV technology.

Besides selecting the most suitable data, other steps of the data analysis (reference data, pre-processing and classification) should be precise and advanced to ensure the production of the most accurate outputs; however, in reality this can be difficult to assure. In our case, we see some possibility for further improvements for example in enhancement of the illumination consistency of UAV imagery. This is a major constraint in data acquisition in mountainous areas, as illumination conditions are rarely ideal and change extremely quickly even if the flight lasts only 15 min.

Another processing-related issue is found in training and validation. For a detailed species-level classification, this step requires thorough field data collection, and it might be challenging to find a sufficient area in the field for some species/communities. Some species do not form uniform and large patches, have sparse growth and/or are small/narrow-leaved, such as *AF* and *CB* in our case. For the validation purpose, either all pixels or a certain number of randomly selected points generated within the validation polygons can be utilized. For the two types of data (UAV and PS), we adopted different strategies (random points for UAV and all pixels within validation polygons for PS). Random points that had been generated within the validation polygons while accounting for spatial autocorrelation are considered more robust compared to using all pixels (Foody, 2009; Jensen, 2005). However, for PS, such a method could not be applied due to the limited validation dataset, considering the size of the PS pixel and the study area. Therefore, to ensure sufficient data (number of pixels) for the validation of PS products, we had to use all the pixels within the validation polygons. We tested the complementarity of the two methods by using UAV data, and

the results were similar, indicating that the two methods are comparable. We also tested multiple random sampling of validation/training data and multiple evaluation of classification accuracy in the case of UAV data. The results were independent of the spatial distribution of the training/validation data, i. e. the resulting accuracies were very similar (maximal differences $\pm 2\%$) for all the tests.

The selection of a classification method is essential for image analysis. Classification of hyperspectral data can be more challenging than classification of multispectral data due to high data dimensionality and noise. However, data preprocessing techniques reducing dimensionality and noise, which are also applied in our study, allow traditional multispectral classification approaches to be used for hyperspectral data (Burai et al., 2015). On the other hand, methods developed for classification of hyperspectral data, in particular the subpixel approach, have recently been widely used for classification of multispectral data (Radoux et al., 2016; Senf et al., 2020). When choosing a method, the purpose of data analysis must be taken into account. In the case of vegetation classification, subpixel methods may not yield the highest classification accuracy (Tran et al., 2014; Růžicka, 2022). As our results show, traditional methods (Maximum Likelihood) can be effective, and machine learning methods are highly recommended for accurate classification of multispectral and hyperspectral data, as demonstrated not only by our findings (results of RF classifications) but also by other studies (Sabat-Tomala et al., 2020; Liu et al., 2021).

In our study, three classifiers were employed to cover the main types of classification approaches (OBIA and pixel-based), and including both classical (MLC) and progressive advanced methods (RF and SVM). Our previous studies (Kupková et al., 2017; Suchá et al., 2016) concluded that for relatively patchy mosaics of vegetation, especially for data with an extremely high spatial resolution, OBIA would be more suitable. Our assumption was confirmed, in the case of UAV data, as OBIA outperformed the pixel-based classifiers (OA for both MS and HS sensors and both mono-temporal and multi-temporal approaches). Meanwhile, for PS, in terms of OA, the most successful classifier was RF (except for mono-temporal data when MLC was slightly better).

As for individual species, OBIA was the best method for the majority of the analyzed species in the case of UAV data (considering F1-score) and RF in the case of PS. A comparison of various classifiers has been widely used to seek the best method not only from an OA perspective but also with regard to the classification of individual species/categories. Liu et al. (2021) applied four classifiers – SVM, RF, artificial neural networks (ANN), and spectral angle mapper for mapping alpine plant species of northern Tibet using close-range HS imagery. They demonstrated that the ANN classifier yielded the highest OA, while RF and ANN performed well for the species identification. Suchá et al. (2016)

tested MLC, SVM, ANN, and OBIA classifiers for vegetation above the tree line in the Krkonoše Mountains from orthoimages and WorldView-2 data, where OBIA exhibited the best results. As in our study, [Pande-Chhetri et al. \(2017\)](#) achieved the best performance (OA = 70.8%) for wetland vegetation at the species level using OBIA (SVM) in comparison with pixel-based classifiers (MLC and ANN) for UAV data (GSD 8 cm). Recently, OBIA has been frequently used for UAV data analyses ([Müllerová et al., 2017](#); Lu and He, 2017; [Mishra et al., 2018](#); [Prošek and Šimová, 2019](#); [van Iersel et al., 2018](#); [Yan et al., 2019](#)). However, our results highlight the importance of testing various methods, because different features of the data (especially spatial but also temporal resolution) and different categories (species in our case) may require a tailored approach to maximize the accuracy of the results. Furthermore, our results confirmed the findings of [Müllerová et al. \(2021\)](#) that particular attention must be paid to each step in the workflow and be adapted to both the characteristics of the target vegetation and to the purpose of the study.

5. Conclusions

The goal of our study was to explore the potential of remote sensing (RS) for nature conservation applications, specifically to establish a workflow for reliable and operational monitoring of grasslands in Central Europe tundra at the species level. The conclusions of our study are listed below:

- We confirmed that UAV MS and HS data with GSD of 3 cm were suitable for the monitoring of dominant grass species in tundra with high accuracy.
- The abundance/density/homogeneity of the species and its cover were essential for classification accuracy. The dedicated tests, by mainly using other classifiers, and other improvements should be continued in the future to increase the mapping accuracy of sparse growth and low-density species.
- Fine grain UAV data considerably outperformed coarser PS satellite data, even when dense temporal coverage of PS was employed. However, PS data can be useful for a general overview and monitoring of dominant grass species and their changes from a long-term perspective.
- We showed that adding a temporal dimension can be very beneficial, as the multi-temporal approach increased the accuracy in all cases. Our findings indicate that two dates might be sufficient for highly accurate classification results in the case of UAV MS and HS data, and three dates for PS data. Of the individual months, the best results for the classified species were obtained in July.
- Unexpectedly, the higher spectral resolution of HS data did not increase accuracies, and the results for the UAV MS and HS data were comparable. Spatial resolution was more important for the classification accuracy at the species level than the spectral resolution.
- These findings provide useful implications for nature conservation practices, because the price of suitable multispectral sensor/s and complexity of processing are significantly lower in comparison to hyperspectral data. Moreover, given weather constraints and costs, it is possible to reduce the number of dates to just two within the growing season without compromising the overall accuracy of the results.
- Of the applied classification methods, the object-based approach was found to be the most accurate for both types of UAV data. For PS data, the pixel-based RF classifier yielded the best results. Further tests of RF and other classifiers (convolutional neural network, subpixel classification) are recommended.
- The high spatial match of different UAV data classification outputs highlights the reliability of the analyses. This is especially true for the multi-temporal approach and dominant grass species. This finding underlines the relevance of RS technology for monitoring dominant grass species.

- The areas where overlaid classification outputs detected the same species can be considered as the core zones where the occurrence of the species is almost 100% accurate. Such core zones can be used as a basis for modeling, experiments, and monitoring changes in the spatial distribution of vegetation composition.

Based on the results of our research we recommend, as the most effective and at the same time satisfactorily accurate and reliable, the workflow based on/using: (1) UAV MS data with GSD in cm (~3 cm), (2) multi-temporal composite of imagery from July and August (acquired ideally in the middle of these months), (3) OBIA SVM or RF classifier. Special attention should be paid to all pre-processing and processing steps as described above in order to ensure the highest classification accuracy. This workflow can provide a high level of confidence for detailed vegetation monitoring at the species level using remote sensing not only in the arcto-alpine tundra of the Krkonoše Mts., but in general.

CRedit authorship contribution statement

Lucie Kupková: Conceptualization, Methodology, Investigation, Formal analysis, Validation, Writing – original draft, Writing – review & editing, Funding acquisition. **Lucie Červená:** Methodology, Formal analysis, Validation, Investigation, Writing – review & editing. **Markéta Potůčková:** Conceptualization, Methodology, Writing – review & editing. **Jakub Lysák:** Investigation, Formal analysis, Software, Writing – review & editing. **Markéta Roubalová:** Formal analysis, Validation. **Záboj Hrázský:** Methodology, Writing – review & editing. **Stanislav Brežina:** Methodology, Funding acquisition. **Howard E. Epstein:** Supervision, Writing – review & editing. **Jana Müllerová:** Investigation, Methodology, Formal analysis, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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Appendix 9.

PAPER 9. **Müllerová** J., Vítková, M., Vítek, O. (2011). The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient poor environment. Science of the Total Environment 19: 3839-3849.
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The impacts of road and walking trails upon adjacent vegetation: Effects of road building materials on species composition in a nutrient poor environment[☆]

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ABSTRACT

Roads represent an important landscape element affecting both biotic and abiotic components. Alteration of soil properties along roads (addition of nutrients) is assumed to have a great impact on vegetation structure especially in nutrient poor ecosystems. Existing studies focus mainly on road dust. In our study we assessed the overall effects of roads upon adjacent alpine tundra vegetation and soils in Krkonoše Mts, Czech Republic. Our aims were to (1) reconstruct the road-related changes using aerial data and GPS mapping to study colonization of roadside plant species; (2) assess the road effects on physical–chemical soil properties and vegetation composition along transects; and (3) propose conservation measures to stop further damage. Changes were reconstructed from historical multispectral aerial photography (1986 to 1997), measured by GPS device (1997, 2004), and accompanied by detailed soil (1998, 2000 and 2001) and vegetation (2000 and 2004) surveys along transects. Along alkaline roads, fast and profound shifts in physical–chemical soil properties (pH increased from 3.9 up to 7.6, base saturation from 9–30% up to 100%), and species composition were recorded. The roadside vegetation doubled in area during the studied decade. Stress-tolerant tundra species were replaced by meso- to nitrophilous species and species preferring man-made habitats. The intensity of changes depended significantly on the type of road material and the position relative to the road (slope position, distance from the road). Our findings support the assumption that alkaline gravel is the main cause of changes along roads in the area, and indicate the leading role of water transport in the soil and consequent vegetation alteration. To prevent the further damage we recommended replacement of alkaline gravel by granite, even though expensive and technically complicated. Based on our recommendations, the National Park authorities started to reconstruct the trails, although recovery is expected to be slow.

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1. Introduction

Roads and paths represent important landscape elements having large impacts on the surroundings. They affect both the biotic and the abiotic components of landscape by changing the dynamics of populations of plants and animals, altering flows of material, introducing exotic species, and changing levels of available resources, such as light, water and nutrients (Angold, 1997; Coffin, 2007; Hill and Pickering, 2006; Spellerberg, 1998). The extent and intensity of the effects vary with the position of the road relative to pattern of slope, prevailing winds and surrounding land cover (Forman and Alexander,

1998). The road-effect zone is highly asymmetrical, due to nature's directional flows and the spatial patterns on opposite sides of a road, and has convoluted boundaries (Forman and Deblinger, 2000).

Disruption of the chemical environment (alteration of chemical soil properties) along roads affects plant growth and species diversity and composition (Cape et al., 2004; Spellerberg, 1998; Trombulak and Frissell, 2000; Forman and Alexander, 1998). Many studies on roadsides indicate strong relationship between the spread of non-native plant species and soil nutrient levels (Cale and Hobbs, 1991; Forman, 2000; Johnston and Johnston, 2004). While considerable research has been carried out on the influence of deicing salt (Green et al., 2008; Bryson and Barker, 2002; Cunningham et al., 2008), and pollutants from vehicle exhausts (Angold, 1997; Cape et al., 2004; Djingova et al., 2003; Hooda et al., 2007; Truscott et al., 2005) and brake linings (Grantz et al., 2003; Thorpe and Harrison, 2008; Ward, 1990), the effects of road construction material have been little investigated. The impact is especially profound if alkaline gravel is used in predominantly nutrient-poor environments dominated by stress tolerant plants (Hill and Pickering, 2006). Liming in general significantly increases the soil pH, enhances the rate of decomposition

Abbreviations: (KRNAP), Krkonoše Mts National Park; (GPS), Global Positioning System; (AB), amygdaloidal basaltic rock; (D-AB), mixture of dolomite and amygdaloidal basaltic rock.

[☆] Nomenclature source: IUCN categories of threatened species – according to Holub and Procházka (2000).

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of organic matter, provides the basic nutrient cations (Ca and Mg), increases the solubility of Mo and P (Bolan et al., 2003) and increases the amount of NO_3^- in the soil (Bertrand et al., 2007; Schimel et al., 1996). Such processes facilitate colonization by more competitive, often non-native species with greater nutrient uptake efficiency and higher biomass, such as weeds (Dulière et al., 1999; Hobbs and Huenneke, 1992; Chapin, 1987).

Studies on alkalization effects of roads on the vegetation of acidic soils are relatively few. In Belgium it is reported that a limestone paved road in the acid forest environment can create a locally neutral to alkaline soil in the adjacent community (Godefroid and Koedam, 2004). An early example is a Roman limestone road that locally resulted in alkaline soils in a natural acidic podsol community (Detwyler, 1971). In Alaska along the Dalton Highway the calcareous road dust altered the soil chemistry and microbial decomposition, and in some cases elevated the soil pH to a level toxic to tundra acidophilic plants (Myers-Smith et al., 2006; Reynolds and Tenhunen, 1996; Walker and Everett, 1987). These tundra studies deal with one aspect of the alkaline road influence on grassland vegetation – the effect of calcareous road dust deposition. Our scientific concern – to evaluate the influence of different environmental factors, mainly the overall effect of alkaline road material, the road age, seasonality, tourist load, and position relative to the slope and wind on soil properties and plant species composition of acidophilic grasslands – has not yet been much investigated. Our aims were to (1) reconstruct a decade of road-related changes using aerial data and a GPS device to study the trends and rate of colonization of roadside plant species; (2) assess the impact of roads on physical–chemical soil properties and vegetation composition along transects, especially the effect of stabilization with alkaline gravel; and (3) propose conservation measures to stop further damage.

2. Methods

2.1. Study area

The Krkonoše Mts National Park and Biosphere Reserve (Fig. 1) represents the highest mountain range in the Czech Republic. Uppermost areas situated above the timberline are covered by a particular mosaic of tundra types: (a) lichen tundra (on topmost summits), (b) grassy tundra (grasslands and peat bogs on the two summit plateaus, focus of our study), and (c) flowery tundra (leeward slopes on glacial cirques of the Krkonoše Mts). The ecosystem, called “alpine” or “arctic-alpine tundra”, displays affinities with both sub-arctic and high-mountain regions (Gordon et al., 2002), and hosts many endemic, glacial relic, and rare species, and unique geomorphologic components (Jeník and Sekyra, 1995; Štursa, 1998; Müllerová, 2004). The alpine tundra covers 47 km², i.e. 7.4% out of the whole area of the Krkonoše Mts (32 km² in the Czech part and 15 km² in the Polish part of the Krkonoše Mts). It is exposed to extreme climatic conditions, such as strong north-western winds, average temperature of 0 to +1 °C, snow cover for more than 180 days, annual precipitation of 1400 mm, and periodical soil regelation and deflation (Soukupová et al., 1995). It is formed from granitoid massifs and metamorphic rocks (mostly mica schist and phyllite) covered with rankers (typical, podzol and lithic), podzols (humus podzol), organozems (pH 3.7 to 5.1) and patches of peat and raised bogs (Štursová, 1985).

Vegetation cover of grassy tundra is composed of mosaic of grassland, scrubland, fens and peat bogs. The most typical plant species include *Pinus mugo* Turra, creating large dense krummholz; *Nardus stricta* L., a typical low competitive stress tolerant grass dominant of dense uniform stands; *Molinia caerulea* (L.) Moench and *Calamagrostis villosa* (Chaix) J. F. Gmelin forming communities of tall grasses and



Fig. 1. Location of the study area in the Krkonoše Mts National Park, Czech Republic.

flowering herbs on wet, wind-protected soils; *Deschampsia cespitosa* (L.) P. Beauv., found on mezotrophic to eutrophic deeper, permanently humid soils; peat mosses; and *Trichophorum cespitosum* (L.) Hartm. forming oligotrophic communities of boreoarctic and alpine raised bogs.

Despite the fact that the Krkonoše Mts were declared a National Park in 1963 and a bilateral Biosphere Reserve in 1992, the increasing numbers of visitors (more than eight million per year, with half a million visitors to the tundra zone per year; Gordon et al., 2002) result in trampling, soil erosion, noise, pollution, dispersal of alien plant diaspores, building activities and fragmentation of habitats (Štursa, 1998). Even on the high plateaus, there are numerous chalets, footpaths and roads.

The study site is located in grassy tundra of the western plateau (1300–1350 m a.s.l., 15° 33' E, 50° 45' N, app. 1.5 km², Fig. 1). It was selected according the available aerial MS photography. Road density in the area is 24 meters per hectare. From the 1970's to 1980's most of paths and roads were stabilized with foreign material – dolomite, amygdaloidal basaltic rock (AB), or dolomite-amygdaloidal basaltic rock mixture (D-AB) – in order to prevent erosion. The only road open for vehicles was stabilized by thick layer of dolomite and AB gravel and covered by asphalt in 1980. Today, extensive strips and lobes of roadside vegetation are present along roads and trails constructed with alkaline material. In the project, six and a half km of roads/walking trails were analyzed, with more than five km of them hardened or paved. The longest were asphalt (2.2 km) and AB roads (1.4 km), dolomite covered 0.8 km and D-AB 0.9 km. The width of stabilized trails was 2 m in average, whereas that of the asphalt road was 3.5 m with 0.3–1 m wide verges of loose gravel. Historical development of trail network was reconstructed from historical and tourist maps (since the end of 16th Century), and from aerial photographs (since 1936). Quantification of traffic intensity was based on data from 1997. During 10 days in the high tourist season the numbers of walking tourists, cyclists and cars were recorded for each hour (9 a.m. till 6 p.m.) in both directions.

2.2. Spatial analyses

Road-related changes were reconstructed using multispectral aerial photographs of 1986 (scale – 1:22000; channels – 0.48, 0.54, 0.66, 0.84 nm), 1989 (scale – 1:22000; channels – 0.54, 0.60, 0.66, 0.84 nm), and 1997 (scale – 1:15000; channels – 0.54, 0.60, 0.66, 0.84 nm), created and provided by the Agency for Nature Conservation and Landscape Protection in Prague. The roadside vegetation could be traced on the multispectral data because it is much taller, has broader leaves and produces a higher biomass than the natural vegetation. The photographs were analyzed digitally – negatives were scanned at 1000 dpi, co-registered by image-to-image registration, and georeferenced using panchromatic orthophotographs (year – 1997; final pixel resolution – 0.5 m; created by Geodézie Krkonoše; provided by the Krkonoše National Park Authority). Second order transformation and the nearest neighbor rectification method were applied at final pixel size 0.5 × 0.5 m with forty to fifty ground control points. Visuality and separability of roadside vegetation were improved by contrast enhancement (histogram equalization) and principal component analysis (Jensen, 2004). The roadside vegetation was classified using parallelepiped classification (non-parametric supervised method defining the lowest and the highest values of classes in every spectral band; for details see Müllerová, 2004) using software Chips (version 4.3, University of Copenhagen, Copenhagen) and Geomatica (version 10.0, Geomatics Enterprises Inc., Ontario, Canada). Evaluation areas used for the accuracy assessment were randomly positioned (100 samples within roadside vegetation layer, and 100 samples outside the layer but within 50 m of road). User's (the measure of commission error), and producer's accuracy (the measure of omission error) of roadside vegetation class was calculated from the confusion matrix (Congalton, 1991).

Since in 1997 multispectral aerial photographs covered only small part of the study area. To fill the gap in data, a GPS device was used to map the roadside vegetation in 1997/98 and partly in 2004 (due to limited financial sources). The boundaries between roadside and natural vegetation were mapped as areal features with attributes, such as species composition (dominant and abundant species), and position relative to the road (above, below, or in flat terrain). Roads, road edges and cross-drains were mapped as linear features with attributes, such as type of stabilizing material, and width.

A GPS mapping receiver Trimble Pathfinder ProXR was used for measurements with PDOP mask set to 6.0 and elevation mask to 15. The differential correction was processed with base data from a Prague station with the final accuracy of the output data better than one meter. Nonetheless point features representing reference points or single occurrences of species were of higher accuracy due to position averaging. For point measurements minimum of 10 positions was collected in one second frequency. For line and polygon measurements positions were read each 2 s. The RS and GPS data from the overlapping area were statistically tested for the discrepancy. A grid of 5 × 5 pixel squares (number of pixels of roadside vegetation in each square) was used for the analysis instead of direct pixel-to-pixel comparison to eliminate the mis-registration errors and to reduce the large amount of data. Chi-square goodness of fit and regression analysis were performed on the data (Zar, 2010).

The extent of roadside vegetation was spatially examined between years to determine vegetation changes and trends in a GIS environment using ArcInfo (Environmental Research Institute, Redlands). Relations among the extent of roadside vegetation and several factors were tested by variance analysis methods (one-way analysis of variance, ANOVA), and by linear regression (STATISTICA 6 software). The tested variables included: (1) road characteristics, such as type of stabilizing material, construction period, road width, seasonality (accessible all year/summer/winter/closed), traffic intensity (average daily number of walkers/cyclists/cars), and road position to the slope (situated in flat terrain, along or across the slope), and (2) environmental variables, such as vegetation position relative to the road, indicating the effect of runoff water; and prevailing wind direction to or from the road, indicating the wind transport of road particles. Average wind directions were obtained from meteorological station (Czech Hydrometeorological Institute), automatic meteorostation (KRNAP), and the study of tree flag forms (KRNAP).

2.3. Vegetation and soil samples along transects

Seven permanent transects were selected randomly at sites of corresponding bedrock and similar terrain morphology to analyze the effects of different road/trail construction material, such as: i) asphalt (transects A1 of 40 m, and A2 of 181 m), ii) AB (transect AB of 46 m), iii) dolomite (transects D1 of 32 m, and D2 of 34 m), iv) D-AB (transect D-AB of 14 m) and v) granite (transect N of 7 m). Transects followed the slope and were perpendicular to a road/trail, with the start and end in undisturbed natural vegetation. Transects were evaluated as a complex comprising of both affected and natural parts, with both ends of transect reaching the natural vegetation considered as controls, comparable to natural stands. A higher number of transects was not possible due to the small extent of vulnerable alpine tundra ecosystem and high risk of ecesis of roadside plant species at sites disturbed by soil sampling.

Vegetation was studied on seventy 1 × 1 m permanent plots. Vascular plant species, bryophytes and lichens were recorded using Braun-Blanquet's nine-grade semi-quantitative scale of abundance and dominance (Braun-Blanquet, 1964) in 2000, and repeated in 2004 with supplementary information on elevation, slope, aspect, and soil type. Relevés were loaded into TURBO(VEG) 9.39 database (Hennekens and Schaminée, 2001). Permanent plots were distributed along seven transects in the following scheme: the first was positioned above the road in natural vegetation, the others were placed below the road at a two meter and five meter distance, and then every 5 m up to natural

vegetation not affected by the road. The interval between plots was enlarged to 10 m starting from the distance of 60 m below the road.

Cover values of species were modified by van den Maarel transformation (Jongman et al., 1995) prior to gradient analysis in Canoco for Windows 4.0 (ter Braak and Šmilauer, 2002). Ordination methods based on the model of linear species response to the underlying environmental gradient (PCA, resp. RDA) were used, because a monotonic distribution of the plant species was assumed. The species were separated into roadside or natural vegetation using PCA. The influence of the soil and landscape characteristics on species composition was studied by redundancy analysis with forward selection (RDA; Jongman et al., 1995). Monte Carlo permutation test (Jongman et al., 1995) with 499 permutations (blocks defined by covariables – codes of transects) was chosen to determine the effect of each environmental variable on 52 relevés and 79 species.

Soil was sampled at the end of the vegetation season (second half of September of 1998, 2000 and 2001) at a total number of 52 sampling points – 23 for asphalt, 10 for AB, 13 for dolomite, 3 for D-AB and 3 for granite. The first and the last sampling points represented controls. Sampling points were positioned on transects at the same scheme as the vegetation permanent plots. At the A1 transect (180 meters long), starting from the forty meter distance below the asphalt road the soil samples for analyzing selected parameters (pH, actual moisture, dry matter) were taken every ten meters, samples for the complete analysis every thirty meters. The D-AB transect differed significantly from others, as it was situated: 1) on a trail closed to the public at the end of the 1970's, whereas other trails are still in use; and 2) in flat terrain, whereas the other transects were situated on slopes. Its' verges were therefore much narrower with only three sampling points.

Soil samples were gathered with a soil probe next to the permanent plot. Part of the sample used for examining actual moisture, dry matter, pH, content of nitrates, and exchangeable phosphorus, was immediately sifted through a 2 mm sieve and transported to the laboratory in airtight 100 ml bottles placed in cooler. The fine earth of the sample was dried at room temperature for other analyses. The soil skeleton was calculated as a ratio of inorganic particles up to 2 mm and fine earth. Values of active pH were measured according to McLean (1982). Methods of Moore and Chapman (1986) were used to determine base saturation by exchangeable cations (Ca^{2+} , Mg^{2+} , K^+ , H^+ , Al^{3+}) and the content of nitrates. Exchangeable phosphorus was measured by the photometric method following Olsen (1982). Total carbon and nitrogen content were analyzed according to Monar (1972). Carbonate concentration was determined by ISO/DIS 10693 (1995). Potential direct solar irradiation (PDSI) was calculated for each plot from data on exposition, slope and angular height of the horizon at these cardinal points following Jeník and Rejmánek (1969). To identify the most important environmental gradients, principal components analysis (PCA; Jongman et al., 1995) was used to detect correlations among site attributes (slope, PDSI), road distance, type of paving material, physical-chemical soil properties (soil skeleton, dry matter, pH, Ca^{2+} , Mg^{2+} , K^+ , Al^{3+} , H^+ , base saturation, $\text{N-NO}_3/\text{N}$, carbonates, N, C, and P_{ex}), and vegetation characteristics (vegetation cover, total number of plant species, number of roadside plant species, and natural composition represented by rate of autochthonous species in relevé). Since the number of environmental characteristics was relatively high (29) compared to the number of soil sampling points (52), the environmental characteristics were used as species data in Canoco (scaling and standardizing were needed because of different units).

3. Results

3.1. Reconstruction of road-related changes using aerial data and GPS mapping

The area of roadside vegetation grew considerably from 2% of the study area in 1986 (2.5% considering the grassland area only – i.e.

excluding Dwarf Pine stands) up to 6.2% (7.6% of grasslands) in 1997 (Fig. 2). The measured rate of spread (1986/1997) was 0.6 hectare per year, with an increase of 0.28 times per year. Based on the measured increase (0.25 times per year in 1997/2004), roadside vegetation was estimated to cover 7.7% (9.4% of grasslands) in 2004 (Fig. 2). Between-year-changes at the pixel level (0.25 m^2) were analyzed using the 1986 and 1989 multispectral aerial photographs and 1997 GPS data. Four different responses of the roadside vegetation were recorded – increase (6.3% of the area), decrease (2.5%), stable (i.e. remained constant; 0.6%) and irregular (3.5%). The results showed a significant increase in roadside vegetation in time. Changes in vegetation along hardened roads were significantly greater (up to 4.7 times in 1997) than along unhardened; with the asphalt road (built of several layers of dolomite and AB gravel) having the greatest change (Fig. 2).

Of the total 6.5 km of roads, 3.1 km were bordered by roadside vegetation in 1986, 3.5 km in 1989, and 5.1 km in 1997. In 1997 asphalt, dolomite and D-AB roads were nearly all bordered with roadside vegetation. The most rapid increase during the decade was recorded along AB (2.7 times) and asphalt roads (2.1 times). D-AB and unhardened trails were relatively stable, with more than 90% of the first and less than 20% of the second bordered with roadside vegetation over the whole period.

The area of roadside vegetation in the vicinity (within 50 m) of the asphalt road enlarged almost five times over a period of ten years, covering 25.5% of the road vicinity in 1997. Along other types of road it increased from 1.5 times (dolomite covering 11.5%, D-AB 9.7%) to 2.7 times (AB 7.2%). Along unhardened walking trails it covered maximally 4%.

From the environmental factors tested, the extent of roadside vegetation was significantly related to the road stabilizing material ($p < 0.001$), and position relative to the road ($p = 0.0087$; Fig. 3). Position to the wind, road frequency, seasonality, and construction period did not show significant relationships. The role of road width and the type of traffic could not be statistically determined, as they were closely interrelated to the type of stabilization material (as the asphalt road was much wider compared to others, and it was the only road used by vehicles).

Results of 1986 and 1989 could not be ground-truthed, so the classification accuracy was evaluated by visual photo interpretation of stratified random samples. The accuracy of the roadside vegetation class in 1986 was 78% (user's), and 92% (producer's accuracy). In 1989 it was 79% (user's), and 87% (producer's accuracy). The overall accuracy was 85.5% in 1986, and 83.5% in 1989. The interpretation of 1989 aerial photographs was also compared with the field map of Fišerová (1991; see Müllerová, 2004). In this case the accuracy reached 73% (user's), and 75.3% (producer's accuracy). However this map focused on natural communities and the roadside vegetation was of marginal interest, and the accuracy therefore reached lower values. In 1997 aerial data were only available for a small part of the study area. Field measurements of roadside vegetation using the GPS device were accomplished, and the two methods (multispectral photography analyses and field GPS measurements) statistically assessed using the data for the overlapping area. The chi-square goodness of fit showed significant differences at $\alpha = 0.05$ but not at $\alpha = 0.01$ ($\chi^2 = 6.41$, $df = 1$, $0.01 < P < 0.05$), so the two methods may be comparable with some limitations.

3.2. The road impact assessment along transects

Based on the PCA, the species recorded on transects were separated into two groups (online supplement). Relevés of natural plant communities were placed at right side of the ordination diagram in Fig. 4, roadside vegetation at left side. The roadside vegetation included: a) species preferring man-made habitats (synanthropic), b) species of lower altitudes, and c) competitive local species favored by the new conditions, which naturally grow in patches of humid tundra richer in

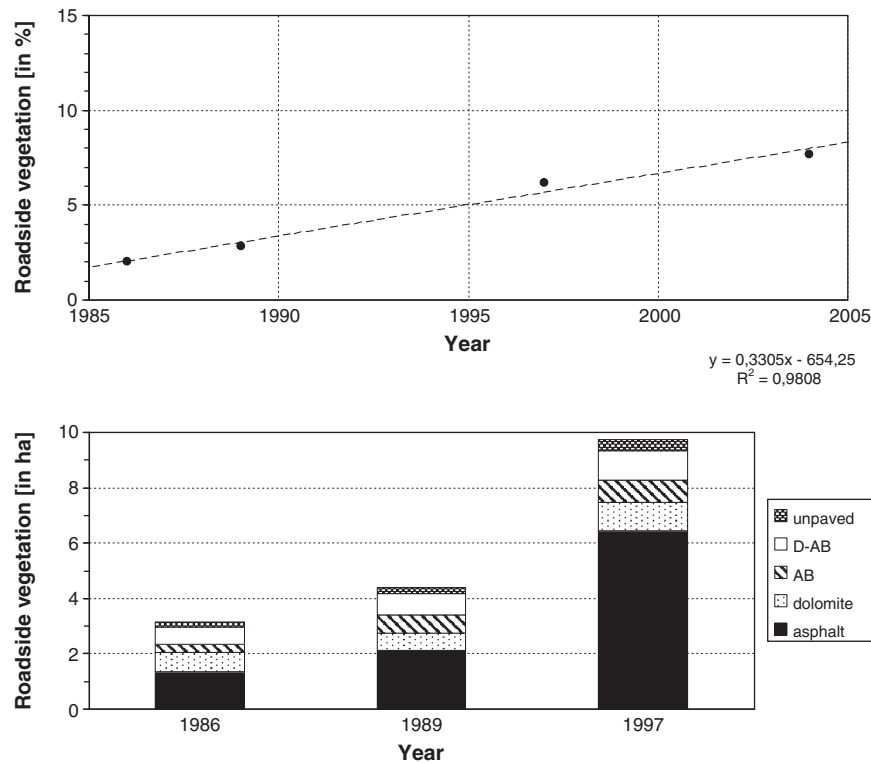


Fig. 2. Dynamics of roadside vegetation changes in percent (measured overall extent with future prospect); and in hectares (divided by the type of road pavement as the main factor explaining the vegetation changes; D-AB – mixture of dolomite and amygdaloidal basaltic rock, AB – amygdaloidal basaltic rock). In 2004, only part of the study area was investigated due to the limited financial sources. Based on the measured increase (1997/2004), the share of roadside vegetation in 2004 was estimated.

nutrients, such as terrain depressions, stream alluviums and stands of *Pinus mugo*, and at sites with long-lasting snow cover (Table 1). In the road vicinity (within 10 m from the road, down the slope), the proportion of roadside species was significantly higher than at distances greater than 20 m, or above the road (up the slope).

Soils covered by natural vegetation showed low values of pH (3.9 to 4.2) and base saturation (9 to 30%) with hydrogen and aluminum playing the main role among exchangeable cations (Figs. 5 and 6). High accumulation of soil organic carbon, nitrogen, and N/P_{ex} ratio can be ascribed to the high ratio of poorly decomposable biomass of grasses in O_h soil horizon of autochthonous communities. Physical-chemical soil conditions along roads were significantly different from

natural stage (Figs. 5 and 6). Near the road the active pH reached up to 7.6 with base saturation 100%, representing slightly alkaline, eubasic and highly saturated soils, found nowhere else in the study area. PCA ordination (Fig. 6) showed that compared to the natural conditions, the soils were drier with more skeleton. Ca²⁺ and Mg²⁺ played the main role in adsorbing complex. Organic biomass mineralization ran faster, N-NO₃/N ratio reached higher values, and contents of total carbon and nitrogen were much lower.

Chemical soil characteristics (pH and base saturation) depended strongly on sample position relative to the road (Fig. 5). Samples situated above the built roads (up the slope) reached values corresponding to natural stands while below such roads (down the slope) the values were

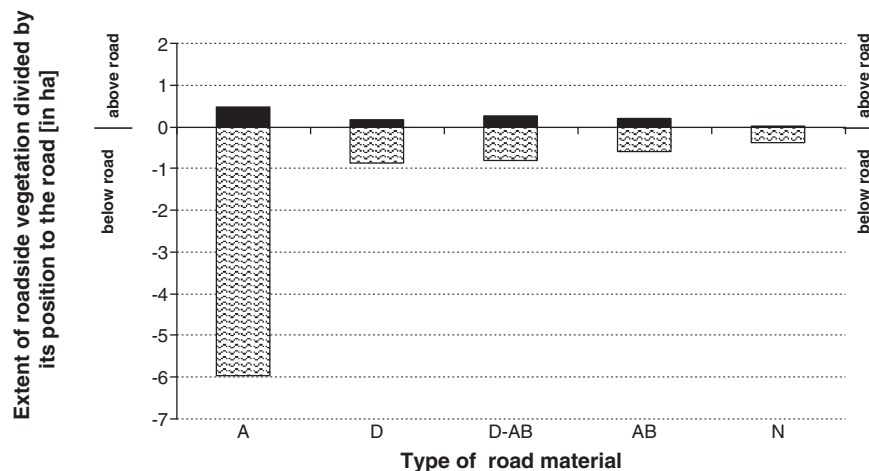


Fig. 3. Extent of roadside vegetation along differently stabilized roads in 1997 divided by its position relative to the road (above or below; A – asphalt; D – dolomite; AB – amygdaloidal basaltic rock; D-AB – dolomite-amygdaloidal basaltic rock mixture; N – granite).

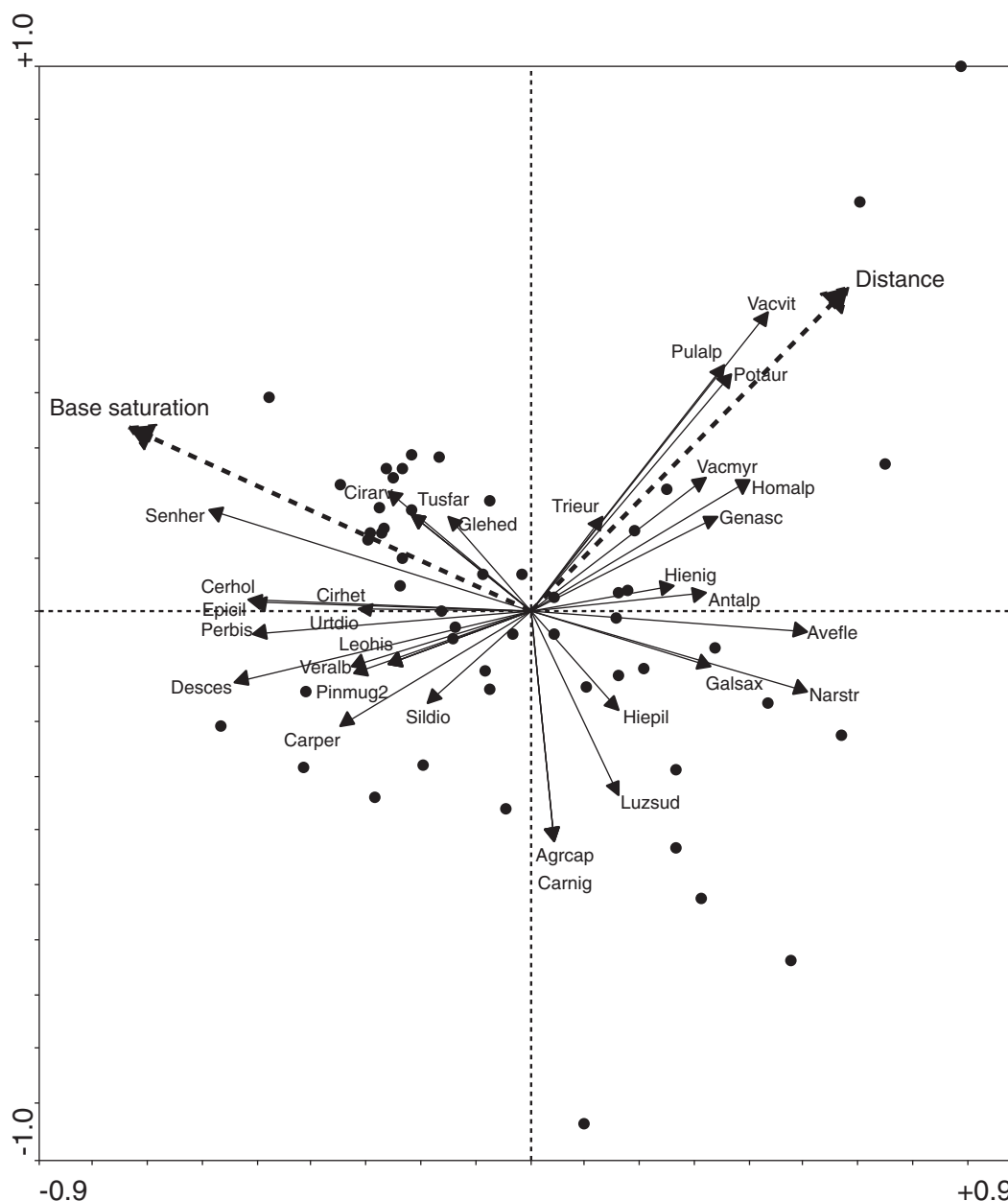


Fig. 4. RDA ordination diagram of 52 relevés from seven transects across differently paved roads arranged according to the linear response of 79 species (arrows). Dashed arrows indicate the most important environmental variables explaining the changes in vegetation along roads – base saturation in soil horizon A and distance from the road. Plant abbreviations include the first three letters of both the genus and species names given in online supplement; only species with fit $\geq 10\%$ are shown. Relevés were separated into road-altered (left side of the diagram) and natural vegetation (right side). The two canonical axes explain 22.3% of the variability in the dataset. Monte-Carlo permutation tests of the first canonical axis and of all canonical axes were significant.

comparably augmented. Dolomite and asphalt had the strongest effects, with maximum values of active pH 7.4 and 7.6, respectively, and base saturation up to 100% (Fig. 5). Mg^{2+} and Ca^{2+} in the adsorption complex along dolomite and asphalt roads reached much higher values compared to natural stands, with a positive content of carbonates detected. Along dolomite trail, the maximum values of $pH(H_2O)$ and base saturation were recorded right below the trail (within 1–2 m), while below the asphalt road the peak occurred at a distance of 9.5 m. Along AB trail soil physical–chemical conditions were similar to the natural conditions. Although an increased Ca^{2+} content of the adsorption complex was detected below such trail, Al^{3+} was still the dominating exchangeable cation at all distances, just as in natural stands.

The most important environmental variables associated with the changes in vegetation along roads, indicated by RDA, were base saturation in soil A horizon ($p = 0.002$) and distance from the road

($p = 0.002$, Fig. 4). These two variables explained 22.3% of the overall variability in the data; base saturation itself explained 16.5%, road distance 11%. The next environmental variables with the large influence such as pH, concentrations of Ca^{2+} , Al^{3+} , total carbon and nitrogen were narrowly correlated with the base saturation and they were not statistically significant after adding this variable into the analysis. Other physical–chemical soil properties and landscape elements had only low and non-significant influence.

Changes in vegetation structure affect comparably large areas of the alpine tundra ecosystem, unique to Central Europe, hosting many species of high conservation (some endemic). While meso- to nitrophilous species of tall grasses and robust herbs spread along the roads, many local stress-tolerant low competitive tundra species either disappear, or survive only in a sterile form. This applies also to the rare and protected species (Table 1). Sixteen IUCN threatened

Table 1

Responses of vascular plants to the road disturbance with examples of typical species. Endangerment by IUCN Red list criteria is marked in brackets (CR – critically endangered, EN – endangered, VU – vulnerable, NT – near threatened).

Responses to the road disturbance	Type	Species
Favored species	Species of man made habitats (synanthropic)	<i>Cirsium arvense</i> <i>Epilobium angustifolium</i> <i>Epilobium ciliatum</i> * <i>Plantago major</i> <i>Ranunculus repens</i> <i>Rumex alpinus</i> * <i>Taraxacum sect. ruderalia</i> <i>Urtica dioica</i>
	Species of lower elevation	<i>Achillea millefolium</i> <i>Hypericum perforatum</i> <i>Lotus corniculatus</i> <i>Poa compressa</i> <i>Prunella vulgaris</i> <i>Senecio ovatus</i> <i>Thlaspi perfoliatum</i> <i>Calamagrostis villosa</i>
Disappearing species	Competitive local species favored by the new conditions	<i>Campanula bohemica</i> (EN, endemic) <i>Cirsium heterophyllum</i> <i>Deschampsia caespitosa</i> <i>Persicaria bistorta</i> <i>Senecio hercynicus</i> <i>Veratrum album</i> subsp. <i>lobelianum</i> (NT) <i>Malaxis monophyllos</i> (CR)
	Rare species preferring open stands Rare species preferring alkaline soils Local stress-tolerant low competitive species	<i>Botrychium lunaria</i> (EN) <i>Gentianopsis ciliata</i> (VU) <i>Anemone narcissiflora</i> (CR) <i>Calluna vulgaris</i> <i>Gentiana asclepiadea</i> (NT) <i>Hieracium nigrescens</i> (EN, endemic) <i>Hieracium alpinum</i> (VU) <i>Homogyne alpina</i> ** <i>Hypochaeris uniflora</i> ** (VU) <i>Nardus stricta</i> <i>Potentilla aurea</i> (NT) <i>Pulsatilla alpina</i> subsp. <i>austriaca</i> (VU)

* Non-indigenous.

** Only sterile plants survive.

species have disappeared along roads in the area. Only during 2001–2004 period, four protected species reduced their cover or disappeared on transects itself (mostly from 30 to 120 m below the asphalt road).

4. Discussion

Our results showed fast changes in soil properties and species composition along roads in the study area. The expansion of roadside vegetation reflects improved nutrient availability resulting from the increase in pH (Fig. 7). In ecosystems with predominantly nutrient-poor soils dominated by stress tolerant plants, addition and augmented release of nutrients constitute a major disturbance, which has been shown in many examples to facilitate colonization by more competitive, often non-native species (Cale and Hobbs, 1991; Hobbs and Huenneke, 1992). Recorded augmentation of soil pH and base saturation agrees with findings of Wagnerová (1995) from the same study area (next to the road the pH reached 6.2 to 7.3) and Auerbach et al. (1997) from arctic tundra (regular pH 4, next to the road pH augmented up to 7.3).

Close to the road we found a high cover of synanthropic species and robust herbaceous plants, with higher number of vascular plant species and lower cover of mosses (Fig. 6, Table 1). With increasing distances from the road the vegetation became dominated by less competitive stress-tolerant species such as *Nardus stricta* L. This shift

in species composition reflects nutrient enrichment and disturbance along roads. The border between the natural and roadside vegetation was sometimes wide with unstable transitional vegetation of both categories.

The spread of roadside vegetation followed the slope. On terrain depressions leading down the slope from alkaline stabilized roads the roadside vegetation formed lobes reflecting the nature of the terrain and reaching far into undisturbed vegetation (up to 156 m from the asphalt road). In flat terrain, *Deschampsia caespitosa* L. (P.) Beauv. formed continuous narrow edges on both sides of stabilized trails. Changes in soil properties were also significantly dependent on the position relative to the road. This provides evidence of the role of water erosion in transporting particles leaching from road building material into the surroundings (c.f. Tossavainen and Forsberg, 1999). Dissolved nutrients from the road stabilizing material were transported down the slope and deposited on existing soil and vegetation (c.f. Forman and Alexander, 1998), gradually enriching originally nutrient-poor soils. This process is enhanced by high precipitation in the area. In other tundra studies (such as Auerbach et al., 1997) the road dust deposition was suggested to be the leading driver of road related vegetation changes. However, in our study the role of wind transport of alkaline particles was not found to be significant. On the other hand our results indicated that water transport plays an important role in soil alteration process (Fig. 7), and therefore we believe it deserves more attention in tundra ecosystem studies.

Asphalt road constructed with large amounts of dolomite and AB gravel was found to have the strongest effects on vegetation and soil properties. Compared to others, the peak in pH and base saturation values along asphalt road was shifted to 9.5 meters distance below the road. One of the reasons for such a shift could be the differences in water flow. During heavy rains the water flows fast over impermeable asphalt surface and graveled surfaces benching, and alkaline particles can thus drift further from the road. The slowly weathering AB had significantly less of an effect on soil and vegetation than easily dissolving dolomite. This could be explained by different times of building of the roads (dolomite road in 1970's, AB road in 1980's). Although AB seems to be less harmful than dolomite, its chemical composition with four times less CaO and MgO and 25 times more SiO₂ is still very different from natural bedrock.

While many rare or threatened tundra species disappear from the road surroundings, it can also provide suitable habitat for some rare species preferring nutrient rich, open or alkaline stands (Table 1). Among the local rare species favored by the roadside disturbance are endangered *Campanula bohemica* Hruby (endemite of Krkonoše), and near threatened *Veratrum album* subsp. *lobelianum* (Bernh.) Arcang. There are also new rare species appearing along alkaline stabilized roads that are present nowhere else in the area and illustrate dimension of road disturbance. Vulnerable *Gentianopsis ciliata* (L.) Ma is basiphilous species preferring xerophilous habitats and occurring rarely in mountain areas. Its natural elevational maximum in the Krkonoše Mts. is 850 m a. s. l. It was probably introduced to the alpine tundra (altitude of 1370 m a. s. l.) with dolomite used for road pavement. Its flourishing population is exclusively tightened to the body of former dolomite trail that was closed to the public thirty years ago and the population is slowly enlarging. Endangered *Botrychium lunaria* (L.) Sw. occurs naturally on meadows, pastures, screes, as well as in light forests, growing on alkaline to slightly acid soils. In the studied area it is found on disturbed stands on road edges with open trampled vegetation without respect to the type of paving material. It usually occurs in fertile solitary individuals, rarely forms more continuous stands. In 2005 three flowering individuals of critically endangered orchid species typical for colder and mountain areas *Malaxis monophyllos* (L.) Sw. were found in the road vicinity (1365 m a. s. l.). This occurrence represents the new elevational maximum of the species in the Czech Republic, and in Krkonoše Mts. the only other occurrence is in similar biotope of lower altitude (1198 m a. s. l.).

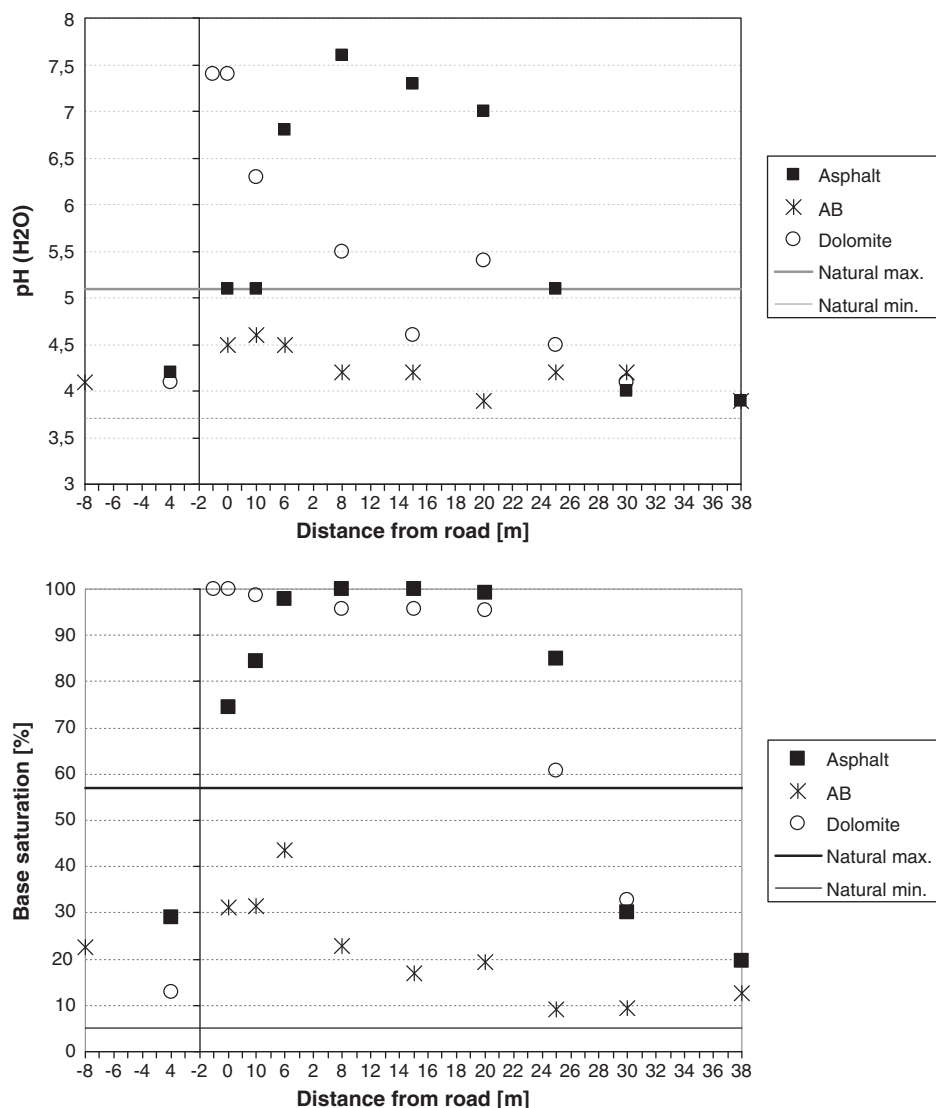


Fig. 5. Relationships among soil pH, base saturation, and the distance from roads stabilized with different material (AB — amygdaloidal basaltic rock). Transects of similar length A2, D1 and M were used in the figure. The orientation of transects followed the slope. Negative values for distance indicate the sample location “above” the road (up the slope); positive values indicate location “below” the road (down the slope, in the direction of flow of particles leaching from the road material). The first and the last samples were located in natural vegetation and represent the controls. The range of natural values (minimum–maximum) indicated by the lines is set according to Štursová (1985).

From such examples we can see profound shifts in species composition in the area. The extent of the road effect and high rate of spread of roadside vegetation indicated that the affected area has grown considerably. Repeated GPS measurements in 2004 confirmed high rate of roadside vegetation increase (0.28 times per year in 1986/1997, 0.25 in 1997/2004). According to these findings the hypothetical constant rate the road-affected area could cover is 13% of the study area by 2020. Expressive changes in vegetation structure of the alpine tundra might happen if no effective conservation measures were applied.

Considering the dimension and rate of changes in vegetation composition and biodiversity losses we proposed replacing the alkaline gravel by granite, especially from the asphalt road, even though expensive and technically complicated. Instead of macadam pavement we recommend the use of flagstone granite pavement to stabilize the roads suffering from water erosion. Although we consider the removal of alkaline material necessary to stop the alpine tundra ecosystem damage, we are aware that the reconstruction of trails (substitution of alkaline gravel by granite) represents a large interference with the fragile tundra ecosystem. During reconstruction roadsides (ca 2 meters wide) are often disturbed and cleared of vegetation, and such stands become subjected to ecesis of synanthropic species.

The ability of alpine tundra to recover in the extreme climatic conditions of Krkonoše summit plateau is limited and the process is expected to be slow. Estimates of the time required for recovery of severely degraded tundra range from more than 15 years (Scherrer and Pickering, 2006) to more than a century (Willard et al., 2007), or the recovery may not happen at all (Harper and Kershaw, 1996; Strandberg, 1997). Still, regarding the comparably fast recovery of disturbed sites in the study area (bodies and surrounding of the two former roads closed thirty years ago), although not so severely damaged, we consider the restoration possible. Based on our recommendations, the National Park Authorities started to reconstruct the trails in 2005.

5. Conclusions

The results of this study revealed that the changes in tundra ecosystem can be fast. The study recorded expansion of roadside and local competitive species deep into the natural vegetation (doubled in size during the studied decade), which resulted in the displacement of local plant communities and suppression of valuable and threatened species. Our findings support the assumption that the alteration of environment that resulted from the building of alkaline roads in the

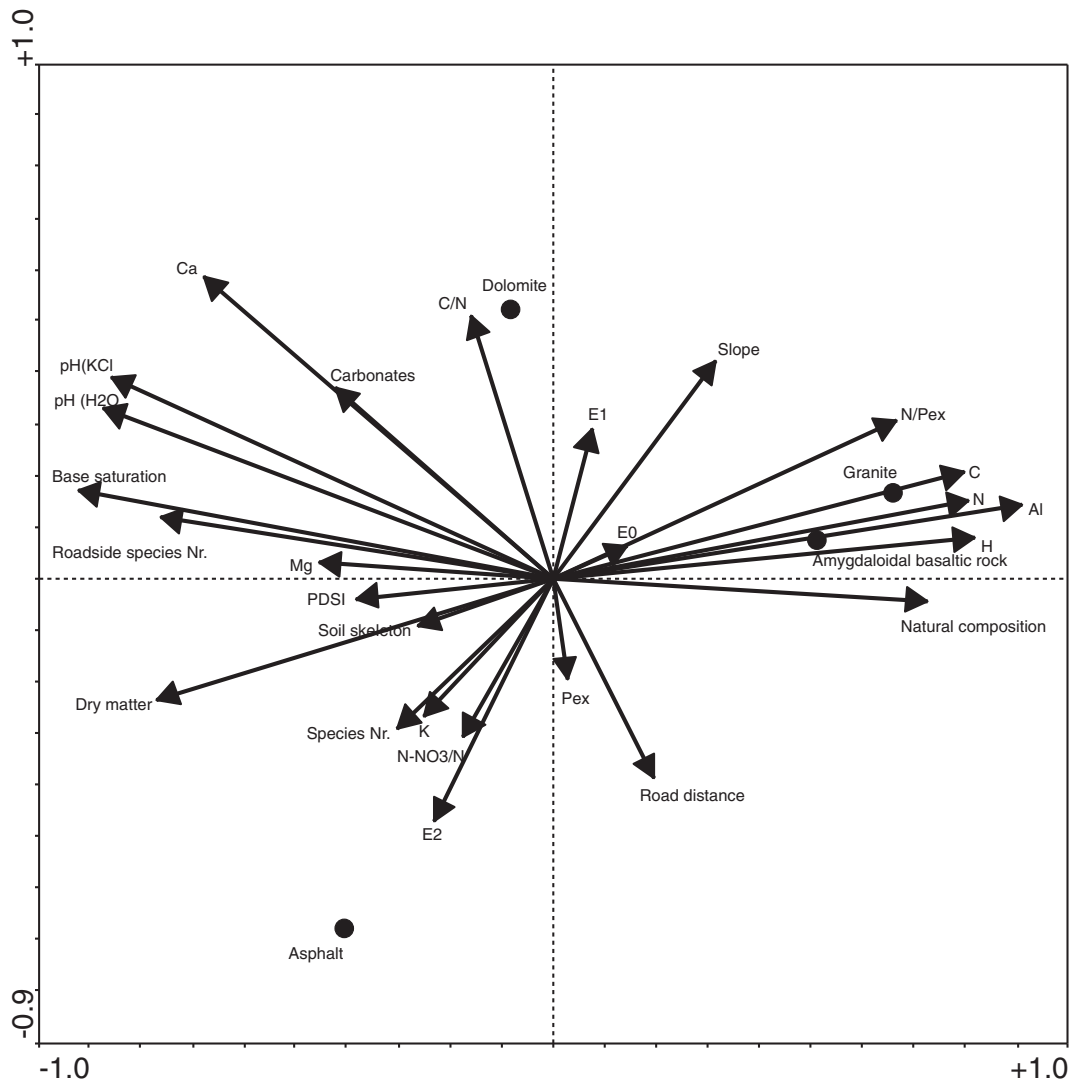


Fig. 6. Correlations among soil, landscape characteristics and species composition. PCA ordination diagram of 52 relevés from seven transects across differently paved roads. Points display categorical variable as the type of paving material (granite, amygdaloidal basaltic rock, dolomite, asphalt). Arrows represent quantitative variables as the site attributes (slope, PDSI), road distance, physical–chemical soil properties (soil skeleton, dry matter, pH, Ca^{2+} , Mg^{2+} , K^+ , Al^{3+} , H^+ , base saturation, $\text{N-NO}_3/\text{N}$, carbonates, N, C, and P_{ex}), and vegetation characteristics, such as cover of the shrub (E_2), herb (E_1), and moss layer (E_0 , no lichens were present); total number of plant species; number of roadside plant species; and natural composition (scores of plant species on first PCA axis expressing rate of autochthonous species in plot; see online supplement). These variables (29) were used as species data, scaling, and standardizing were performed due to usage of different units. The first axis explains 31.2% of the variability in the dataset.

1970's to 1990's represents a major driving force of changes. The expansion of roadside vegetation reflects improved nutrient availability resulting from the shifts of physical–chemical soil properties along roads stabilized with alkaline material with water transport playing the crucial role.

Arctic-alpine tundra represents a unique ecosystem in Central Europe of high conservation value hosting many rare and protected species including endemites. Long-term monitoring and detailed research of abiotic and biotic processes is important for its correct and effective management. Because future climate warming is expected to increase soil nutrient availability in tundra (Hobbie et al., 2002) similarly to the described road effect, the response of this sensitive ecosystem to climate warming could be similar to the vegetation changes described by our research (yet without supply of synanthropic

species such as in our case). Ongoing successive changes along roads of arctic-alpine tundra environment and vegetation recovery along reconstructed trails will be monitored in further research.

Supplementary materials related to this article can be found online at doi:10.1016/j.scitotenv.2011.06.056.

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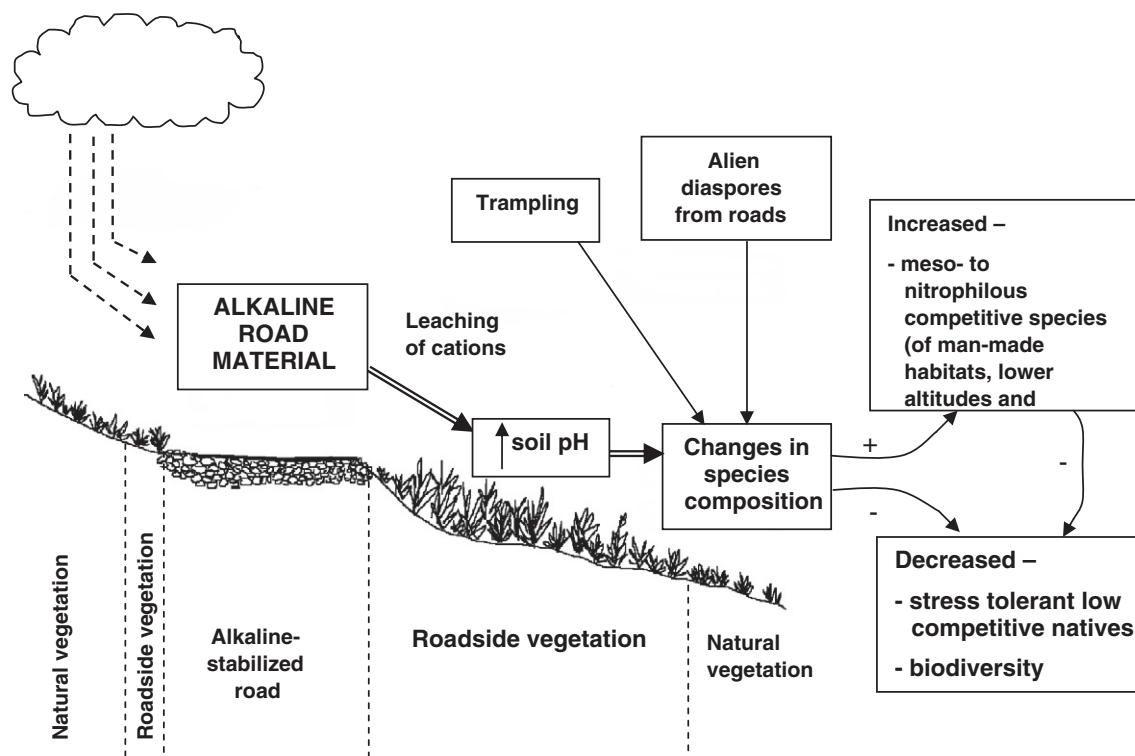


Fig. 7. Conceptual model of driving forces of studied changes in vegetation and soil conditions along alkaline roads.

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Appendix 10.

PAPER 10. Potůčková, M., Kupková, L., Červená, L., Lysák, J., Krause, D., Hrázský, Z., Březina, S. & **Müllerová, J.** (2021). Towards resolving conservation issues through historical aerial imagery: vegetation cover changes in the Central European tundra. *Biodiversity and Conservation* 30(12): 3433-3455. <https://doi.org/10.1007/s10531-021-02255-y>



Towards resolving conservation issues through historical aerial imagery: vegetation cover changes in the Central European tundra

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Abstract

Mountain ecosystems are considered to be sensitive to global change and human disturbance. Our retrospective analysis of archival aerial imagery showed dynamics of arctic-alpine tundra vegetation in the Krkonoše Mountains, Czech Republic; image classification revealed a change in land cover classes in 44% of the study area over the past eighty years. This particular ecosystem holds many rare features, such as high numbers of endemic, glacial relict and rare species as well as relict geomorphological components such as sorted patterned ground. Our study revealed an accelerating expansion of the native and planted shrub, *Pinus mugo*, from 30.6% of the study area in 1936 to 48.6% in 2018, mostly at the expense of grasslands that decreased from 59.3% in 1936 to 44.2% in 2018. Shrub expansion represents a threat to relict periglacial landforms, covering 8% of the sorted patterned ground in 1936 and 26.5% in 2018. Shrub encroachment was shown to be due to artificial planting of the pine in the past as well as the cessation of former farming (mowing and cattle grazing) and, most probably, also by global change. Both dwarf pine stands and tundra grasslands hold high conservation value (Natura 2000 habitats); a balance between different nature protection interests must, therefore, be ensured. Detailed spatio-temporally, explicit outputs of the remote sensing analysis can serve as a baseline for nature conservation in order to prepare corresponding management plans.

Keywords Krkonoše Mountains · Shrub encroachment · Relict tundra · Management · Spatial–temporal analysis · Remote sensing

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Introduction

High mountain ecosystems are generally regarded as relatively untouched. In recent years, however, mountains have been subject to increasing threats due to globalisation, global change, changing land use, and growing human pressure (Pauchard et al. 2009). Because of their steep environmental and climatic gradients, mountains are especially sensitive to climate change (Beniston 2003) and atmospheric nitrogen deposition (Bowman et al. 2006; Lavoie et al. 2011). Subalpine and alpine zones are predicted to be the most affected by increased temperatures and reduced snow cover, resulting in a major impact on biodiversity (Klanderud 2005). Besides global change, increasing human disturbance represents a major threat since these ecosystems are fragile and sensitive to any kind of direct human impact, such as trampling, ruderalisation and eutrophication (Becker et al. 2005). This is due to a number of factors, including short growing seasons, low temperatures, low primary productivity and the sensitivity of vegetative and organic surface layers to any disruption of their physical integrity or the thermal régime (Reynolds and Tenhunen 1996).

The Krkonoše Mountains represent the highest mountain range in the Czech Republic. They are placed along the border with Poland. Its two subalpine plateaus (1300 m to 1600 m a. s. l., 50°44' N, 15°42' E and 50°46' N, 15°33' E) above the timberline form a particular landscape system called “alpine” or “arctic-alpine tundra”, displaying affinities to both subarctic and high-mountain regions (Gordon et al. 2002; Fig. 1). Despite its small size (47 km²), the tundra represents one of the most valuable ecosystems in the Krkonoše National Park (NP) and in the country. Since it hosts many endemic, glacial relict and rare species as well as unique habitats and valuable periglacial landforms, it is also unique in Europe (Soukupová et al. 1995; Štursa 1998; Flousek et al. 2007).

Nature conservation of such a specific ecosystem poses many challenges, including competition between tourists' interest in the country's highest mountains and the protection of these vulnerable habitats. Owing to its remoteness, extreme weather conditions and

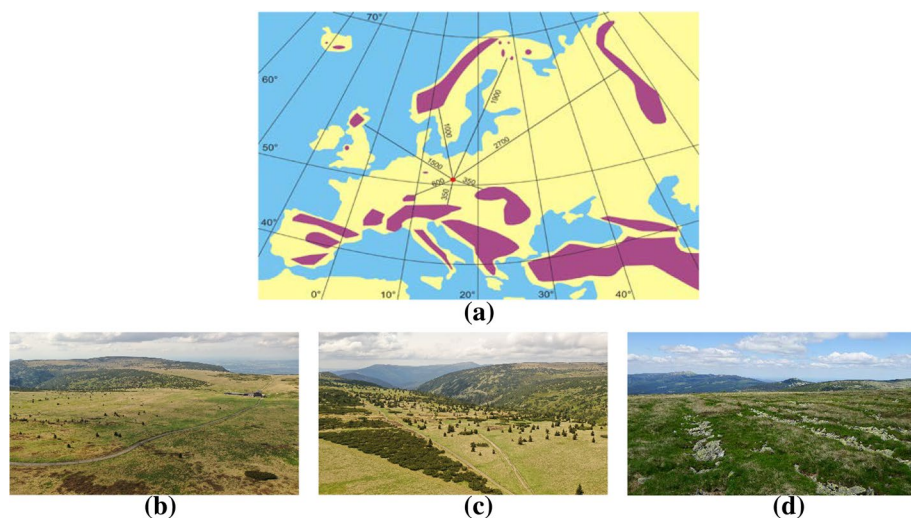


Fig. 1 Geographic location of the Krkonoše Mountains arctic-alpine tundra in relation to European subarctic and high-mountain regions; approximate distances in km (adopted from Kociánová et al. 2015) (a). A view of tundra grasslands (b), areas of planted dwarf pine (c) and patterned ground (d)

very low productivity, the area was traditionally considered as almost untouched by human activities. The truth is, however, that for centuries, humans have, to certain degree, interfered with the Krkonoše arctic-alpine tundra. Remnants of historical management (though not very extensive) together with current high tourism impact and effects of global change can, on the one hand, threaten this fragile ecosystem and, on the other, possibly support biodiversity. Traditionally, this area was considered to be the best protected by non-intervention. In light of the history of human presence in the uppermost areas of the Krkonoše Mountains, the question remains as to what extent the mosaic of tundra unique habitats and plant communities was actually supported by past human activities. Although for inhabited landscape, the role of low-intensity traditional management in conserving grasslands is widely recognised (e. g. Halada et al. 2011), it must be borne in mind that human activities in tundra, especially agriculture, were occasional and extensive. Still, cessation of traditional management (shrub-cutting, irregular hay harvesting, extensive cattle grazing) and afforestation activities possibly could, in the long-term, reduce some of the valuable plant assemblages such as herbs and grasses at the expense of others, typically, woody plants. On top of that, afforestation activities must have largely altered the relative proportion of grasslands and woods.

In our paper, based on time series data from historical aerial photography, we try to answer the question by assessing vegetation change in the Krkonoše tundra over the last eighty years. We focus on habitats of high conservation value, such as the ‘Natura 2000’ habitats, namely, semi-natural, endemic-species-rich habitats. We also deal with relict periglacial landforms (patterned ground) and explore the link between the observed transitions among vegetation types and changes in management (from traditional low-intense farming and logging towards strict nature protection via a non-intervention régime).

Our study aims to evaluate the Krkonoše tundra vegetation cover dynamics between years 1936 and 2018. Archival, remote-sensing data can serve as a valuable (and probably the only) source for such a long-term comparative study. In recent decades, proliferation of shrubs into grasslands was observed in the field, especially at the edges of the trails (Harčarik 2007). Herein, we present a quantitative, time-dependent assessment of grassland to shrub ratio and link the observed patterns to the management history in order to see if the shrub encroachment has accelerated in recent decades. We hypothesise that traditional human activities could, in the past, have played an important role in supporting grasses over shrubs, and that current non-intervention management might not guarantee the preservation of the balance between these key players in the tundra ecosystem. Thus, we also aim to provide a baseline for biodiversity conservation guidelines.

Materials and methods

Study area

Environmental conditions

The study area covers relict arctic-alpine tundra representing one of the most valuable ecosystems of the Krkonoše Mountains NP, Czech Republic (Soukupová et al. 1995; Schwarz 1997; Krahulec et al. 1996; Chytrý et al. 2007). During the cold periods of the Pleistocene and beginning of the Holocene, its typical plateau surface was affected by cryogenic, nivation, eolic and glacial processes and is maintained by the current quasi-periglacial climate

(Sekyra 1964; Fanta 1969; Pelíšek 1974; Traczyk and Migoń 2003). In our study, we focus on the eastern plateau (50°44' N, 15°42' E, 16 km²).

The tundra ecosystem is, to large extent, formed by extreme climate conditions (mean annual temperature from 0 to +1 °C, mean annual rainfall about 1400 mm, strong north-western winds and snow-cover lasting on average 180 days, Soukupová et al. 1995). Bed-rock is either crystalline igneous and/or metamorphic rocks, covered by nutrient-poor acidic soils of the alpine sod podzol type, patches of peatlands, raised bogs and sorted patterned ground (Štursová 1985). Sorted patterned ground represents a unique relict component of the Krkonoše arctic-alpine tundra. These landforms are typical for periglacial environments, showing geometric patterns of polygons, irregular nets and stripes (French 2017) and cover total of 1.7 km², i.e., 10.18% of the study area (Křížek et al. 2019). They originated by frost sorting processes during the last glacial period (Traczyk and Migoń 2003; Křížek and Uxa 2013; Engel et al. 2021) and were not active during the Holocene (Trembl et al. 2010). Thus, they are palaeogeographically significant since their morphometric parameters related to the depth of the former active layer above permafrost can be used to estimate the climatic conditions of their origin (Uxa et al. 2021). Moreover, these periglacial features are unique even from the European perspective since similar landforms in Scandinavia have different age and history of development (Matthews et al. 1998; Trembl et al. 2010).

The tundra vegetation is characterised by a mosaic of subalpine grasslands dominated by matgrass (*Nardus stricta*) and sedges, dwarf pine stands (*Pinus mugo* Turra), subalpine peat bogs, slopes of glacial cirques and rock outcrops, sparse alpine grasslands on base-poor soils and lichen tundra in the highest elevations (Soukupová et al. 1995; Flousek et al. 2007). The tundra hosts a number of rare species, some of them endemic: e.g., various *Hieracium* species, or glacial relicts related to the northern tundra, e.g., *Carex bigelowii* Torr. ex Schwein (Soukupová et al. 1995; Flousek et al. 2007). Habitat mapping of the Czech Republic (AOPK 2019; Härtel et al. 2009) described 29 habitats and 68 biotopes for the Site of Community Interest Krkonoše, and 14 habitats and 29 biotopes specifically for the study area (for details see European Commission 2013; Chytrý et al. 2010).

Human impacts and threats

The first important human impact in the area is connected to the road network and summer farming, the consequent building of the first chalets above the timberline in the sixteenth century (Luční bouda chalet), followed by clear cuts of dwarf pine. The second half of the nineteenth century saw the peak of grazing and regular hay management of the low productive grassy tundra. Matgrass grasslands were considered of low value and were thought to be of human origin following farming and dwarf pine clearcutting. A period of erosion events with several extensive landslides in 1882 to 1900 provoked a first wave of “replanting” the dwarf pine (and, to a certain extent, also the Norway spruce) in the area, continued in the 1930s and again after WWII (Lokvenc 2001). Unfortunately, the planting did not often respect the natural distribution of dwarf pine and was carried out even on valuable patterned ground that could probably never been covered by the shrubs in the past (Sekyra et al. 2002). Just before WWII, a network of fortifications was built on the uppermost areas along the border to protect the country.

Tourism had already started to play a major role in the area in the eighteenth century. Being the highest mountains of the country and a popular destination for cross-country and downhill skiing, hiking and mountaineering, the region has suffered from increasing

tourist pressure ever since. From 1946 to 1949, a chairlift to the country's highest mountain Sněžka was constructed, further facilitating the access to the eastern ridges of the Krkonoše Mountains. The increasing number of visitors (750,000 tourists in Krkonoše in 1938; 1.4 million already in 1950; up to seven million in 1970, and more than eight million nowadays with half a million in the tundra itself per year) cause trampling, soil erosion, noise, pollution, dispersal of alien plant diaspores, building activities and fragmentation of habitats (Gordon et al. 2002; Štursa 1998). To reduce the negative impacts on the fragile mountain ecosystems, national parks (the Karkonosze NP on the Polish side and the Krkonoše NP on the Czech side) were declared in 1959 and 1963, respectively, with the tundra designated as a core zone. In 1992, Krkonoše/Karkonosze transboundary biosphere reserve was established. The region is a part of the Ramsar Convention, the Long-Term Ecological Research Network, EUROSITE and other networks.

The high numbers of visitors cause heavy pressure on the fragile, arctic-alpine tundra ecosystem. There are many tourist facilities built—even in the core zone—such as, chalets and trails/roads, some of them built in the 1970s to 1980s using unsuitable alkaline material that markedly altered the soil properties and caused profound changes in the tundra ecosystem (Müllerová et al. 2011; Vítková et al. 2012). The planting of dwarf pine (1930s, 1960s to 1980s) and the cessation of traditional farming, coupled with an increase in the nitrogen availability and global warming changed the long-term coexistence of grasslands and dwarf pine stands (Wild and Winkler 2008; Štursa and Wild 2014). Dwarf pine and dominant grasses such as *Calamagrostis villosa* (Chaix) J. F. Gmelin and *Molinia caerulea* (L.) Moench were observed to outcompete species rich matgrass communities (Harčarik 2007; Hejčman et al. 2009, 2010), placing many rare species in danger. Overgrowth by dwarf pine can also disrupt the patterned ground structure (i.e., induce movement of clasts from their original position) due to root and branch pressure on individual clasts (Sekyra et al. 2002), and thus poses a danger to these unique features (Trembl and Křížek 2006).

Image processing

The first aerial survey covering the entire area of the Krkonoše Mountains was carried out in 1936. Since the 1950s, the area has been covered approximately once a decade. For the purpose of this study, five surveys in approximate 20 year periods were selected (1936, 1953, 1977, 2001, and 2018). Scanned aerial photographs from 1936 and 1977 needed to be orthorectified. Scanning was performed on the certified photogrammetric scanner with the geometric distortion below 0.002 mm and the resolution of 0.015 mm/pixel. The orthorectification was carried out using PCI Geomatica. The parameters of interior and exterior orientation were not available. Approximations using a camera constant exposed on the image panel and distances between fiducial marks measured in the image-processing software were used. Exterior orientation was determined by means of bundle adjustment using 3D control points derived from existing orthoimages and a digital terrain model (horizontal accuracy of 0.25 m and vertical accuracy of 0.3 m). The rest of the imagery was provided as orthoimage products by the Krkonoše Mountains NP Administration (2001 and 2018) and the Czech Environmental Information Agency (1953) with quoted horizontal error up to 2 or 3 pixels in orthoimages from 2001/2018 and 1953, respectively. All the orthoimages were resampled to a pixel size of 0.5 m. A rigorous visual check of geometrical alignment was performed on well-defined objects over the whole area studied, concluding that the images were aligned on a pixel level and local misalignments exceeding claimed accuracy were not present. Thus, the achieved relative geometric accuracy of

Table 1 General characteristics of orthoimagery used for the land cover classification

Year of acquisition	Type of the camera	Spectral range	Ground sampling distance
1936	Analogue	Panchromatic	0.5 m
1953	Analogue	Panchromatic	0.5 m
1977	Analogue	Panchromatic	0.5 m
2001	Analogue	RGB	0.5 m
2018	Digital	R, G, B, NIR	0.10 m

All images were acquired in June or July, their radiometric resolution is 8bit (for each band in case of multispectral images)

Table 2 The classification scheme applied for all time horizons

Name of the class	Description
Grasslands	Grasslands (dominated mostly by matgrass, <i>C. villosa</i> and <i>M. coerulea</i>), and <i>Vaccinium</i> and <i>Calluna</i> stands
Dwarf pine	Dwarf pine stands
Blockfields	Rocks, scree, stones, blockfields and rubble
Sparse forest	Trees, mostly Norway spruce, above 2 m in height with cover up to 30%
Artificial surfaces	Roads, trails, buildings, parking lots etc
Water bodies	Lakes in the peat bog (water streams are not included since their width was below the image resolution)

the multitemporal dataset was high enough not to affect the changes detected across the time horizons. Table 1 summarises the main characteristics of the orthoimagery used.

Suchá et al. (2016) classified 11 vegetation species (including nine herb categories) from multispectral aerial orthoimages. Spectral resolution and radiometric quality of the scanned panchromatic photographs did not allow individual herb species to be distinguished. Thus, the classification scheme comprises only six categories (Table 2). In 1936, part of the study area was not covered, and the “no data” category was introduced.

The object-based image analysis (Blaschke et al. 2008) was selected as the most suitable classification method due to the high spatial resolution of all imagery and low radiometric quality of panchromatic images. The method allows applying not only spectral but also geometrical (e.g., size and shape of the objects) and spatial (e.g., neighbourhood to a specific class) features. The classification was carried out using Trimble eCognition software. Based on previous experience with segmentation of aerial orthoimagery (Suchá et al. 2016; Müllerová et al. 2013; Brůna et al. 2013) supported by several tests carried out with the above-described datasets, the scale and shape parameters (25 and 0.5, respectively) were applied to segment all orthoimages. The minimal mapping unit thus corresponds to 0.5 m² and 1 m in area and length, respectively. Smaller objects (e.g., small single Norway spruce trees or narrow water streams) were not recognised and were subsumed into the surrounding classes.

Mean brightness was the main parameter used for classification of the panchromatic orthomosaic. Other features such as the ratio of the object height and width, heterogeneity, and shape (asymmetry) were further used in the classification (Fig. 2).

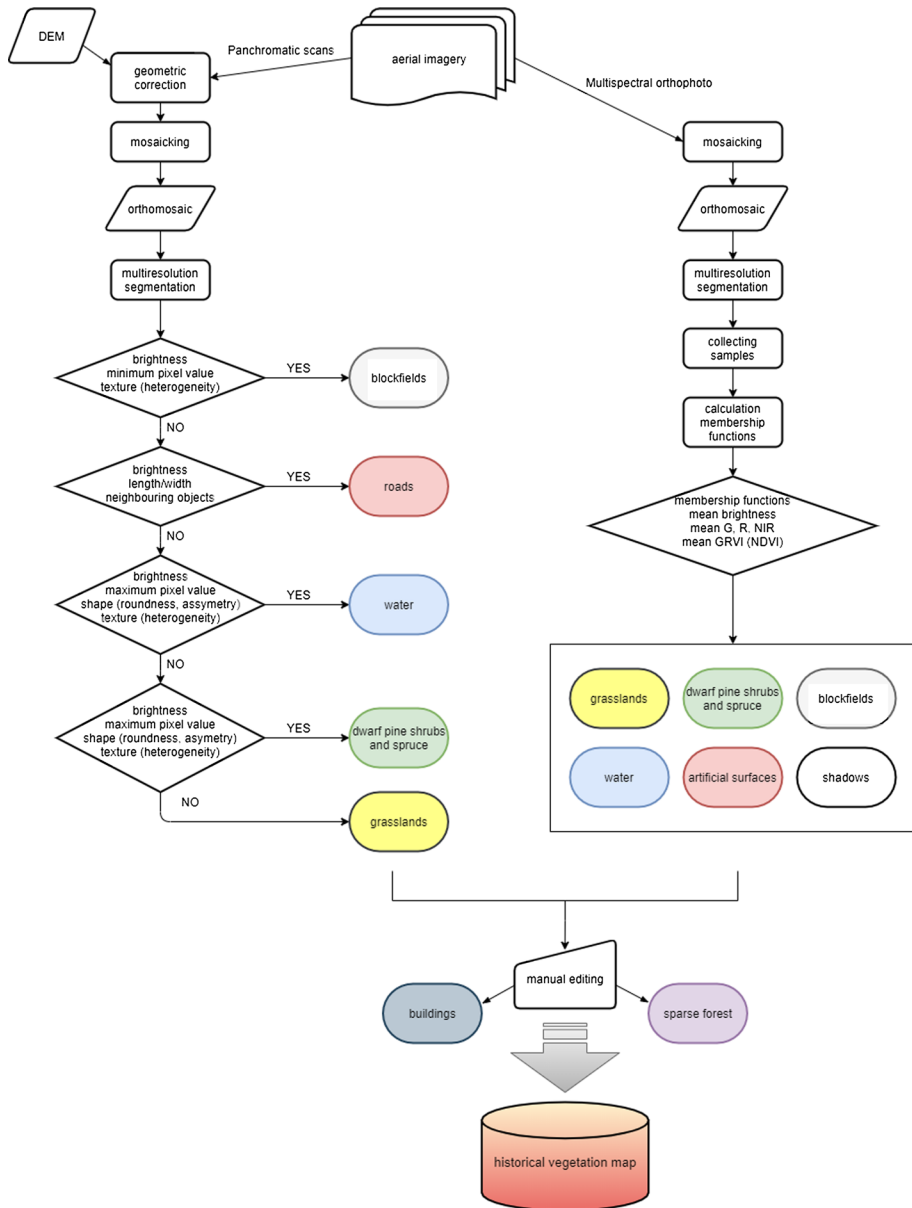


Fig. 2 Classification scheme

In the case of multispectral images from 2001 (R, G, B) and 2018 (NIR, R, G), samples of each class were selected manually in the respective orthoimages, and membership functions of the following features were calculated: mean brightness, mean DN value in the three respective multispectral bands, mean value of the Green–Red Vegetation Index $GRVI = (G - R) / (G + R)$ and, in the case of the 2018 imagery, also the mean value of the Normalised Difference Vegetation Index $NDVI = (NIR - R) / (NIR + R)$. The option

“calculate membership function” of the eCognition software was used to automatically derive the shape and limits of the membership functions.

The outputs of the above-mentioned, automated processes were edited manually with respect to artificial surfaces, shadows, and classification errors. All classified segments were exported from eCognition as a shapefile and further edited in ESRI ArcMap. The segments corresponding to buildings, roads and paved paths were manually attributed as artificial surfaces. In colour images, shadows were originally discriminated as a separate class. After export to ArcMap, based on visual interpretation of the orthoimage, the segments labelled as shadow were manually reclassified as either dwarf pine or grasslands. The majority of segments were checked manually and classification errors were corrected, including any inconsistencies in the time horizons. The retrospective comparison of classification results was especially advantageous in the case of water bodies and blockfields that were difficult to discriminate from panchromatic images. Although the manual check was a very time-consuming process, it was necessary in order to achieve the highest possible accuracy. Except for the 2018 layer, no accuracy assessment was carried out because no external archive data sets of higher quality were available. The accuracy assessment could be performed by means of visual inspection carried out with the same imagery which would not bring any added value because correction of classification had already been done in the same way.

In order to assess classification accuracy, the 2018 layer was independently checked by a visual inspection using a true colour (RGB) orthoimage with an original spatial resolution of 0.1 m pixel. Following Foody (2009), the validation was based on 385 check points with the distribution stratified according to the area of each class, and a minimum of 20 points per class (Table 3). The overall accuracy and the Kappa index achieved 92.3% and 0.89, respectively.

The five layers comprising segments classified into six land cover classes were finally transformed to a five-band raster with a cell size of 0.5 m. Thus, each pixel contained the code of the corresponding land cover category in each of the five studied years. Consistency among time horizons was re-checked. After running an automated procedure, manual checking was carried out only in cases where classification in one time-horizon differed

Table 3 Accuracy assessment of 2018 classification

		Validation data						Sum classification data	User's accuracy [%]
		D	G	W	B	A	F		
Classification	D	166	10	0	1		0	177	93.8
	G	8	145	0	1	0	0	154	94.2
	W	0	3	17	0	0	0	20	85.0
	B	2	3	0	45	0	0	50	90.0
	A	0	2	0	0	18	0	20	90.0
	F	3	1	0	0	0	16	20	80.0
	Sum validation data	179	164	17	47	18	16	441	
Producer's accuracy [%]		92.7	88.4	100.0	95.8	100.0	100.0		

Classes are dwarf pine (D), grasslands (G), water bodies (W), blockfields (B), artificial surfaces (A), and sparse forest (F)

from the other four, and the segment was larger than 100 m². Finally, the extent of all land cover classes in the five studied years, stable areas, and changes between the time-horizons were calculated.

Ancillary data sources

The latest classification results of 2018 were overlaid with the vector layer of the Habitat Mapping of the Czech Republic (AOPK 2019; Härtel et al. 2009) to compare classification results with the vegetation map prepared by field botanists in the scale of 1: 5000. This layer contains polygons classified in vegetation units following Chytrý et al. (2010). These are further referred to as “biotopes”. The share of biotopes within each land cover class was calculated. Biotopes (Härtel et al. 2009) were converted to habitats of Natura 2000 (European Commission 2013) based on the conversion table in Chytrý et al. (2010) and on corrections mentioned in remarks of Table 9 in Appendix 1, and subsequently, the ratios of Natura 2000 habitats were derived for each land cover class.

Polygons with biotopes of high conservation value (Härtel et al. 2009) were extracted to investigate the rate of successional changes in these priority areas. To select the polygons, both parameters “typical species” and “structure and function” (or “quality” and “representativeness in the older version of the database) had to be marked within the most favourable grades (see Härtel et al. 2009 for details). Transitions from grassland to dwarf pine were analysed within these priority polygons (sum area of 283 ha) and the results were related to the dwarf pine expansion over the rest of the study area.

A map of Lokvenc et al. (1992) showing the dwarf pine origin, year of plantation and the density of shrubs as mapped in 1992 was used in order to compare the dynamic of natural expansion and planted dwarf pine at the study area.

Finally, the land cover classification results for the whole study period were compared with the spatial distribution of sorted patterned ground (i.e., areas of sorted polygons, sorted nets and sorted stripes) published in Křížek et al. (2019). The changes in dwarf pine derived from the retrospective image analysis were related to the patterned ground, artificial dwarf pine plantations and natural dwarf pine stands.

Results

Long-term dynamics

Analysis of historical imagery over the last eighty years showed that the Krkonoše tundra constitutes a rather stable landscape (Fig. 3). Over half of the study area did not show any changes during the study period, i.e., pixels were assigned to the same class in all time-horizons (Table 4). The most pronounced changes happened in between dwarf pine and grassland classes—dwarf pine showed a marked expansion from 30.6% of the study area in 1936 to 48.6% in 2018, mostly at the expense of grasslands, which decreased from 59.3% in 1936 to 44.2% in 2018 (See Table 10 in Appendix 1).

During the entire study period of eighty years, dwarf pine stands showed continuous expansion over the former grasslands with maximum shifts happening between 1955 and 2001 (Table 5; for full matrices See Table 11 in Appendix 1). During the most recent period (the twenty-first century), nature conservation began protective measures to reduce dwarf pine in the most valuable parts of tundra (NP core zone). Figure 4 (below Table 5)

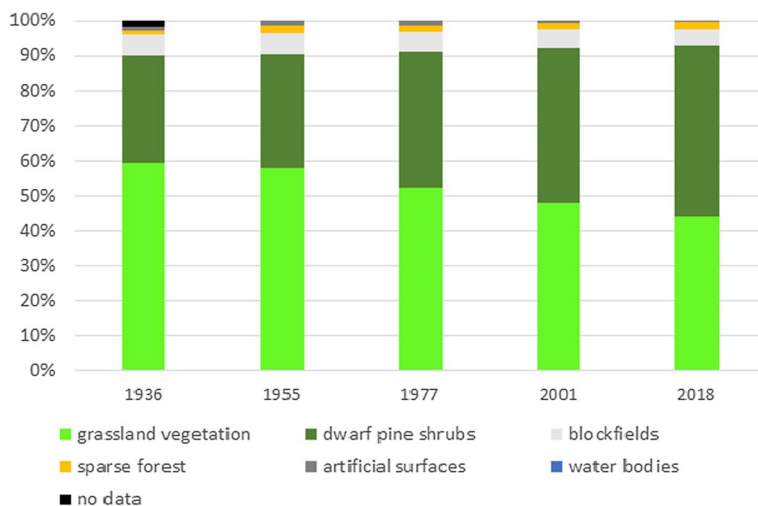


Fig. 3 Proportions of classified land cover classes in the total area of 1675.4 ha in the five evaluated time-horizons. The absolute values can be found in Table 10 in Appendix 1

Table 4 A stable area that did not show any changes during the studied eighty-year period

Class	Stable area [ha]	% of the area of interest
Grasslands	548.1	32.71
Dwarf pine	335.5	20.02
Blockfields	41.4	2.47
Sparse forest	9.7	0.58
Artificial surfaces	2.8	0.17
Water bodies	0.2	0.01
Sum	937.7	55.97

Table 5 Changes of selected land cover classes between the evaluated time-horizons, related to the total study area (1675.4 ha)

Original class	New class	Changed area [% of the total area]				
		Period of change				
		1936–1955	1955–1977	1977–2001	2001–2018	1936–2018
Grasslands	Dwarf pine	6.0	9.7	10.3	7.1	18.3
Dwarf pine	Grasslands	4.7	4.2	5.2	2.9	2.7
Blockfields	Dwarf pine	0.3	0.9	0.9	0.4	1.3
	Grasslands	1.6	1.4	1.3	0.9	1.3
Artificial surfaces	Dwarf pine	0.0	0.1	0.2	0.1	0.2
	Grasslands	0.5	0.6	0.6	0.2	0.6

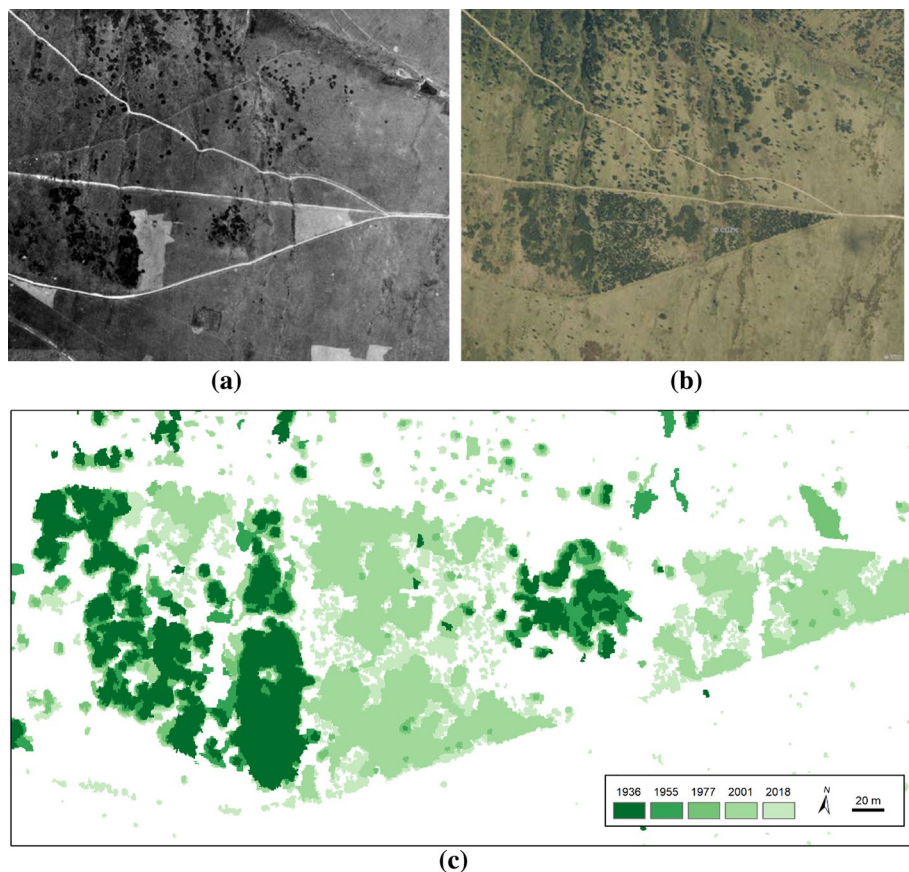


Fig. 4 Historical dynamics of the Krkonoše tundra in the last eighty years. On an aerial image from 1936 (a), freshly-mown patches of grassy tundra (the last documented farming in the area) are visible in white. Some of the former managed grasslands (in the middle part surrounded by trails) were forested with dwarf pine in the 1970s, and are already well developed on the current orthophoto from 2018 (b). Natural expansion of dwarf pine into former grassy tundra is visible mainly in the upper half of the area. The subset c shows the dynamics of dwarf pine based on land cover classification, from the dark (the oldest) to the light green (the youngest)

shows an example of farmed grassy tundra with mown patches on the oldest aerial photograph from 1936, and dwarf pine plantations (dense and regular patterns, often at the place of former farming) as well as naturally expanding pines (usually forming open, irregular patches) on the latest orthophoto from 2018.

Comparison with ancillary data

The land cover map obtained from 2018 images was overlaid with the Natura 2000 habitats. Table 6 shows habitats where only one classification type was expected to be dominant. Habitats showing over 75% correspondence with classification were considered as correctly classified. Six out of eight habitats were expected to be classified as grasslands

Table 6 Representation of land cover classes mapped from 2018 aerial imagery overlaid by Natura 2000 habitats

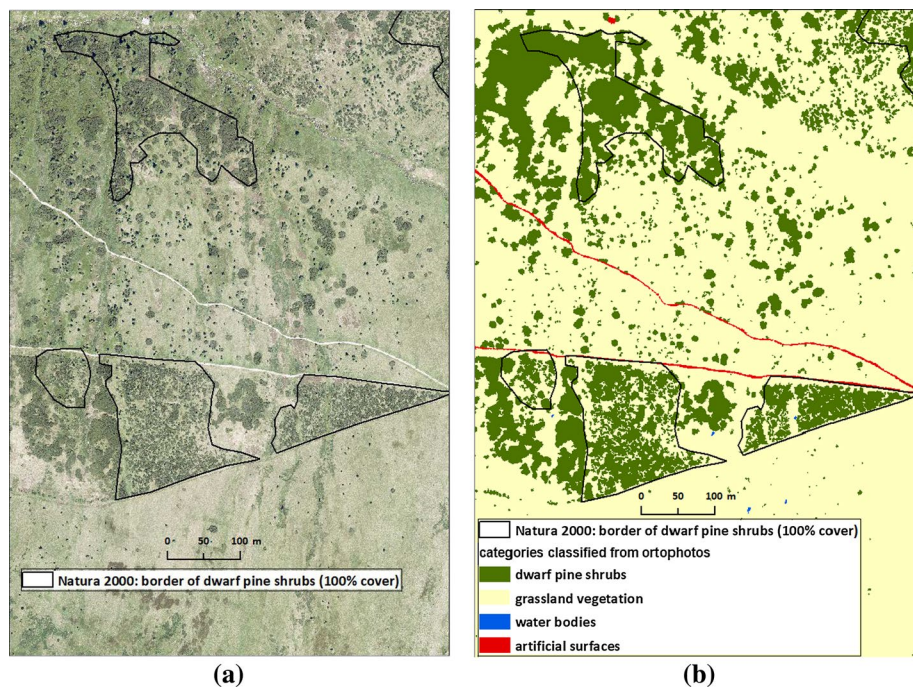
Natura 2000 habitats	D	G	W	B	A	F	Sum
6150 Siliceous alpine and boreal grasslands	13.93	83.53	0.01	2.05	0.46	0.02	100.00
4030 European dry heaths	7.60	90.47	0.00	1.93	0.00	0.00	100.00
4060 Alpine and boreal heaths	20.72	70.64	0.00	7.26	0.61	0.76	100.00
4070 Bushes with <i>Pinus mugo</i> and <i>Rhododendron hirsutum</i> (<i>Mugo-Rhododendretum hirsuti</i>)	81.04	15.58	0.00	1.83	0.23	1.31	100.00
6230 Species-rich <i>Nardus</i> grasslands on siliceous substrates in mountain areas	28.30	68.44	0.00	0.46	2.80	0.00	100.00
4080 Sub-Arctic willow scrub	88.15	10.10	0.00	0.35	0.00	1.40	100.00
6430 Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels	15.95	76.61	0.03	2.92	0.71	3.77	100.00
6520 Mountain hay meadows	14.93	83.32	0.02	0.00	1.73	0.00	100.00
7110 Active raised bogs	15.03	83.32	1.43	0.00	0.22	0.00	100.00
7140 Transition mires and quaking bogs	7.17	91.02	0.10	1.70	0.00	0.00	100.00
8110 Siliceous scree of the montane to snow levels (<i>Androsacetalia alpinae</i> and <i>Geleopsietalia ladani</i>)	34.34	21.24	0.00	43.77	0.20	0.45	100.00
8220 Chasmophytic vegetation on siliceous rocky slopes	29.86	39.46	0.00	28.12	0.06	2.50	100.00
91D0 Bog woodland	40.40	50.27	0.00	1.22	0.00	8.11	100.00
9410 Acidophilous spruce forests (<i>Vaccinio-Piceetea</i>)	57.72	29.98	0.00	1.60	0.27	10.42	100.00
Non-natural habitats	9.84	24.05	0.00	0.56	46.49	19.05	100.00
Other natural habitats	43.87	53.26	1.25	0.87	0.21	0.55	100.00

Values shown are in percentage terms

Key: Dwarf pine – D, Grasslands – G, Water bodies – W, Blockfields – B, Artificial surfaces – A, Sparse forest – F

Table 7 Comparison of Habitat mapping of the Czech Republic (Chytrý et al. 2010) and classification of aerial imagery from 2018

Class	Natura 2000 [ha]	Classification 2018 [ha]	Difference [ha]	Difference in % related to 2018 classification
Grasslands	715.1	738.4	− 23.3	3.2
Dwarf pine	766.1	813.2	− 47.1	5.8

**Fig. 5** Comparison of dwarf pine stands mapped by the Natura 2000 methodology (Habitat A7 – 100% cover of dwarf pine; marked by the black line) (a) and those classified from the 2018 orthoimage (in green) (b)

and both habitats expected to belong to the dwarf pine class were correctly classified. This is opposite to blockfields and sparse forest that were far below the 75% threshold.

The total area of grasslands and dwarf pine obtained from the latest orthophoto of 2018 were compared to Habitat mapping of the Czech Republic (Chytrý et al. 2010) using a simple transformation (See Table 9 in Appendix 1). Their correspondence is high despite very different mapping methodologies and resolution (Table 7; Fig. 5).

Habitats of high conservation value (Härtel et al. 2009, see Methods for details) covered 283.1 ha of the study area, and 9% of them turned from grassland to dwarf pine during the analysed time period. By comparison, the overall change from grasslands to dwarf pine happened in 15% of the study area.

Dynamics of the dwarf pine growth under the natural conditions and in plantations was compared using a digitised map created by Lokvenc et al. (1992). Between 1936 and 2018,

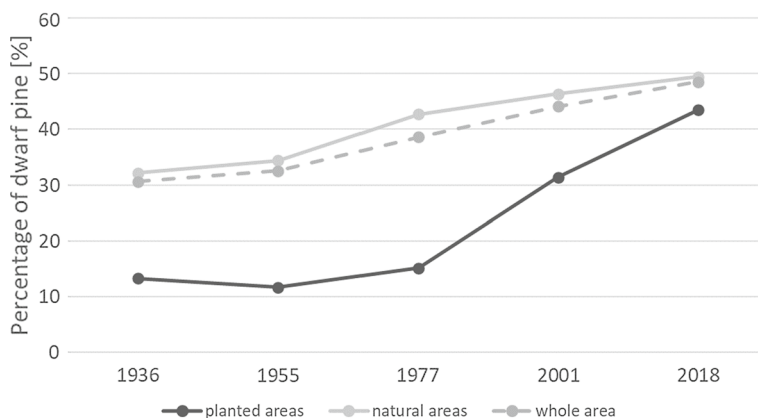


Fig. 6 Percentage of dwarf pine in the planted areas, natural areas and the total area; the planted areas were delineated according to Lokvenc et al. (1992)

Table 8 Area of the aerial-based land-cover classes covering sorted patterned ground (according to Křížek et al. 2019)

Class	Area over the sorted patterned ground [ha]				
	1936	1955	1977	2001	2018
Grasslands	151.4	149.2	144.6	132.4	122.4
Dwarf pine	13.8	16.5	21.1	34.6	45.3
Blockfields	2.9	3.2	4.0	3.4	2.7
Sparse forest	0.0	0.0	0.0	0.0	0.0
Artificial surfaces	0.9	1.7	0.9	0.2	0.1
Water bodies	0.0	0.0	0.0	0.0	0.0
No data	0.1	0.0	0.0	0.0	0.0

the planted area of the study area increased from 8 to 15%. To emphasise the dynamics of the dwarf pine growth, the proportions of the dwarf pine obtained from our classification in the areas marked as planted by Lokvenc et al. (1992) are compared to those in the rest of the study area (so called “natural areas”) in Fig. 6. The figure clearly shows faster increase of planted dwarf pine stands over the natural ones, which signifies that large part of expansion can be related to planting, especially after a new wave of planting starting in 1966. At the end of the monitored period (2018), the proportions of planted and natural dwarf pine stands in related areas were almost equal.

The classification results also show significant changes of sorted patterned ground in the area (Table 8). The dwarf pine increased by 205% from 1936 to 2018, covering 8% of the sorted patterned ground in 1936 and 26.5% in 2018. The increased speed of change starting in the second half of the twentieth century is clearly visible; the area of dwarf pine more than doubled from 1977 to 2018. Approximately 17% of the sorted patterned ground intersects with the dwarf pine artificial plantations as mapped by Lokvenc et al. (1992). Whereas plantations contributed to the dwarf pine spread over the patterned ground, significant increase is also visible elsewhere (Fig. 7). The increase happens almost exclusively at the expense of open grasslands, whereas other classes remain stable.

Discussion

In this research, we assess the long-term dynamics of Central European arctic-alpine tundra vegetation cover over the last eighty years using a time series of archival aerial imagery. Typically, mountain ecosystems respond rather slowly to the changes in environmental conditions and/or human pressure. This slow reaction can be attributed to the extreme climate conditions and short vegetation season, and consequent slow plant growth. Our study revealed, however, that more than a half of the study area in the Krkonoše tundra changed over the studied eighty years.

The main pronounced phenomenon was the proliferation of dwarf pine shrubs in the former grasslands. In eighty years, the pine cover increased markedly, from 31 to 49%. This can partly be attributed to afforestation activities during the twentieth century aiming to reduce erosion risks and prevent landslides by planting the pine shrubs, and (to a limited extent) also the Norway spruce mainly over stream catchments. The increase of pine can, therefore, be largely attributed to the growth after the plantation. In our study, we were interested whether the pine also spreads naturally without the direct human intervention (i.e., planting). Therefore, we used the Lokvenc map of plantations to divide the area into planted and natural parts, and by comparing the wood encroachment at the two types, we were able to study changes in wood cover at natural parts. Our detailed, spatially-explicit analysis showed that shrub encroachment happened naturally as well, with both planted and natural spread showing the same trend. In our study, we were interested as to whether the pine also spreads naturally without direct human intervention (i.e., planting). From comparison of the wood encroachment in the two parts, we could identify if the increase in wood cover can be detected also at natural parts.

Similar spontaneous shrub encroachment may be observed in mountain areas of many parts of the world, as well as in the Arctic (e.g., Tape et al. 2006; Myers-Smith et al. 2011). The phenomenon was studied using historical records, dendrological techniques and remote sensing methods (e.g., Cannone et al. 2007; Danby and Hik 2007; Formica et al. 2014). Reasons for such shrub expansion in tundra ecosystems are inferred to be of both global and local human influence, i.e., climate warming (Cannone et al. 2007) and an

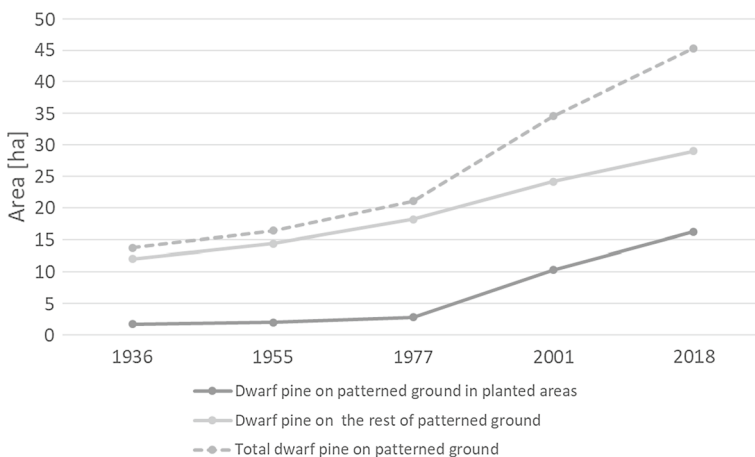


Fig. 7 The spread of dwarf pine stands over sorted patterned grounds related to the dwarf pine origin according to Lokvenc et al. (1992)

increase in nitrogen deposition (Formica et al. 2014) on the one hand, and cessation of traditional farming on the other (Tasser and Tappeiner 2002; Sanz-Elorza et al. 2003). In the case of Krkonoše, it was gradual abandonment of clearcutting, grazing and mowing that ceased completely after WWII (Štursa and Wild 2014).

Dwarf pine polycormons influence microclimate and soil conditions, including acidity, nutrient content and the thickness of soil organic layer, and cause changes in plant composition (Svoboda 2002; Wild and Wildová 2002). Pine encroachment can also destroy unique periglacial relict features of patterned ground by disrupting these rare geomorphologic components (Sekyra et al. 2002; Tremblé and Křížek 2006). At the same time, patterned ground was shown to facilitate the expansion of shrubs (Frost et al. 2013). Continuation of this expansion in the future could lead to the irreparable loss of these unique periglacial landforms in significant portions of the arctic-alpine tundra.

The rapid transition of grasslands to shrubs (as shown by our analysis) has great consequences for nature conservation. This is despite the fact that dwarf pine itself is listed in IUCN Red List as a species of Least Concern and its stands represent Natura 2000 habitat (code 4070) hosting several Red List species, such as *Rubus chamaemorus*. Nonetheless, grassland communities and relict periglacial structures threatened by the pine spread represent the most valuable habitats in the Krkonoše tundra and are among (critically) endangered and/or vulnerable habitats according to the Red List of Habitats of the Czech Republic (Chytrý et al. 2020). The co-existence of pine polycormons and grasses, specifically matgrass, is under constant debate, and both key players of the Krkonoše tundra deserve the highest conservation priority (Štursa and Wild 2014). Whereas pine has an important function in soil protection, hydrology and microclimate, species rich matgrass communities (Natura 2000 habitat code 6230) host many rare and endemic plant and invertebrate species, serve as important habitat for birds, and are considered as important centres of florogenesis (Krahulec 2006; GalvANEK and Janák 2008).

Our analysis was based on a series of archival aerial photography from 1936 to 2018 with varying quality. The old layers of the time series (1936 to 1977) were panchromatic, with small parts of the study area missing in the oldest 1936 layer. Limited spectral information did not allow for detailed vegetation interpretation, and only broad and general land cover classes such as “grasslands” could be distinguished, although this class naturally comprises many different habitats. Many conservation issues, such as the above-mentioned phenomenon of expansive native grasses, *C. villosa* and *M. caerulea*, which can outcompete species rich matgrass communities as with dwarf pine could not therefore be assessed. Nonetheless, the method of semi-automatic photo-interpretation of historical time series represents a powerful tool to assess long-term changes, providing not only practical deliverables for nature conservation but also bringing insights into the effects of global change on fragile high mountain ecosystems. This is because besides changing habitats and threatening valuable species, detected shifts in dominance of plant growth forms from herbs to shrubs may also have coupling and cascading effects on key ecosystem processes that are very difficult to predict (cf. Wookey et al. 2009). Observed fast proliferation of shrubs into the former grasslands signifies that non-intervention management might not be able to preserve all the components of the tundra ecosystem. There is a need to adjust current nature conservation strategies towards more active measures mimicking, to certain extent, former farming practices (cf. Chytrý et al. 2019).

Conclusion

In this study, we focussed on long-term dynamics of Central European arctic-alpine tundra, Krkonoše Mountains. A retrospective approach based on a time-series of historical imagery revealed considerable dynamics with shrub encroachment being the most pronounced phenomenon. Detailed spatiotemporal analysis of processes at a landscape level showed accelerating expansion of native dwarf pine into the former grasslands of high conservation value during the past century. This was caused by both artificial planting in the past and natural processes; pine displaying the same trend in both. In the past, pine was not only planted but also logged to free space for summer farming. The expansion of pine is thus caused by a combination of following factors: (i) the ageing of planted stands, (ii) the cessation of traditional farming after WWII, and (iii) global change, namely, an increase in temperature and nutrient availability caused by atmospheric nitrogen deposition. Important habitats, such as rare Natura 2000 habitats and relict geomorphological features of patterned ground, were shown to be under threat from pine expansion. Nevertheless, dwarf pine stands themselves are also important from the point of view of conservation. A balance between different nature conservation interests must therefore be found to protect all the valuable phenomena in the fragile tundra ecosystem. It is clear that current non-intervention management is not efficient in preserving the important grasslands, in particular semi-natural endemic-species-rich habitats of the tundra. Adjustment is necessary to assure the protection of the most valuable components of such a unique ecosystem. The detailed spatio-temporal information resulting from the analysis will assist nature conservation in updating action plans. Remote sensing, and archival imagery, in particular, have great potential to describe the long-term changes at the landscape scale, and they help our understanding of processes underlying vegetation change in such valuable ecosystems as tundra.

Appendix 1

See Tables 9, 10, 11.

Table 9 Transformation table between the Natura 2000 habitats and classes of grasslands and dwarf pine stands

Natura 2000 habitat code	Natura 2000 habitat description	Classification	Remark
A7	Pinus mugo scrub	Dwarf pine	G: 40%, B: 60%
A8.2	Subalpine deciduous tall scrub		
A1.1	Wind-swept alpine grasslands	Grasslands	
A1.2	Closed alpine grasslands		
A2.1	Alpine heathlands		
A2.2	Subalpine Vaccinium vegetation		
A3	Snow beds		
A4.1	Subalpine tall grasslands		
A4.2	Subalpine tall-forb vegetation		
A4.3	Subalpine tall-fern vegetation		
M1.7	Tall-sedge beds	G: 50%, D: 45%, W: 5%	
R1.5	Subalpine springs		
R2.3	Transitional mires		
R3.1	Open raised bogs		
R3.2	Raised bogs with Pinus mugo		
S1.2	Chasmophytic vegetation of siliceous cliffs and boulder screens		
T1.2	Montane Trisetum meadows		
T2.1	Subalpine Nardus grasslands		
T2.2	Montane Nardus grasslands with alpine species		
T8.2B	Secondary submontane and montane heaths without occurrence of Juniperus communis		
X10	Forest clearings		
X7B	Herbaceous ruderal vegetation outside human settlements, other stands		

The remarks show the percentage of grassland (G), block fields (B), water bodies (W) and dwarf pine (D) classes in the specific Natura 2000 habitat

Table 10 Area of the land cover classes in the five evaluated years resulting from classification of aerial images

Class	Area [ha]				
	1936	1955	1977	2001	2018
Grasslands	994.0	968.1	877.7	802.3	739.8
Dwarf pine	513.0	545.7	647.2	739.4	813.5
Blockfields	102.6	104.7	97.3	91.6	82.6
Sparse forest	17.7	33.9	30.4	30.2	31.0
Artificial surfaces	19.1	22.4	20.2	11.1	7.5
Water bodies	0.6	0.4	0.5	0.6	0.8
No data	28.4	0.2	2.1	0.2	0.2

Table 11 Change detection matrices

		1995						
		N	D	G	W	B	A	F
1936	N	0.0	1.1	0.4	0.0	0.2	0.0	0.0
	D	0.0	24.9	4.7	0.0	0.5	0.0	0.5
	G	0.0	6.0	50.5	0.0	1.4	0.6	0.8
	W	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.0	0.3	1.6	0.0	4.1	0.1	0.0
	A	0.0	0.0	0.5	0.0	0.0	0.6	0.0
	F	0.0	0.2	0.1	0.0	0.0	0.0	0.7
		1977						
		N	D	G	W	B	A	F
1955	N	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.1	27.8	4.2	0.0	0.4	0.1	0.0
	G	0.0	9.7	46.0	0.0	1.4	0.5	0.2
	W	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.0	0.9	1.4	0.0	3.9	0.0	0.0
	A	0.0	0.1	0.6	0.0	0.1	0.6	0.0
	F	0.0	0.2	0.2	0.0	0.0	0.0	1.6
		2001						
		N	D	G	W	B	A	F
1977	N	0.0	0.1	0.0	0.0	0.0	0.0	0.0
	D	0.0	32.7	5.2	0.0	0.6	0.1	0.1
	G	0.0	10.3	40.7	0.0	1.2	0.2	0.1
	W	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.0	0.9	1.3	0.0	3.6	0.0	0.0
	A	0.0	0.2	0.6	0.0	0.0	0.4	0.0
	F	0.0	0.1	0.1	0.0	0.0	0.0	1.7

Table 11 (continued)

		2018						
		N	D	G	W	B	A	F
2001	N	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	40.9	2.9	0.0	0.2	0.0	0.1
	G	0.0	7.1	40.1	0.0	0.6	0.1	0.0
	W	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.0	0.4	0.9	0.0	4.1	0.0	0.0
	A	0.0	0.1	0.2	0.0	0.0	0.4	0.0
	F	0.0	0.0	0.0	0.0	0.0	0.0	1.7
		2018						
		N	D	G	W	B	A	F
1936	N	0.0	1.4	0.2	0.0	0.1	0.0	0.0
	D	0.0	27.1	2.7	0.0	0.3	0.0	0.5
	G	0.0 1	8.3	39.2	0.0	1.0	0.1	0.6
	W	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	B	0.0	1.3	1.3	0.0	3.4	0.0	0.1
	A	0.0	0.2	0.6	0.0	0.0	0.3	0.0
	F	0.0	0.0	0.0	0.0	0.0	0.0	1.7

The values correspond to the changed area in % of the total study area (1675.4 ha) between the classes dwarf pine (D), grasslands (G), water bodies (W), blockfields (B), artificial surfaces (A), and sparse forest (F); no data or non-classified pixels are marked with N

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Authors' contributions MP, LK, and JM carried out the image classification, its validation, the processing of ancillary data; they also prepared statistical and graphical outputs of the spatial-temporal image analysis. JL and LČ developed scripts in ArcGIS for spatial-temporal data analysis and validation. DK contributed with analyses relating vegetation cover and patterned ground. ZH and SB supervised linking the results with the conservation aspects. The manuscript was drafted by JM (Introduction, Discussion and Conclusion), MP and DK (Results). All authors contributed to designing the manuscript's concept and to editing the final version of the manuscript.

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Data Availability The imagery used was provided by (i) the Czech Office of Surveying, Mapping and Cadastre, (ii) the Military Geographical and Hydrometeorological Office, (iii) the Czech Environmental Information Agency, and (iv) the Krkonoše Mountains National Park Administration under licence agreements that do not allow for its further distribution. The classification outputs are a part of the project CZ.05.4.27/0.0/0.0/17_078/0009044 and can be provided on request.

Code availability Not applicable.

Declarations

Conflict of interest No conflicts of interest/competing interests.

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Appendix 11.

PAPER 11. Pergl P., **Müllerová** J., Perglová I., Herben T. & Pyšek P. (2011). The role of long-distance seed dispersal in the local population dynamics of an invasive plant species. *Diversity and Distributions* 17: 725-738. <https://doi.org/10.1111/j.1472-4642.2011.00771.x>



The role of long-distance seed dispersal in the local population dynamics of an invasive plant species

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ABSTRACT

Aim Long-distance dispersal is important for plant population dynamics at larger spatial scales, but our understanding of this phenomenon is mostly based on computer modelling rather than field data. This paper, by combining field data and a simulation model, quantifies the fraction of the seed of the alien species *Heracleum mantegazzianum* that needs to disperse over a long distance for successful invasion.

Location Central Europe, Czech Republic.

Methods To assess the role of random dispersal in long-term population dynamics of the studied species, we combined longitudinal data covering 50 years of the invasion of this plant from its very start, inferred from a series of aerial photographs of 60-ha plots, with data on population dynamics at a fine scale of 10-m² plots.

Results A simulation model based on field data indicates that the fraction of seed that is dispersed from source plants not described by the short-distance dispersal kernel ranges from 0.1 to 7.5% of the total seed set. The fraction of long-distance dispersed seed that provides the best prediction of the observed spread was significantly negatively correlated with the percentage of habitats suitable for invasion.

Main conclusions Our results indicate that the fraction of seeds that needed to be dispersed over long distances to account for the observed invasion dynamics decreased with increasing proportion of invulnerable habitats, indicating that the spatial pattern of propagule pressure differs in landscapes prone to invasion. Long-distance dispersal is an important component of the population dynamics of an invasive species even at relatively small scales.

Keywords

Aerial photographs, biological invasions, *Heracleum mantegazzianum*, invasive plants, land-use change, long-distance dispersal, matrix models.

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INTRODUCTION

Seed production and dispersal are crucial determinants of the colonization processes in sessile plant species and their populations (Crawley, 1997). However, despite recent progress in understanding the important role of seed dispersal in species' population dynamics at larger scales, the frequency of rare long-distance dispersal events is because of the difficulty of measurement and quantification still poorly documented (Cain *et al.*, 2000; Nathan *et al.*, 2003, 2008; Nathan, 2006).

The majority of seeds are dispersed over short distances, and the probability of seeds being dispersed over long distances is assumed to be very low. Still, it has been suggested that long-distance dispersal is the key process that determines the extent and spatial dynamics of plant distributions (Cain *et al.*, 1998, 2000; Clark, 1998; Higgins & Richardson, 1999; Bullock & Clarke, 2000; Wilson *et al.*, 2009), but the evidence for this is still scanty. To date, the importance of long-distance dispersal has been confirmed by simulation studies exploring its role in population dynamics, migration and range shaping (e.g.

Higgins *et al.*, 1996; Clark, 1998; Higgins & Richardson, 1999) rather than quantified by using field data (but see Rouget & Richardson, 2003). These studies indicate that in terms of population spread, occasional long-distance jumps are more effective than numerous small-distance dispersal events (Clark, 1998; Higgins & Richardson, 1999; Pyšek & Hulme, 2005; see Nathan, 2005 for a review). Rapid development of molecular tools enabled some progress in the detection of dispersal events, but the rarity and enormous stochasticity associated with long-distance dispersal make it extremely difficult to measure and quantify its role in plant species' population dynamics. This lack of quantitative data limits our understanding of mechanisms, causes and consequences of long-distance dispersal. This is particularly relevant when considering the spread of invasive alien species (Cain *et al.*, 2003; Nathan, 2005).

However, the difficulties associated with identifying the exact role of long-distance dispersal are not only because of the lack of data but also because of the fact that the scale, at which long-distance dispersal may be addressed, ranges across many orders of magnitude, from inter-continental distances to those between patches of habitats. To account for differences between the scales, the long-distance dispersal is therefore usually defined as seed travelling beyond some absolute distance threshold or as a certain small fraction of seed that travel the farthest distance from the maternal plant (Bullock & Clarke, 2000; Nathan *et al.*, 2003; Soons & Ozinga, 2005; Wilson *et al.*, 2009). For the purposes of this study, we define long-distance dispersal as uniform random dispersal independent of distance from maternal plant.

The major difficulty in assessing the role of long-distance dispersal results from its elusive nature, which defies quantification. For short-distance dispersal, reliable estimates can be based on density functions (seed dispersal kernels) and dispersal distance (Bullock *et al.*, 2006), inferred using various observational, experimental or inverse modelling methods (Jones & Muller-Landau, 2008; Jongejans *et al.*, 2008; Schurr *et al.*, 2008; Soons & Bullock, 2008; Hardy, 2009; Kamm *et al.*, 2009). A number of estimates of maximal dispersal distance hence exist, and the effects of long-distance dispersal on shaping species distributions, metapopulation dynamics or genetic structure of populations are documented (Davies *et al.*, 2004; Bohrer *et al.*, 2005; Bialozyt *et al.*, 2006; He *et al.*, 2009) as well as how the dispersal vectors affect the dispersal kernels (Kuparinen, 2006; Westcott *et al.*, 2008; Heinken & Winkler, 2009). Development of complex spatio-temporal dispersal simulation models is thus a promising tool for obtaining a better understanding of the processes underlying population dynamics that act in concert with environmental conditions (Malanson & Armstrong, 1996; Levey *et al.*, 2008; Franklin, 2010). Such models can include a variety of environmental parameters, but their use is often limited by inadequate field and observational data to parameterize the models (Neilson *et al.*, 2005; Gallien *et al.*, 2010). Therefore, empirical studies that assess the importance of long-distance dispersal at a reasonably large scale are needed, namely studies that link

long-term observations of species distribution with species traits rather than by inferring long-distance dispersal from static data.

Identifying the role of long-distance dispersal is extremely difficult because of the long presence of species in current landscapes. Consequently, it may be more appropriate to study such dynamic dispersal processes in newly established populations, which is the case of ongoing invasions by alien species. Therefore, introduction of species into new ranges represents natural experiments ideally suited for studying the spread of the species and dynamics of their ranges (Sax *et al.*, 2005; Cadotte *et al.*, 2006; Xu *et al.*, 2010), including long-distance dispersal (Nehrbass *et al.*, 2007). However, few invasions are recognized and described early enough to capture the complete temporal dynamics of the process (but see Robinson, 1965; Richardson & Brown, 1986; Lonsdale, 1993; Müllerová *et al.*, 2005). Therefore, our incomplete understanding of the role of long-distance dispersal in species' population dynamics results from the lack of reliable long-term data on how the distribution of a species changes over time. A well-documented pattern of spread at a finer scale, from local to regional, and over a sufficiently long period of time therefore would provide a unique opportunity to study the role of dispersal in shaping a species distribution and (meta-) population dynamics. Unfortunately, such data are rarely available for individual species.

One exception is *Heracleum mantegazzianum* (giant hogweed), a serious plant invader in many European countries and North America (Nielsen *et al.*, 2005; Pyšek *et al.*, 2007; DAISIE, 2009). Owing to its large and conspicuous flower heads and strong negative impacts, it has been the subject of many studies that yielded data on its distribution on different scales. By using aerial photographs, it was possible to analyse 50 years of its invasion dynamics at the landscape scale (Müllerová *et al.*, 2005), and floristic records were used to analyse the invasion by this species at the country and continental scales (Jahodová *et al.*, 2007; Nielsen *et al.*, 2008; Pyšek *et al.*, 2008). The existing detailed knowledge of various aspects of this species' population biology (Moravcová *et al.*, 2006; Pergl *et al.*, 2006; Perglová *et al.*, 2006) acquired during the recently accomplished EU FP project Giant Alien (<http://www.giant-alien.dk>; Pyšek *et al.*, 2007) allowed to properly understand the life cycle of the species and thus develop appropriate models.

The aims of the study were, using the model species *H. mantegazzianum*, to (i) identify the fraction of seeds dispersed at long distance that provides the best fit to the prediction of actually observed spread at a landscape scale and (ii) provide an insight into how these seeds contribute to the invasion dynamics over several decades, since the initial introduction of the species to the region. This was made possible by combining detailed data on the long-term invasion dynamics of *H. mantegazzianum* at a large scale (from a longitudinal series of aerial photographs) with detailed knowledge of its local fine-scale population dynamics. The estimate of the fraction of long-distance dispersed seeds was obtained by fitting a set of scenarios of stage-based matrix

model linked to a spatial landscape dispersal model, and the outputs from these models were compared with the real *H. mantegazzianum* longitudinal data. Furthermore, we asked whether there is a relationship between the availability of habitats suitable for invasion and fraction of seed entering the long-distance dispersal.

METHODS

Study species

Heracleum mantegazzianum (giant hogweed, Apiaceae) is native to the western Greater Caucasus (Jahodová *et al.*, 2007; Otte *et al.*, 2007) where it grows on wet and nutrient-rich soils on mountain slopes in forests. In central Europe, *H. mantegazzianum* invades mainly semi-natural grassland communities, nutrient-rich sites, forest edges and anthropogenic habitats (Pyšek & Pyšek, 1995; Thiele *et al.*, 2007). It is able to develop large populations harbouring thousands of individuals, although more often populations consist of small groups of a few individuals scattered along linear landscape structures such as roadsides, water streams or in abandoned gardens and parks and unmanaged meadows. *Heracleum mantegazzianum* is the tallest herbaceous species in Europe; it reaches 200–500 cm in height, with leaves up to 300 cm long and a flowering stem that may reach up to 15 cm in diameter. The species is monocarpic, i.e. it can persist as a vegetative rosette for several years, then flowers and dies in the same year. Plants of *H. mantegazzianum* usually live 3 to 5 years, but a 12-year-old individual is recorded (Pergl *et al.*, 2006). *Heracleum mantegazzianum* reproduces entirely by seed and can produce enormous numbers of fruits; on average 10,000–20,000 seeds with maxima occasionally reaching up to 50,000 (Perglová *et al.*, 2006, 2007). The seeds start to germinate early in the season, and the species has a short-term persistent seed bank with the majority of the seed (92%) germinating in the first year (Moravcová *et al.*, 2005, 2006). Inflorescences of *H. mantegazzianum* are large compound umbels (up to 80 cm in diameter) (Perglová *et al.*, 2006), which makes it easy to identify flowering or early fruiting patches of plants or even individuals on aerial photographs taken during the flowering or early fruiting period (Müllerová *et al.*, 2005).

Under natural conditions, timing of flowering and mortality are dependent on the amount of accumulated resources, but do not seem to be significantly affected by local density (Pergl *et al.*, 2007), although in artificial conditions in an experimental garden with two distinct regimes of density, competition is important (Pergl *et al.*, unpublished). Only a very small proportion of the emerged seedlings (700–1700 seedling per m²) survive to the flowering stage (0.5–1.0 plants per m²) (Pergl *et al.*, 2007). Most of this population self-thinning occurs during the first season when the mortality is very high – maximum densities of plants older than 1 year vary between 20 and 31 per m² in the Czech Republic and Germany (Pergl *et al.*, 2007).

Study region

The study region is located in the western part of the Czech Republic, near the place where *H. mantegazzianum* was first introduced into the country in 1862 (Appendix S1 in Supporting Information). However, the spread of the species in this area, inferred from aerial photographs, started only after 1947 (Pyšek, 1991; Müllerová *et al.*, 2005). This region is now very heavily infested with *H. mantegazzianum* because of a radical change in land use that occurred 50 years ago; after the World War II, the inhabitants were displaced and a significant part of the region became a military area with restricted access. In 1974, 617 km² of this area was declared a landscape-protected area, Slavkovský les. It is sparsely inhabited, with remnants of natural vegetation consisting of beech and spruce forests, peat bogs and pine forests on serpentine (Neuhäuslová & Moravec, 1997). However, natural vegetation was replaced over much of its original extent by extensive wet grasslands with high species diversity, pastures and spruce plantations that cover 53% of the area (Kos & Maršáková, 1997).

Small-scale analysis: demographic data

To obtain the information about the species' small-scale demography, two field studies were carried out: (i) demographic data sampling in permanent plots that were used to construct the matrix models and (ii) analysis of transect data to describe the short-distance dispersal.

Eight permanent plots (1 × 10 m) were monitored in the study region to determine environmental heterogeneity and range of *H. mantegazzianum* populations in terms of size and density; at each site, the invasive population occupied at least an area of 30 × 30 m (see Pergl *et al.*, 2007 for details). The plots were located at sites for which demographic data are collated and the ecology of the species studied (Krinke *et al.*, 2005; Perglová *et al.*, 2006, 2007). Population dynamics of *H. mantegazzianum* were followed from 2002 to 2006 twice a year, in late spring (May/June) and summer (July/August). For the purpose of this study, only the late-summer censuses are used, in particular the 4 year-to-year transitions at each study plot.

All plants within the plots with leaves larger than 8 cm were mapped and their (i) height, (ii) number of leaves, (iii) length of the longest leaf blade and (iv) stalk length recorded. These plants were classified directly in the field according to their size as: (i) a seedling, (ii) juvenile, (iii) vegetative rosette or (iv) a flowering plant. The position of the plants within the plot was mapped using a Laser/Angle encoder (Laser technology, Inc.) and software Field map (ver. 8.1.203; <http://www.fieldmap.cz>), which enabled their identification at subsequent visits. At each visit, new seedlings were recorded and included in the study.

Based on the detailed knowledge of its biology (e.g. seed bank dynamics, emergence and mortality) and data on the growth, survival and emergence, matrix population models were constructed for each plot and between-year transition. The matrices used were four-stage matrices without persistence

of seed in a seed bank. At sites where the information for all diagonal and subdiagonal cells in a given year was not available, the demographic data were pooled for the following years within that site.

Data on successful short-distance dispersal was collected along eight transects 40 cm wide and at least 10 m long. These transects were located in the study region and established in summer 2005 at sites where solitary *H. mantegazzianum* had flowered in 2004. The number of seedlings per 10 cm length of each transect that emerged in 2005 was recorded. The phenomenological dispersal model was chosen to accommodate the two aspects of the dispersal curve: density functions at a very short distance from the mother plant (exponential) and the tail of the dispersal kernel (hyperbolic) (Bullock & Clarke, 2000). Mechanistic dispersal models were not considered owing to data limitations (Bullock *et al.*, 2006).

Large-scale analysis: aerial photographs

Five *H. mantegazzianum*-dominated sites (subset of sites for demographic monitoring) were chosen for determining the role of long-distance dispersal. The sites were selected to minimize possible human-mediated directional seed dispersal along roads or pathways and natural dispersal along water courses from surrounding landscapes. Aerial photographs from 1947 to 2000 recorded the invasion since the first occurrences of individual *H. mantegazzianum* plants (for details see Müllerová *et al.*, 2005). At Žitná I study site, the first occurrence of *H. mantegazzianum* was documented in 1957, giving the longest period of 39 years; however, most sites were first invaded between 1962 and 1973, with the invasion history spanning 13–31 years (Table 1).

For the present analysis, each study site of 60 ha (750 × 800 m) was divided into 2.5 × 2.5 m grid cells. Using the aerial photographs (for details on the interpretation of the photographs, see Müllerová *et al.*, 2005), each cell was assigned presence/absence of *H. mantegazzianum* and suitability for invasion (see model description for details) based on the type of land use detectable from the photographs: individual trees in the neighbourhood, vicinity of roads or railways (5-m buffer along the corridor), tree plantations, open or young forest, forest clearings, surrounding of buildings and other disturbed areas, and edges of pastures were considered as suitable habitats; pastures and arable fields as partly suitable; and forest, buildings and water bodies as unsuitable. The suitability of land-use categories was classified based on long-term field observations in the study area by the authors and monitoring of other study plots invaded by *H. mantegazzianum* (Pergl *et al.*, unpublished data). This yielded two sets of grids for each site and year recorded in the aerial photographs: (i) grid of habitat suitability and (ii) grid of *H. mantegazzianum* distribution.

The sites studied markedly differed in the proportion of suitable, partly suitable and unsuitable habitats, with area suitable for invasion ranging from 10.4 to 53.4% of the total area of a site. The availability of suitable habitats decreased over time at the Arnoltov site (from 11.2 to 5.3%), increased at Žitná I (32.6–55.4%) and remained the same at the three other sites (Table 1).

The model

The purpose of the model was to create sets of scenarios of the population dynamics differing in the level of long-distance dispersal. Based on the knowledge of the species biology, a

Table 1 Geographical location (centroid) of the five 60-ha study sites and percentage of suitable, partly suitable and unsuitable habitats.

Site	Suitability	1957	1962	1973	1987	1991	1996	2000
Arnoltov	Suitable	–	–	11.2 (1.1)	12.1 (13.5)	10.8 (3.1)	13.1 (5.9)	5.3 (6.6)
N 50°6.801',	Partly suitable	–	–	59.7 (0.1)	56.1 (0.8)	57.7 (2.3)	58.0 (6.4)	59.7 (11.8)
E 12°36.147'	Unsuitable	–	–	29.2 (0.0)	31.8 (0.6)	31.5 (0.7)	29.0 (0.1)	35.0 (1.2)
Dvorečky	Suitable	–	–	16.3 (0.0)	n.a.	22.4 (11.4)	18.6 (18.1)	–
N 50°5.982',	Partly suitable	–	–	38.6 (0.5)	n.a.	29.7 (0.6)	29.8 (2.5)	–
E 12°34.137'	Unsuitable	–	–	45.1 (0.0)	n.a.	47.9 (0.6)	51.6 (0.0)	–
Krásná Lípa	Suitable	–	–	–	40.7 (1.9)	40.4 (1.3)	36.5 (3.2)	40.7 (3.1)
N 50°6.306',	Partly suitable	–	–	–	52.9 (0.2)	52.4 (0.0)	56.1 (0.7)	52.1 (0.1)
E 12°38.393'	Unsuitable	–	–	–	6.4 (0.0)	7.2 (0.0)	7.3 (0.0)	7.2 (0.0)
Žitná I	Suitable	32.6 (3.0)	30.5 (7.1)	42.7 (10.8)	45.4 (30.0)	57.5 (32.0)	55.4 (21.4)	–
N 50°3.754',	Partly suitable	45.5 (0.0)	48.3 (1.1)	36.0 (1.0)	37.8 (10.3)	35.1 (1.7)	38.0 (15.2)	–
E 12°37.569'	Unsuitable	22.0 (0.0)	21.3 (0.0)	21.3 (0.0)	16.8 (1.2)	7.4 (0.2)	6.6 (0.0)	–
Žitná II	Suitable	–	39.7 (4.6)	43.3 (10.7)	50.6 (25.0)	69.6 (29.3)	63.9 (16.4)	–
N 50°3.837',	Partly suitable	–	36.0 (1.3)	33.0 (4.7)	31.8 (6.9)	20.7 (1.0)	32.1 (4.3)	–
E 12°37.304'	Unsuitable	–	24.4 (0.0)	23.8 (0.0)	17.6 (0.7)	9.7 (0.3)	4.0 (0.0)	–

Values in brackets show the percentage of the total area invaded by *Heracleum mantegazzianum*. See Methods for details of the classification of the suitability of habitats. –, the lack of distributional data before the start of the invasion; n.a., distributional data for the given period not available

simple simulation model was developed that takes into account land-use structure and suitability for *H. mantegazzianum*, species traits included in a stochastic matrix model and short- and long-distance dispersal at a large scale. This model was based on stage-classified matrix models, which were extended using dispersal functions that allowed the spatial development of a population to be simulated. The local population dynamics was simulated at the level of patches. The dynamics at each patch were modelled using density-dependent (logistic growth), stage-specific transitions with a 1-year transition interval (see Münzbergová *et al.*, 2005 for details of the model used). At each step, each element in the predicted population vector was replaced by a Poisson-distributed deviate with the mean given by that element. The temporal stochasticity was simulated by randomly drawing one matrix from a pool of transition matrices at each step. The probability of drawing each matrix from the pool was the same.

Size and land use type of the patches (which determines their suitability for *Heracleum mantegazzianum*) were obtained by analysing the aerial photographs. The patches were represented as sets of neighbouring cells with the same land use and maximum size of 30 × 30 m. Three habitat quality categories were used in the model based on classification of aerial photographs: (i) habitats with no regular management were assumed to be suitable for establishment, growth and reproduction, i.e. full matrices with both growth and reproduction were used in the model; (ii) habitats with regular management like pastures or meadows were classified as partly suitable for *H. mantegazzianum*; instead of full matrices, matrices with reproduction set to zero were used, and (iii) in unsuitable habitats (forest, buildings, water bodies), no growth and reproduction was allowed.

The simulations were run on a simulation plane that was modified with respect to dates for which historical data inferred from the aerial photographs was available. Changes in landscape characteristics were implemented starting in the year when they were first recorded, resulting in discrete changes in landscape suitability. The rules of plant growth and reproduction at patches followed the changes in suitability; e.g. if plants occurred in patches that changed from suitable to unsuitable, all plants were deleted, or if it changed to partly suitable, their reproduction output was set to zero.

The dispersal in the model had two forms: (i) independent of distance (henceforth referred to as long-distance dispersal) and (ii) combined exponential and hyperbolic (short-distance dispersal). To minimize the potential bias in wrong parameterization of the model owing to stochasticity in seedling emergence and survival, instead of seeds the dispersed stage in the model was seedlings that survived to late summer (but henceforth referred to as seed dispersal). Short-distance dispersal in the model was performed numerically in a cell grid put over a plane with absorbing boundaries (see Münzbergová *et al.*, 2005; Herben *et al.*, 2006 for details). Absorbing boundaries were used because the plots were selected so that seed input from outside could be assumed to

be minimal; this was confirmed by a previous analysis of the long-term dynamics at study sites (Müllerová *et al.*, 2005), which indicates that the spread is from foci within sites and not the surroundings.

Number of seeds arriving at cell i by short-distance dispersal was defined as

$$n_i = \frac{1}{T} \sum_k \sum_j I_{jk} \frac{x_{0k}}{A_k} \left[a_1 \exp(-\alpha_1(d_{ij} + c_1)) + \frac{a_3}{[\alpha_3(d_{ij} + c_3)]^\theta} \right] \quad (1)$$

where x_{0k} is the number of seeds produced in patch k , A_k is the area (number of cells) of the k -th patch, α_1 , α_3 and θ are dispersal shape parameters, a_1 and a_3 are weights of these dispersal shapes, c_1 and c_3 are additive constants of these dispersal shapes, d_{ij} is the distance between cells i and j , I_{jk} is 1 if cell j lies in the habitat k , and 0 otherwise, and T is a constant to normalize the sum of dispersal function values ($\sum [a \exp(-\alpha_1(d_{ij} + c_1)) + \frac{a_3}{[\alpha_3(d_{ij} + c_3)]^\theta}]$) to unity; j means indexing over all cells in the grid, and k summation over all patches.

Number of seeds arriving by long-distance dispersal was assumed to be independent of distance to potential seed sources. This distance independence was modelled by removing a fraction of seeds at each step from each patch and redistributing them randomly over the whole simulation plane. The number of seeds arriving at the l -th patch by distance-independent dispersal is thus proportional to the area of that patch as follows:

$$N_{dil} = p_f \frac{A_l}{A} \sum_k x_{0k} \quad (2)$$

where p_f is the proportion of seeds dispersing long distance, x_{0k} is the number of seeds produced at the patch k , A_l is the area (number of cells) of the l -th patch and A is the total area of the simulation plane. The seeds dispersed into unfavourable patches within the study site were considered as not contributing to the population dynamics.

Model parameterization and initialization of simulations

For the majority of sites, the number of individuals within a plot or for some transitions between stages was insufficient for developing robust transition matrices for each year. Thus, only 14 transition matrices were available for the stochastic simulations. Three matrices pooled across years 2002–2006 and eleven year-to-year transitions were developed for the model. The values for the population growth rate (finite rate of population increase – λ) varied within the range of 0.684–1.301. The estimate of the mean population growth rate of *H. mantegazzianum* based on 9999 random simulations (Caswell, 2001) was 1.081.

Maximum distance of seedlings from the maternal plant in these transects was 5.3 m, with the highest density of seedlings within the range 0.0–0.5 m, where ca 40% of the seedlings occurred, and with 89.2% of the seedlings within 2.5 m. Dispersal parameters for short-distance dispersal were esti-

mated by fitting the combined exponential and hyperbolic model (Equation 1) to the data obtained from transects (Fig. 1). The model used for parameterization explained 78.1% of the variance in the data, and the adequacy of the fitted model was checked by plotting standardized residuals against fitted values, and by a normal probability plot.

The simulations for each study site started with an initial population corresponding in size to the distribution when *H. mantegazzianum* was first observed in photographs, and with the mean plant density and proportion between stages based on data from permanent plots.

Apart from local population dynamics, the following parameters were also estimated from field data. Density of *H. mantegazzianum* stands ranged from 0.2 to 23.4, with a mean of 6.7 individuals m^{-2} (eight permanent plots; SD 7.4). The mean density value was used for initialization of occupied cells in the initial occupancy layer, and maximum density was used for the carrying capacity (K). Initial occupancy layer was based on the observed species distribution obtained from aerial photographs with the proportion in the four stages (seedlings, juveniles, rosettes, flowering) based on a stable stage distribution as obtained from the fourteen matrices, namely 0.31:0.30:0.26:0.13.

Simulation experiment and sensitivity analysis

To identify the contribution of long-distance seed dispersal to overall landscape population dynamics not described by the short-distance kernel, sets of simulations with different fractions of randomly distributed seeds (p_R from 0 to 10%, henceforth referred to as scenarios) were run for each site. To keep the number of seeds dispersed by short-distance kernel constant at simulations differing by the fraction of randomly dispersed seeds, we changed the number of produced seed in matrix accordingly. The simulations were run for an additional 10 years from the date of the last aerial photograph, and for each scenario, 20 simulations were run.

Twenty simulations were used as the variability between the individual runs within the scenarios was relatively low. To compare whether the scenarios conform with the observed trends in occupancy of patches and reduce the bias owing to possible overlooked individuals in managed habitats, only data for patches in suitable habitats were used. As rosettes cannot be clearly detected from aerial photographs, only habitats that hosted at least one flowering plant were considered as occupied. The selection of the best scenario was based on visual inspection and on the comparison of the sum of squares between the average patch occupancy and the real number of occupied patches taken from aerial photographs.

The additional analysis of sensitivity for the whole model was performed for two parameters that are known to significantly affect the extrapolation of short-term data to long-term dynamics: density dependence expressed through the carrying capacity and average population growth rate (Mildén *et al.*, 2006). Five alterations in both parameters were used, giving 25 parameter combinations. The effect of changing the carrying capacity was tested by using 20% smaller, 10% smaller, unchanged, 10% bigger and 20% values of the carrying capacity. For population growth, five pools of matrices were used: lowest population growth (removing from the pool of available matrices the two matrices with the highest lambda, $\lambda = 1.01$); low population growth (removing one matrix with the highest lambda, $\lambda = 1.06$), unchanged pool of matrices (1.08), faster population growth (removed matrix with the smallest population growth, 1.11); and the fastest population growth (removing two slowest matrices, 1.15). The sensitivity analysis was carried out for the following fractions of long-distance dispersed seeds: 0, 0.2, 0.5, 1 and 5%. Owing to the computer-demanding simulations, this sensitivity test was performed only for one locality (Žitná I). Sensitivity was assessed by visual inspection and by using the sum of squares between individual scenarios and the real number of occupied patches taken from aerial photographs.

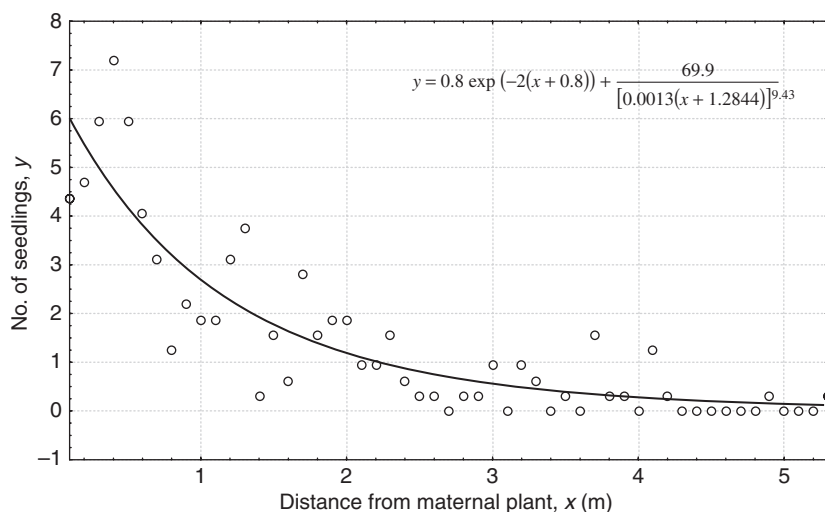


Figure 1 The pattern of short-distance dispersal showing data from the transects and estimated parameters for the dispersal curve (combined exponential and hyperbolic model), Equation 1.

RESULTS

Fraction of long-distance seed dispersal

The simulation scenarios in which the fraction of long-distance dispersed seed was manipulated showed that at all the sites studied this fraction must have been larger than zero. The scenarios in which this fraction was zero clearly showed that the predicted increase in the occupancy rate of patches within the simulation plane was much slower than that actually observed in aerial photographs. This indicates that the short-distance dispersal alone cannot account for the observed invasion dynamics (Fig. 2, Appendix S2 in Supporting Information). At the five study sites, the scenarios providing the best correspondence with aerial photograph data indicated fraction of long-distance dispersed seed to be in the range between 0.1 and 7.5% (Table 2). At two sites, it was higher or equal to 1%, and in the remaining three between 0.1 and 0.4%. In the

scenario with the highest fraction of long-distance dispersed seed in the model (10%), *H. mantegazzianum* occupied the majority of suitable habitats at all study sites at a rate that was approximately double that observed. The relationship between the fraction of long-distance dispersed seed and sum of squares is clearly U-shaped for all the studied sites (Fig. 2, Appendix S2 in Supporting Information).

Sensitivity analysis

The sensitivity analysis assessing the effects of uncertainty of the estimates of carrying capacity and population growth rate (λ) was performed for the locality Žitná I where the monitored period of invasion was longest and the estimated fraction of long-distance dispersed seeds was intermediate. The simulations for each combination of parameters and changed fraction of long-distance dispersed seeds revealed that the model was very robust to varying values of the carrying

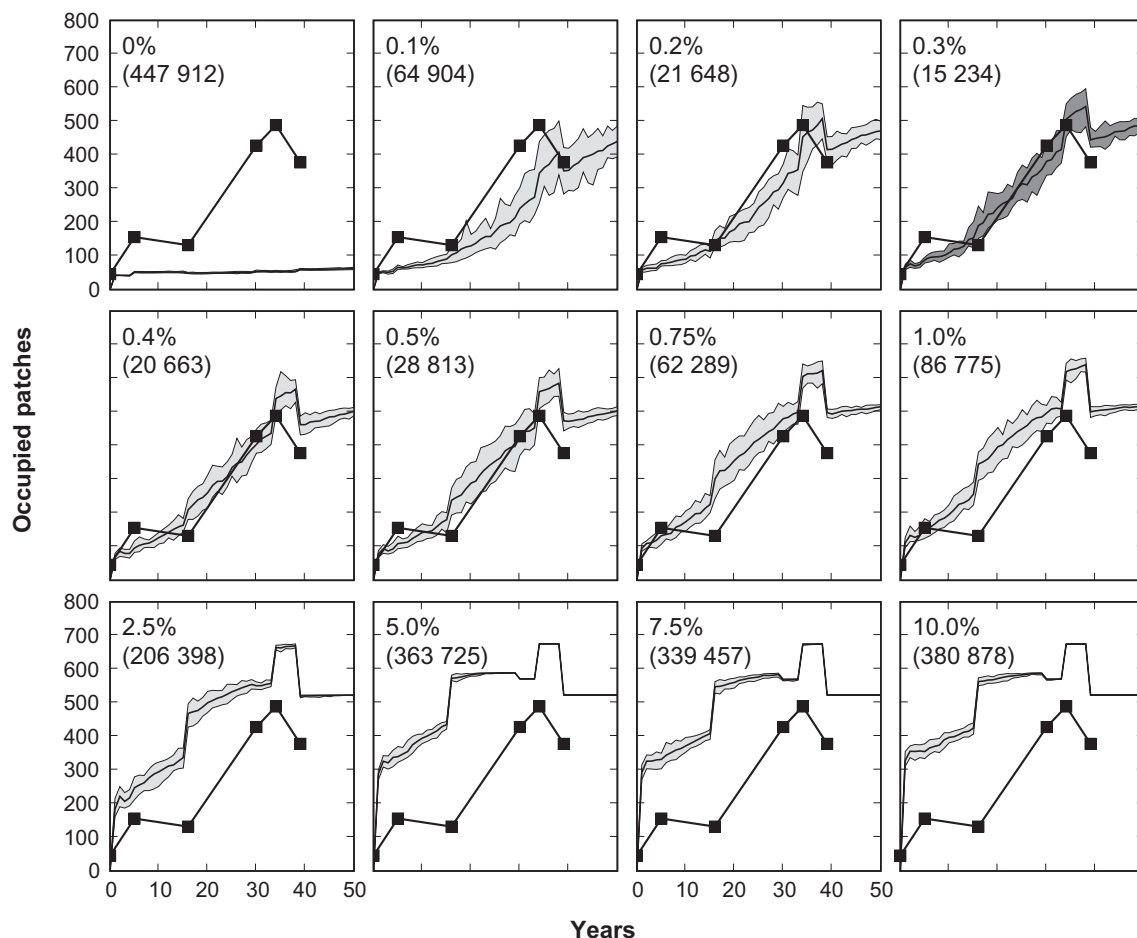


Figure 2 Simulations with different fractions of seeds dispersed over long distances (study site Žitná I). The solid line with squares shows observed number of occupied patches; the squares indicate the years for which aerial photographs were available. Black line shows the average patch occupancy predicted by simulations for each scenario, and grey lines show the 90% confidence interval. Numbers in graphs indicate fraction of seeds dispersed over long distances. The values in brackets show the sum of squares between the average patch occupancy and real number of occupied patches taken from aerial photographs. Graphs with dark grey indicate the scenarios that best fit to the observed data based on the minimal sum of squares. The sharp decrease in the number of occupied patches in the last year was because of an occasional management action.

capacity (Fig. 3, Appendix S3 in Supporting Information), but sensitive to changes in the estimates of population growth (average for CV over-carrying capacities was 0.096, while the CV for lambdas was 0.842). In case of the 0.3% fraction of long-distance dispersed seed, the 2% change in population growth resulted in 50–100% change in sum of squares (Table 3). Nevertheless, the sensitivity analysis of the model indicates that even in case of highly over- or underestimated population growth parameters with *c.* 7% change of lambda (1.01 or 1.15), the minimal sum of squares and therefore the best fit to the real data from aerial photographs with the estimates of fraction of long-distance dispersed seeds within a site does move between 0.2 and 1% fraction of the long-distance dispersed seed (Table 3, Fig. 3).

Correlation between long-distance dispersal and suitable habitats

The percentage of the area of habitats that were invaded ranged from 2.4% (site Krásná Lípa; first record of invasion in 1987) to over 17% at Žitná I and Žitná II (invaded between 1957 and 1962) and reflected the differences in the time that has elapsed since these sites were invaded (averages over the years) (Table 2). There was no clear correlation between the fraction of long-distance dispersed seeds and

invaded area, or its percentage of the total site area (averages over the available years), but the fraction of long-distance dispersed seeds providing the best fit to the prediction of the observed spread in a given site was significantly negatively correlated with the percentage of suitable habitats at that site (both variables log-transformed, $r = -0.916$, d.f. = 3, $P < 0.05$) (Table 2).

DISCUSSION

In this study, the combination of long-term observational data at two different scales, based on monitoring the invasion from the beginning, allowed for the first quantitative insight into the importance of long-distance dispersal in the invasion of an alien plant species. The results illustrate how an analysis of a well-documented invasion of an alien species can contribute to a better understanding of general ecological phenomena, including species dispersal and spread (Kinlan & Hastings, 2005; Lewis *et al.*, 2006), and support the theories on how availability and spatial pattern of habitats shape the rate and population dynamics of species (Hill *et al.*, 2001; With, 2002; Soons & Ozinga, 2005; Murrell, 2006).

The proportion of seed that is randomly dispersed beyond the prevailing distance predicted by a density function, i.e. over relatively long distances from the source plants of

Table 2 Estimated fractions of seeds dispersed over long distances at each study site, average values of the percentage of suitable habitats at each study site and invaded area (averages over years with available data).

Locality	Fraction of seeds dispersed over long distances (%)	Suitable habitats (%)	Invaded habitats (%)	Invaded area (max. area invaded; m ²)	Mean rate of spread (areal; m ² year ⁻¹)	Mean rate of spread (linear; m year ⁻¹)
Arnoltov	5.0–7.5	10.4	6.0	47,000	1241	12.8
Dvorečky	1.0	19.0	9.9	23,817	730	17.4
Krásná Lípa	0.1	39.6	2.4	9,000	350	3.8
Žitná I	0.3	44.0	17.4	113,000	2831	8.0
Žitná II	0.1	53.0	17.2	111,000	3275	8.2

Maximum area invaded and mean rates of areal and linear spread are taken from Müllerová *et al.* (2005).

Table 3 Sensitivity analysis based on sum of squares for the correspondence of the simulations of patch occupancy compared to real data from the locality Žitná I.

Population growth scenario	Sum of squares					Average lambda (change in %)
Fraction of long-distance dispersed seeds (%)	0.2	0.3	0.5	1.0	5.0	
Lowest λ	183,422	121,729	59,561	20,475	351,693	1.01 (93.5)
Low λ	51,228	22,507	16,773	54,107	361,130	1.06 (98.1)
Average λ	19,922	15,679	32,920	86,008	364,270	1.08 (100.0)
High λ	19,805	32,557	62,751	124,376	377,765	1.11 (102.8)
Highest λ	43,339	68,346	102,407	161,767	381,490	1.15 (106.5)

See Methods for details on modelling the sensitivity. The table shows averages of sum of squares for individual scenarios with varying fraction of long-distance dispersed seed and different population growth models differing by average lambda. Fraction of 0.3% was identified as fitting the best to the real data. Bold value indicates the scenario with the smallest sum of squares.

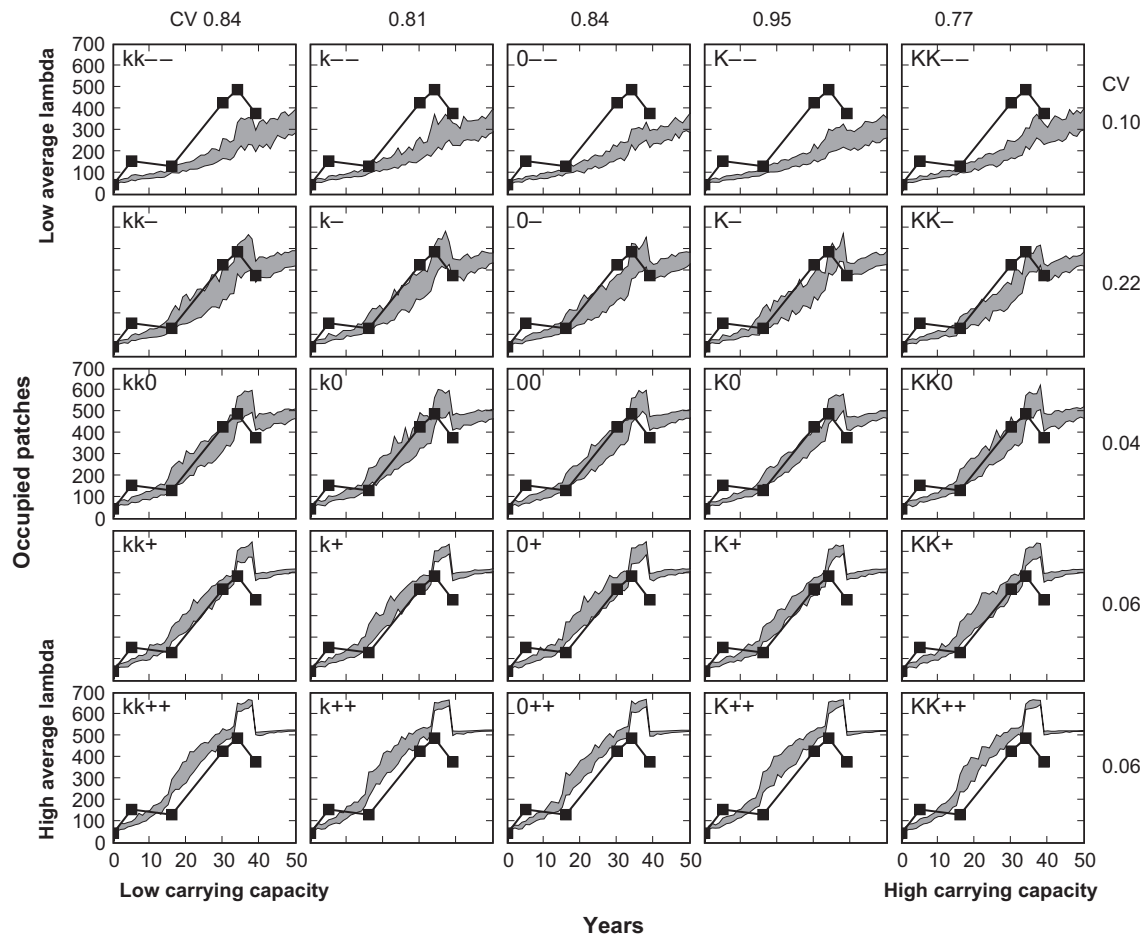


Figure 3 Results of sensitivity analysis for locality Žitná I and 0.3% fraction of long-distance dispersed seeds. The solid line with squares shows observed number of occupied patches. The squares indicate the years for which aerial photographs were available. Grey lines show the 90% confidence interval of patch occupancy predicted by simulations for each scenario. kk – indicates lowest, k – low, K – high and KK – highest population growth (lambda); – indicates lowest, + high and ++ highest carrying capacity used in the model. 00 indicates the standard values used in the simulations. See Methods for details. Above each column (carrying capacity constant) and on the left of each row (lambda constant), the values of coefficient of variation (CV) of sum of squares are shown.

H. mantegazzianum, ranged from 0.1 to 7.5% of the total seed set. Previous studies on long-distance dispersal indicated up to c. 5% of the seed travelled relatively far from mother plants, with a long and fat tail to the dispersal curve (see e.g. Higgins *et al.*, 2003 and examples therein; but see only 0.02% of *Rhododendron ponticum* seed estimated to travel further than 50 m; Stephenson *et al.*, 2007).

Although the existing estimates of long-distance dispersal (e.g. in Higgins *et al.*, 2003) seem to be directly comparable with ours, available data are mostly for tree species where distances over which seeds are dispersed are larger because of seeds being released from higher up and many species have specialized structures that support passive dispersal by wind. As seeds of *H. mantegazzianum* have no specific adaptation to dispersal vectors and the only indication of wind dispersal is flat and thin seed margins, water dispersal was suggested as a more important mode of its distribution (Walker *et al.*, 2003). Compared to other alien species in the Czech Republic, *H. mantegazzianum* exhibits an average capacity for dispersal

by water and wind (Moravcová *et al.*, 2010). This indicates that, compared to species possessing special adaptation for dispersal such as wind-dispersed trees or animal-species species, its long-distance dispersal is rather random, depending on landscape structures, especially water streams, and human activities.

It may be argued that the size of the study sites in relation to the overall seed production in these sites and the shape of the long-distance dispersal kernel may significantly affect the output of our study. The scale of the study generally affects the interpretation of the colonization patterns found in ecological studies because the same size of initial population will play a different role at a small study site or if it covers only a small proportion of a large area. As we were aware of these constraints, we attempted to take into account all possible aspects of landscape dynamics in our study: individual study sites were of the size that allowed to capture the dispersal at landscape level and chosen so as to be comparable in terms of the initial proportion of invaded area that ranged from 0.5 to

5% of the suitable area (Table 1). We believe that by taking these issues into account, we achieved a sound basis for analysing the long-distance dispersal at the used level.

Furthermore, it may be argued that long-distance dispersal can follow similar rules, in terms of density dependence on distance, as short-distance dispersal, and dispersal models combining both short- and long-distance dispersal should be used. However, such models are more suitable for larger distances and suffer by the need of precise estimate of dispersal parameters (Jongejans *et al.*, 2008; Münzbergová *et al.*, 2010). Therefore, we preferred, for our relatively small study sites, a general model with completely random dispersal being constant throughout the simulation plane instead of using a more accurately parameterized dispersal model for long-distance dispersal with higher uncertainty of the parameters. The distance function is therefore integrated only in the short-distance dispersal kernel.

Monitoring by using aerial photographs provides excellent information on spatio-temporal dynamics, despite lack of information on links between mother plants and offspring, which means that the inferred rates of spread are conservative estimates (Müllerová *et al.*, 2005). However, it needs to be noted that individual plants can be overlooked on aerial photographs, especially in the close neighbourhood of shrubs or in the forest understorey. This might be a source of two types of potential bias in the simulation models: underrepresented distribution in the initialization of the simulations and underrepresented distribution of the species used for comparison with simulation outputs. The former would lead to the overestimation of needed proportion of long-distance dispersed seed, while the second to its lower estimates. Even though such bias can be hidden in the presented results, the data in this study are the best that are available. Another issue potentially results from the fact that only flowering plants were clearly detected on aerial photographs. Therefore, the lag owing to the existence of vegetative plants (rosettes) outside the identified patches in the beginning of simulations might cause a delay in the modelled invasion dynamics compared to the observed data. However, this difference is only minor because the life span of the species is short, with the majority of plants flowering in their 3rd to 5th year (Pergl *et al.*, 2007).

Nevertheless, aerial photographs also provide a good way of analysing the role of landscape structure in shaping the patterns of long-distance dispersal and allow the use of habitat-specific models of species' population dynamics. Although the model used in the present study was based only on stochastic non-directed long-distance dispersal at a large scale, the results demonstrate the importance of relatively small but significant amounts of seed that are dispersed over long distance across the landscape. The advantage of our long-distance dispersal model is its simplicity, by using uniform random dispersal that fits the relatively small area of homogeneous landscape without strong corridors. However, in contrast to a pilot study by Nehrbass *et al.* (2007), our approach shows that reliable estimates of long-distance dispersal can be obtained only if

environmental heterogeneity is taken into account. At the Arnoltov study site, which was used in both studies, the estimated values of long-distance dispersed seed are 5.0–7.5% (this study) and 2.5% (Nehrbass *et al.*, 2007). This difference is likely to result from different population growth model (matrix vs. IBM) based on different population data, with the latter overestimating local dispersal at the expense of random dispersal (Nehrbass *et al.*, 2006).

The interplay between the dispersal of species and landscape structure affects the dynamics and survival of many species (e.g., Hanski, 1999; Soons & Ozinga, 2005; Trakhtenbrot *et al.*, 2005). In our study, the variation in the fraction of long-distance dispersing seeds that provides the best fit to the prediction of observed spread was attributable to the suitability of landscape to invasion, determined by land-use structure. Bearing in mind that a more rigorous statistical analysis was constrained by the low number of study sites, the results, nevertheless, strongly suggest that the fraction of long-distance dispersed seed needed to account for the observed invasion dynamics decreases as the proportion of the landscape made up of habitats that are suitable for invasion increases. In addition to identifying the fraction of dispersed seeds over long distances as critical, the simulations also showed that the level of long-distance dispersal significantly differs among individual study sites, even among those that experience similarly low levels of human pressure. This emphasizes the crucial role of habitat (and its invasibility) in plant invasions (Chytrý *et al.*, 2008a, 2008b) and indicates that in disturbed landscapes where a large proportion of area is covered by suitable habitats, the long-distance seed dispersal needed for a successful invasion needs to be much lower than in landscapes that are less disturbed. This highlights the smaller size of the window of opportunity for invasion for alien species in undisturbed habitats and increased potential of highly disturbed habitats that are generally suitable to invasion and exposed to a higher propagule pressure (Catford *et al.*, 2009; Davis, 2010). However, although the dispersal along streams and roads is crucial for this species (Pyšek *et al.*, 2008), these pathways are unlikely to play a role in our study sites owing to their relatively small area and the absence of the respective dispersal vectors. In addition, as these dispersal modes increase the availability of seeds at sites far away from the seed source, our results are rather conservative estimates of the study species' spread patterns.

The results of this study point to an important conclusion for management of both invasive and rare native species (see e.g. Trakhtenbrot *et al.*, 2005; Jongejans *et al.*, 2008). While the general recommendation is that the eradication of invasive species should first target satellite rather than central populations (Moody & Mack, 1988), our results indicate the importance of monitoring as large an area as possible. It needs to be noted that 1% of the seed set of an average *H. mantegazzianum* plant represents about 200 highly germinable seeds (Moravcová *et al.*, 2006; Perglová *et al.*, 2006). In the context of sustainable management of large infestations of *H. mantegazzianum* where complete eradication is unrealistic,

our results show that reduction in the seed set even at small amounts is likely to significantly affect the invasion dynamics. This can be extrapolated to other invasive species where control methods focus on reducing the seed set; the results of our study suggest that the more important effects of such methods may be in decreasing the number of seeds that are available for dispersal to a large distance from mother plants rather than in simply reducing the total seed set.

In this paper, we present a case study of an invasive species, invasion dynamics of which was modelled by incorporating long-distance seed dispersal. The study also indicates how linking long- and short-term population studies can improve the application of spatially explicit models that are currently in use. Based on the results, it is concluded that long-distance dispersal is an important component of the population dynamics of a species in the early phase of invasion, even at relatively small (regional) scales. Furthermore, by using the model species *H. mantegazzianum*, it was possible to show that the effects of long-distance dispersal on population dynamics can be demonstrated without direct measurements of dispersal events if long-term observations on a species distribution and land-use change accompanied by detailed population data are available. But, it has to be kept in mind that the data presented and conclusion drawn in this study are only valid for the scale used here and the species studied, while at different landscapes and for species with different dispersal mechanisms and life history, the effect of long-distance dispersal might be different. Therefore, our conclusions can only be generalized to a limited group of monocarpic perennial species in a comparable habitat that reproduce by seed, are extremely prolific and lack any specialized dispersal mechanisms, such as some other invasive Apiaceae (e.g., *Myrrhis odorata*, *Imperatoria ostruthium*, *Angelica archangelica*); more case studies covering a wider range of species with different life histories and addressed at a variety of spatial scales are needed.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Map of the study sites.

Appendix S2 Results of simulations of the sites.

Appendix S3 Results of sensitivity analyses.

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BIOSKETCH

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Appendix 12.

PAPER 12. Dostál P., **Müllerová** J., Pyšek P., Pergl J., Klinerová T. (2013). The impact of an invasive plant changes over time. Ecology Letters 16: 1277–1284. <https://doi.org/10.1111/ele.12166>

LETTER

The impact of an invasive plant changes over time

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Abstract

Many exotic plant invaders pose a serious threat to native communities, but little is known about the dynamics of their impacts over time. In this study, we explored the impact of an invasive plant *Heracleum mantegazzianum* (giant hogweed) at 24 grassland sites invaded for different periods of time (from 11 to 48 years). Native species' richness and productivity were initially reduced by hogweed invasion but tended to recover after ~30 years of hogweed residence at the sites. Hogweed cover declined over the whole period assessed. A complementary common garden experiment suggested that the dynamics observed in the field were due to a negative plant–soil feedback; hogweed survival and biomass, and its competitive ability were lower when growing in soil inocula collected from earlier-invaded grasslands. Our results provide evidence that the initial dominance of an invasive plant species and its negative impact can later be reversed by stabilising processes.

Keywords

Central Europe, coexistence, diversity, giant hogweed, native plant communities, plant invasions, recovery, soil pathogens, stabilising mechanisms.

Ecology Letters (2013) 16: 1277–1284

INTRODUCTION

Exotic plant invasions may have detrimental impacts on native plant communities by reducing their native species diversity (Levine *et al.* 2003; Vilà *et al.* 2011). Exotic invaders can displace resident species through superior competitiveness or the production of novel allelochemicals (Vilà & Weiner 2004; Lankau *et al.* 2009; but see Dostál 2011). The dominance of exotic species at the expense of native plants is also often explained by the modification of nutrient and material fluxes within the invaded community (Ehrenfeld 2003; Levine *et al.* 2003).

The impact of an invasive species does not necessarily remain constant over the course of invasion (Strayer *et al.* 2006; Strayer 2012), and both ecological and evolutionary processes may increase or attenuate the impact of invaders on the resident community. For example, Mitchell *et al.* (2011) found fewer native species in older vs. younger stands of exotic cattails (*Typha* sp.) due to an increasing litter layer. In contrast, the cover of native woody species in the forest understory invaded by *Alliaria petiolata* increased in sites where invasive populations were present for a long time, which was attributed to them losing an advantage due to becoming less allelopathic (Lankau *et al.* 2009). Similarly, selection for native genotypes tolerant to allelopathy can equalise the fitness of invaders and that of resident species (Callaway *et al.* 2005).

Along with these equalising processes, the coexistence of resident and invasive species depends on stabilising processes such as the density-dependent specialist enemy attack (Janzen 1970; Connell 1971; Chesson 2000; MacDougall *et al.* 2009). The initial advantage of exotic species due to missing enemies may translate into improved performance (Keane & Crawley 2002; Reinhart *et al.* 2003; DeWalt *et al.* 2004) and, most likely, also into local dominance at the expense of native species. Over the course of invasion, however, specialist pathogens or herbivores, subsequently introduced

from the previous range (Zangerl & Berenbaum 2005) or recruited from native pests (Carroll *et al.* 2005), are expected to reduce the dominance of the invader, facilitating the recovery of the native species (Flory & Clay 2013). Simberloff & Gibbons (2004) list several examples of boom-and-bust cycles of invaders' populations in their new ranges together with changes in their impact, and hypothesise that diseases could be the proximal cause of the collapse of the invaders. To date, there are several examples of increased enemy richness and control over the performance of exotic species that have colonised novel ranges at an earlier time (Hawkes 2007; Diez *et al.* 2010; Mitchell *et al.* 2010). To our knowledge, however, there are no rigorous data documenting pest accumulation and a subsequent modification of the invaders' impact along an invasion chronosequence (see discussion in Strayer 2012).

Heracleum mantegazzianum Sommier & Levier (giant hogweed) is a stout, up to 5 m tall, monocarpic perennial umbellifer native to the western Greater Caucasus that was introduced to Europe in 1817 (Jahodová *et al.* 2007). Following its introduction, it became invasive in a number of European countries, including the Czech Republic (Pyšek *et al.* 2012). Giant hogweed predominantly invades grasslands, where it can form large and dense stands and significantly reduce native species richness (Thiele & Otte 2007; Hejda *et al.* 2009) due to the reduction in light availability and changes in soil properties (Thiele *et al.* 2010). Hogweed also produces allelopathic compounds (Junttila 1975), yet its significance in competitive interactions remains to be proven.

In this study, we used spatially explicit knowledge of the invasion of giant hogweed in the western part of the Czech Republic, which was derived from a sequence of aerial photographs previously used to analyse the dynamics of invasion in this region (Müllerová *et al.* 2005, 2013; Nehrbass *et al.* 2007). The mapping of invading populations in particular years made it possible to perform vegetation surveys at sites invaded for different periods of time. At the same

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sites, we also sampled soil inocula for an experiment to evaluate the effects of soil biota on hogweed and native species performance and competitive ability. Our goal was to test the hypothesis that native species richness and native biomass production will be most reduced in recently invaded communities but will recover in older hogweed stands. If true, we hypothesised that this pattern was driven by the accumulation of soil pathogens in the older hogweed stands, thus reducing hogweed performance and/or its competitive ability.

METHODS

Survey of plant communities

We performed vegetation surveys in the Slavkovský les Protected Landscape Area, which is located in the western part of the Czech Republic (Fig. 1). Hogweed was introduced to this region as an ornamental plant in 1862 but began to spread massively only after WWII, presumably as a consequence of the lack of appropriate grassland management after the displacement of the German popu-

lation (Pyšek 1991). To obtain the information on sites invaded for different periods of time, we used data explored in the study by Müllerová *et al.* (2005, 2013), who reconstructed the hogweed invasion dynamics in this region over the past 50 years using a series of aerial photographs. We chose five areas (Fig. 1; Appendix S1) and in each of them identified grassland sites that were invaded (1) in 1962 or earlier, (2) between 1963 and 1973, (3) between 1974 and 1991, (4) between 1992 and 2006 and (5) were free of hogweed prior to 1962 and remained uninvaded until 2006. These intervals were further classified by the estimated mean age of the hogweed stands, yielding a chronosequence of invasive populations of differing age, i.e. (1) a minimum of 48 years, (2) 42 years, (3) 28 years, (4) 11 years and (5) 0 years (indicating hogweed-free sites). Mean age of 42 years, e.g. was calculated as $(2010 - 1963 + 2010 - 1973)/2$, with 2010 being the year when this study was initiated and 1963 and 1973 the years when aerial photographs were taken.

In 2010, sites were surveyed for the presence or absence of hogweed. In total, we included 24 sites of five different invasion histories as outlined above, each represented by five (or four) replicates (Fig. 1; Appendix S1). We assumed independent invasion dynamics within the individual areas; this assumption is justified by the maximum distance between sites within the areas being 1316 m (mean = 491.3 m; SD = 305.3 m) and the minimum distance between the area centres 2497 m (mean = 6935.3 m, SD = 2951.8 m). We also assumed that the sites involved in this study were similar in environmental conditions prior to the invasion because the historical aerial photographs indicate that the sites now colonised by hogweed used to be managed grasslands, as are the hogweed-free sites at present. However, as in all space-for-time-substitution studies, we cannot rule out the possibility that the pre-invasion differences in the abiotic and community characteristics also influenced the hogweed invasion and its temporal dynamics (see Appendix S2 for more details).

During the vegetation peak in June 2011, we determined plant species composition and species cover (in %). At each of the 24 sites, we installed three transects separated by a distance of 7 m, with three 2×2 m plots per transect; the centres of the neighbouring plots were 7 m apart. At the sites with hogweed populations present, we located the grid in the middle of the hogweed stands. At several sites, we were only able to install two transects due to the linear shape of the hogweed populations growing, e.g. along road edges. The sampling was thus done in nine or six plots per site.

The species data collected in all plots at a particular site were pooled for further analyses. For each site, we calculated the cumulative number of native species (S , species richness), the Shannon diversity index (H') and evenness (J'), which was calculated as $H'/\ln S$ (Magurran 1983). Shrub and tree species were excluded from the data set ($n = 11$ species), as were the four neophytes (alien species introduced since the end of the Medieval Period) from a set of 155 species that were recorded during a vegetation survey. The mean species cover was used for the calculation of H' and J' . Diversity of sites represented by six plots was not significantly different from diversity of sites where nine plots were sampled ($P > 0.5$ in all three diversity parameters).

At the same time, we also harvested the native species biomass 2 cm above the ground in 25×25 cm squares located in each plot. The biomass was then dried to a constant mass at 70 °C. In addition, we harvested the hogweed biomass in three 2×2 m plots

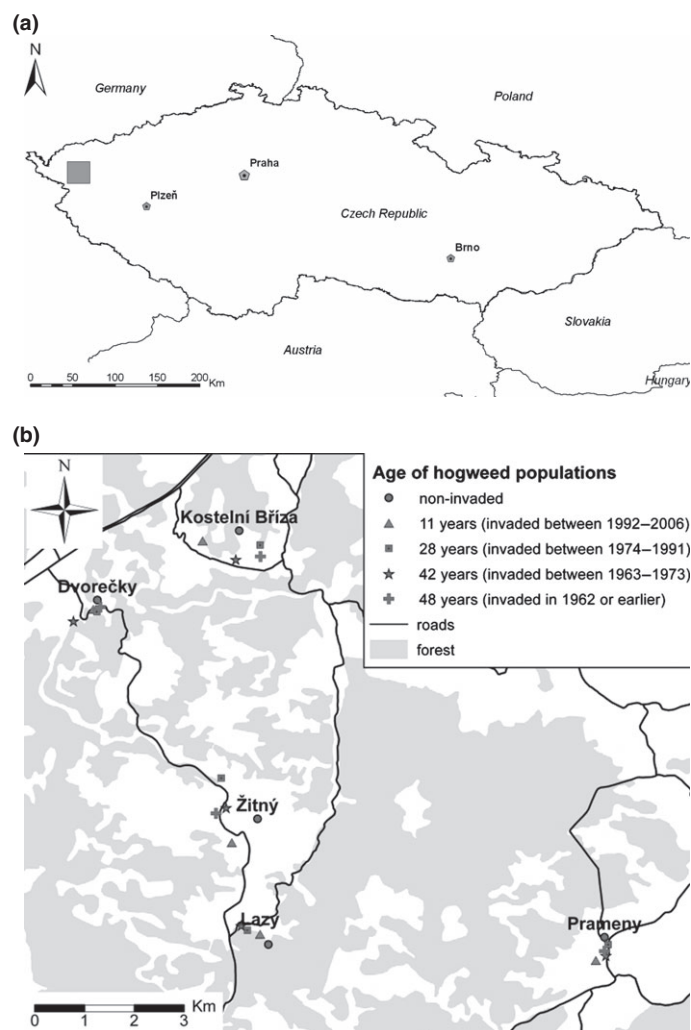


Figure 1 (a) Map of the Czech Republic with a square indicating the study location. (b) Map of the sites included in the study. Within each area, there were uninvaded grasslands and grasslands invaded for 11 to 48 years.

at the invaded sites for a total productivity analysis (i.e. sum of mean native and hogweed biomass), with the value recalculated for an area of 0.0625 m². The biomass sampling was performed prior to the any mowing or grazing applied by managers at the hogweed-free sites.

We also used the same plots to calculate the mean hogweed cover at the invaded sites. All invaded sites were free of any management during the community selection in 2010, but a hogweed eradication campaign was initiated at six sites in 2011 prior to data collection (see Appendix S1). We included native community measurements but not hogweed cover measurements (and total biomass) from these six sites in our further analyses.

Common garden experiment

In addition to the vegetation survey, at 20 sites, we sampled soil blocks along four transects (5 m apart) with 10 sampling points each (5 m apart) during late June 2010 (Appendix S1; soil sampling was not performed in the 'Lazy' area). The sampled blocks were approximately 10 × 10 × 8 cm in size. At certain sites, we were able to install two transects only; in such cases, the soil was sampled at 20 sampling points per transect.

The soil from the same site was then bulked, homogenised and sieved through a 10-mm mesh to remove large stones and roots. Half of the soil from each site was sterilised by 25 kGy gamma irradiation, and the other half was left untreated; both were mixed with sterile sand in a 2 : 3 ratio. The sterilization treatment was crossed with the addition of activated carbon to control for possible hogweed allelopathic effects (Junttila 1975), adding 20 g of carbon per litre of substrate mixture (particle size of 0.075 mm; Resorbent, Ostrava, Czech Republic). The factorial manipulation of sterilization and activated carbon gave four soil treatments.

The soil treatments were combined with three planting schemes. In 2.5 l pots, we added either (1) one hogweed seedling alone, (2) a mixture of native seed or (3) one hogweed seedling along with the native seed mixture. Hogweed seedlings were obtained in the field and their roots were surface-sterilised with 2% bleach for one hour. Each seedling was also measured for root length and width to estimate its below-ground biomass; the product of the two measured parameters effectively predicted the root biomass ($R^2 = 0.737$, $P < 0.001$; based on $n = 20$ seedlings). The native seed mixture consisted of forbs *Plantago lanceolata* and *Centaurea jacea* (10 seeds each) and 20 seeds of *Dactylis glomerata* (grass). These are native grassland species observed to occur in the study area, with *D. glomerata* being the most abundant and *C. jacea* the rarest plant species. *Dactylis glomerata* was found in all of the communities whereas *P. lanceolata* and *C. jacea* tended to occur at uninvaded sites or at those harbouring old hogweed stands. The native seeds used in the experiment had no prior contact with hogweed (purchased from Planta Naturalis, Sobotka, Czech Republic), i.e. the results of the experiment were not confounded by possible evolutionary adaptations of the native species to hogweed.

The experiment was initiated in early July 2010 and consisted of 480 pots (20 sites of soil origin × four soil treatments × three planting schemes × two replicates) randomly placed in beds of the experimental garden of the Institute of Botany in Průhonice, Czech Republic (49°99'N, 14°57'E). In addition, we prepared four replicates per site that were left untreated and without native seed addition to check for the presence of the three native species in the

soil inoculum; no seedlings of the native mixture germinated in these controls. The experiment was maintained by watering, if necessary, and by fertilization using 0.25-strength Hoagland solution, 100 mL per litre of substrate, which was performed biweekly until the end of September 2010 and again from early May 2011 until mid-July 2011, when the experiment was terminated. The hogweed seedlings that died during the first month of the experiment were replanted. The pots were weeded regularly to remove non-sown species.

We recorded the number of native germinants by the end of August 2010 and hogweed survival by mid-October 2010, early May 2011 and mid-July 2011. We separately harvested the above-ground biomass for each species in mid-October 2010. In mid-July 2011, we performed the final harvest and sampled the above-ground biomass separately for each species and the below-ground biomass separately for hogweed and the natives. The biomass was dried at 70 °C. Herein, we report the total native and hogweed biomass and the hogweed survival recorded during the final harvest.

Statistical analyses

Survey of plant communities

First, we analysed the effect of hogweed invasion (i.e. of hogweed presence/absence at the sites) on native species richness and productivity. Within invaded sites, we tested the effect of hogweed cover on richness and productivity. We used linear mixed models with area as random effect.

Second, we tested the effect of invasion history (time since community invasion) on the native species diversity (expressed as the species richness, H' and J'), native productivity and total productivity. In addition, we tested whether the invasion history was a significant predictor of the variation in native species composition. For the latter, we used detrended correspondence analysis (hereafter DCA) to calculate the axis 1 and axis 2 (that explained 19.8 and 12.0% of the variance respectively) site scores from the species composition data (with species cover included). We also analysed hogweed cover at sites differing in invasion history.

We ran three models for each of the above eight response variables (see also Appendix S3), one with the time variable entered as a linear term only, another one with both linear and quadratic terms for time, and the third one with intercept only. We used linear mixed models to test for the fixed effects of time, with area included as a random effect. The statistical significance of the fixed effects was estimated using likelihood ratio tests, and the model with the best fit was also identified based on Akaike's Information Criterion.

Common garden experiment

We searched for effects of soil origin (i.e. for differences between soils with different invasion histories measured as time since the site was invaded), sterilization, the addition of activated carbon, and competition on the performance of hogweed and that of native plants. We analysed hogweed survival and total biomass, separately for hogweed and the native species, harvested in mid-July 2011.

We constructed a full model that included all four treatments as the main and interacting effects (entered as fixed effects), producing a four-way interaction model. Area and site nested within area were included as random effects. Likelihood ratio tests were used to estimate the statistical significance of main effects and their interactions,

and to obtain a minimum adequate model. Binomial errors were used in the models for hogweed survival.

For the total hogweed biomass, we ran an additional model using the mean biomass per site of inoculum origin (instead of the biomass from individual pots used in the above-described models). Time, sterilization and their interaction were used as predictors (fixed effects), with area included as random effect.

In the analyses of hogweed survival and biomass, the initial root biomass of the hogweed seedlings from early July 2010 was entered as a covariate, $\log(x \times 1000)$ -transformed.

The hogweed total biomass was square-root-transformed to meet the assumptions of homoscedasticity and normality of residuals. The outliers [determined by the $1.5 \times$ interquartile range (IQR) rule] for the hogweed ($n = 5$ values) and native total biomass values ($n = 3$) were replaced by the mean values. Alternative models with outliers retained or removed yielded similar results (data not shown) as those with outliers replaced by the mean. The native mixtures initially planted with hogweed that died by May 2011 were entered in the analysis as hogweed-free (competition-free) pots based on the observation that hogweed had no effect on the native above-ground biomass during the harvest in mid-October 2010 ($p = 0.387$). Raw data can be found in Appendix S5.

Mixed-effects models were developed using R version 2.14.2 (R Development Core Team 2012), specifically with the R packages *lme4* and *nlme* (Bates *et al.* 2012; Pinheiro *et al.* 2012). Marginal R^2 (proportion of variance explained by the fixed factors alone) and conditional R^2 (proportion of variance explained by both the fixed

and random factors) were calculated according to Nakagawa & Schielzeth (2013). DCA was performed using CANOCO (ter Braak & Šmilauer 2002).

To assess the native community recovery in invaded sites, we used measurements at uninvaded sites as a reference point. We also included soil inocula from uninvaded sites in the experiment to estimate the effects of initial soil conditions. Including uninvaded sites could, however, prevent the detection of temporal changes within invaded sites as the dynamic view of invasion impacts predicts (Strayer *et al.* 2006). To overcome this problem, we repeated the analyses with measurements from invaded sites only, and also with plants grown in soil inocula originating from there.

RESULTS

Survey of plant communities

Hogweed invasion was correlated with low native species richness: we found $40.8 (\pm 1.4 \text{ SE})$ species at hogweed-free sites, whereas communities colonised by *H. mantegazzianum* hosted an average of $31.3 (\pm 1.6 \text{ SE})$ species (t -value = -2.975 , $P = 0.004$). The invaded communities were also less productive in terms of native biomass ($18.2 \pm 2.2 \text{ g vs. } 10.8 \pm 1.2 \text{ SE g of dry biomass/0.0625 m}^2$ (mean $\pm$ SE) in uninvaded vs. invaded communities; t -value = -3.122 , $P = 0.004$) but not in terms of the total biomass ($18.2 \pm 2.2 \text{ g vs. } 16.4 \pm 1.3 \text{ g of dry biomass/0.0625 m}^2$ (mean $\pm$ SE) in uninvaded vs. invaded communities; t -value = -0.516 , $P = 0.54$). Within invaded sites, greater

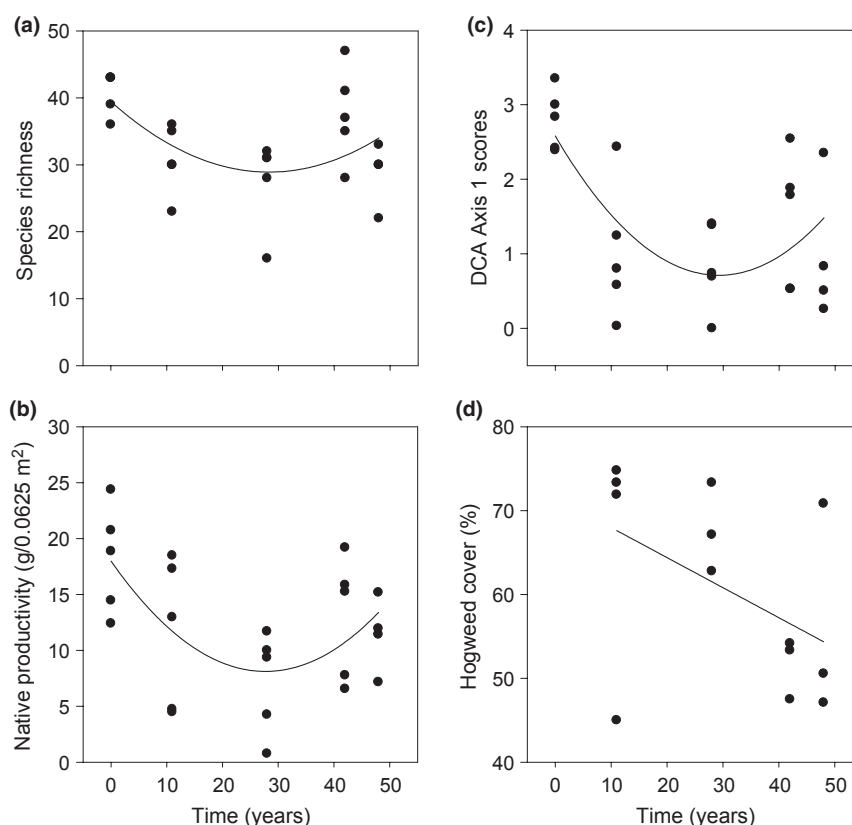


Figure 2 Regression of species richness (a), native productivity (b), community composition (as DCA axis 1 scores; c) and hogweed cover (d) against the time since the sites ($n = 24$) were invaded by hogweed *Heracleum mantegazzianum*. The best fits included linear and quadratic terms for time (both always significant at $P \leq 0.05$) in (a–c) and a linear term for time ($P = 0.046$) for (d). Time = 0 years indicates uninvaded sites.

hogweed cover reduced both the species richness (t -value = -1.983 , $P = 0.088$) and native productivity (t -value = -2.288 , $P = 0.056$), though the effect was only marginally significant.

The impact of hogweed changed during its invasion history. The best fit models in the analysis of hogweed impact included both linear and quadratic terms for the time since community invasion. Specifically, the native species richness and productivity consistently decreased with time from the beginning of invasion; they were most strongly reduced in the 28-year-old stands but increased again in the older populations (Fig. 2a, b; Appendix S3). This unimodal pattern was also found for Shannon diversity H' and DCA axis 1 scores of the community composition data (Fig. 2c). Evenness J' , total productivity and DCA axis 2 scores were, however, similar across the sites of different invasion history (Appendix S3).

Maximum hogweed cover ($66.2 \pm 7.1\%$, mean $\pm$ SE) was recorded in the earliest invasion stage, in 11-year-old stands, but declined linearly with the time since invasion ($P = 0.046$), reaching $56.2 \pm 7.4\%$ in the 48-year-old populations (Fig. 2d; Appendix S3).

Common garden experiment

Of the 320 hogweed seedlings that were initially planted, one hundred and sixty-one survived until mid-July 2011. The survival was reduced by competition (χ^2 -value = -6.121 , $P < 0.001$; Appendix S4), the effect of which was further modified by sterilization (competition $\times$ sterilization: χ^2 -value = 4.149 , $P < 0.001$); without competition, more plants survived in the sterile ($n = 59$ plants) than non-sterile substrate ($n = 44$ plants). In the presence of native species, twice as many hogweed plants survived under the non-sterile condition than in pots with the sterile inoculum (38 vs. 20 plants). Although the biomass of native species grown with hogweed was larger in sterile than non-sterile inocula (18.7 ± 0.8 g vs. 13.4 ± 0.7 g, mean $\pm$ SE) and could thus have a more detrimental effect on hogweed survival, the effect of sterilization treatment remained significant even if the native biomass was used as a covariate (χ^2 -value = 2.272 , $P = 0.023$). Survival was also less likely in the substrate with activated carbon (χ^2 -value = -2.198 , $P = 0.028$).

Consistent with our hypothesis, soil inocula collected at sites with longer invasion history had a greater negative effect on the survival of hogweed plants. Importantly, this trend was found in pots with non-sterile inoculum only (time $\times$ sterilization: χ^2 -value = -2.515 , $P = 0.012$; Fig. 3a). Addition of activated carbon modified this relationship (see Fig. S1 in Appendix S4) as indicated by a marginally significant three-way interaction (activated carbon $\times$ time $\times$ sterilization: χ^2 -value = -1.896 , $P = 0.058$). When analysed separately, a significant time $\times$ sterilization interaction was detected in pots without addition of activated carbon but not in pots with carbon (Appendix S4).

The hogweed total biomass was smaller in pots with the non-sterile (13.8 ± 1.6 g, mean $\pm$ SE) than sterile inoculum (28.8 ± 2.4 g, mean $\pm$ SE; t -value = -4.698 , $P < 0.001$) and was also reduced by the competition with native species (t -value = -8.407 , $P < 0.001$; Appendix S4). When the hogweed total biomass (taken as the mean per site of inoculum origin) was regressed against the invasion history in an additional model, a pattern similar to that for hogweed survival was found: plant size decreased with the soil inoculum collected in the older hogweed stands but only if not treated by sterilization (a marginally significant time $\times$ sterilization interaction: t -value = -1.960 , $P = 0.059$; Fig. 3b, Appendix S4).

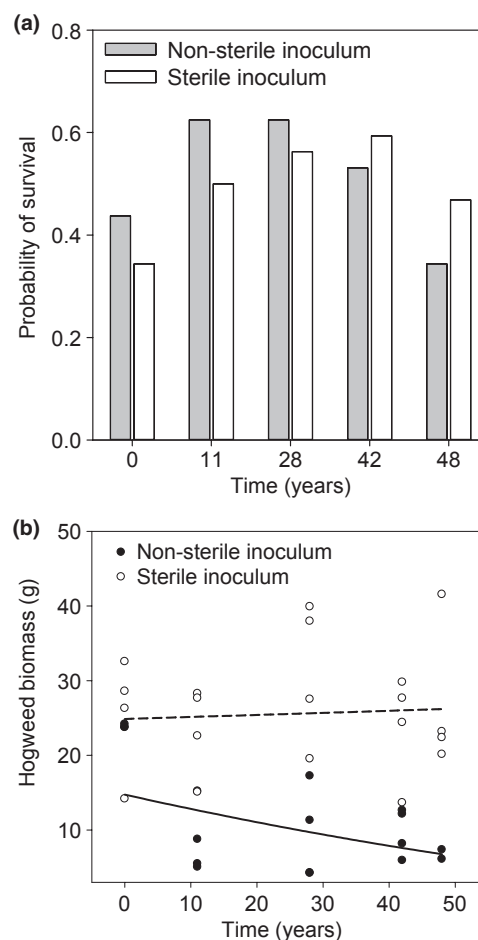


Figure 3 Survival probabilities (a) and total biomass (b) of hogweed plants by July 2011 in the common garden experiment. The plants were grown in substrates that included non-sterile and sterile soil inocula sampled from sites with different invasion histories (including uninvaded sites and sites invaded for 11 to 48 years). In (a), hogweed plants were less likely to survive in non-sterile inocula sampled at sites invaded for longer time ($P = 0.012$ of time $\times$ sterilization interaction). In (b), biomass (mean per site of inoculum origin) decreased with longer invasion history, but in non-sterile (full line) rather than sterile inocula (dashed line; $P = 0.059$ of time $\times$ sterilization interaction).

The native total biomass was reduced in pots with the non-sterile (13.5 ± 0.5 g, mean $\pm$ SE) compared to the sterile inoculum (18.9 ± 0.5 g, mean $\pm$ SE; t -value = -7.683 , $P < 0.001$). Hogweed presence also decreased the biomass of native species (t -value = -2.526 , $P = 0.012$), but its competitive effect was dependent on the origin of the soil inoculum. Specifically, when grown with the invader, the native biomass increased with inocula collected at sites with longer invasion history (time $\times$ competition: t -value = 2.382 , $P = 0.018$; Fig. 4, Appendix S4). The significant time $\times$ competition interaction associated with native biomass was mostly due to plants grown in sterile rather than non-sterile inocula (Appendix S4). Further, the effect of time on the biomass of native species was independent of the biomass of hogweed plants (treated as a covariate) growing together with natives (t -value = 2.262 , $P = 0.045$).

Re-analysing the data with invaded communities only

When uninvaded sites were excluded from the analyses of field community measurements, evenness J' (Fig. S1 in Appendix S3) and

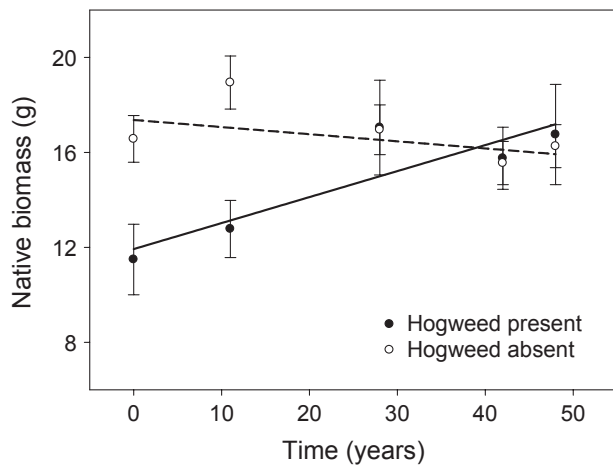


Figure 4 The native total biomass (mean $\pm$ SE) grown with (full line) and without (dashed line) hogweed in a common garden experiment. The presence of hogweed significantly ($P = 0.012$) reduced the native biomass, but its competitive effect was dependent on the invasion history of the community from which the soil inoculum was sampled ($P = 0.018$ of time $\times$ competition interaction).

Shannon diversity index increased with the age of hogweed stands (although the effect was only marginally significant in case of the latter parameter). Variation in all other parameters including species richness and composition (DCA axes scores) was not, however, related to the invasion history (Appendix S3).

Regarding the experiment, similar temporal trends as those found for a complete data set were indicated for hogweed survival and native species' biomass but not for hogweed total biomass (with mean per site of inoculum origin; Appendix S4).

DISCUSSION

The rapidly growing interest in biological invasions is closely associated with their potential impact on native communities (Levine 2008). In most studies, the impact is usually derived from a comparison of invaded and invasion-free plots of presumably similar environmental conditions (e.g. Hejda *et al.* 2009) without further reference to the invasion history. However, such an approach cannot properly estimate the long-term effects of the invader on the native community, as these can change over time (reviewed by Strayer *et al.* 2006). In accordance with this argument, we found that the hogweed impact on the diversity and productivity of native species is dynamic: the invader exerted the strongest effect on native communities in the early stages of invasion, up to approximately 30 years, with the impact diminishing after 40–50 years since the beginning of invasion. We showed that temporal changes occurred also within invaded sites only as the evenness and Shannon diversity index increased linearly since the beginning of the invasion. There was, however, little evidence for an increase of species richness or change in species composition in older hogweed stands when uninvaded sites were excluded from the analyses.

Changes in the hogweed impact are likely associated with the decreasing dominance of this species in the invaded communities over time. Our results indicate that hogweed cover in the oldest populations (48 years old) was smaller by 10% than at the begin-

ning of invasion (11 years), with 66% cover on average. Müllerová *et al.* (2005) analysed the same chronosequences derived from aerial photographs and recorded that hogweed patches reached their maximum size after 20–25 years but decreased later on. Nehrbass *et al.* (2006) used a modelling approach and demonstrated that the probability of sampling negative population growth of hogweed increased with time since first invasion, which also supports observed declines in hogweed cover over time. The ongoing process of native community recovery in less dense hogweed stands corresponds to findings of Thiele *et al.* (2010) who showed that cover of 50% (i.e. similar to that in the oldest stands of our study) was the threshold above which the adverse effects of hogweed on native species richness start to manifest. Studies from other invaded communities also support the view of a greater negative impact being associated with increasing exotic dominance (e.g. Ortega & Pearson 2005).

The second, experimental part of our study indicated a possible explanation for hogweed decline and recovery of the native community. Specifically, we showed that the survival and biomass of hogweed decreased most markedly when growing in the soil from sites with the longest invasion history. Importantly, the relationship of hogweed performance and invasion history was detectable in the non-sterile rather than sterile soil. This indicates that hogweed performance was controlled by soil pathogens but their effect depended on the number of successive generations of hogweed occupying the same site (e.g. Packer & Clay 2004). As the negative plant–soil feedback is likely to develop slowly, hogweed can grow in high densities at sites invaded for a short time. With increasing number of hogweed generations, soil pathogens accumulate and increase their control over the hogweed performance. Alternatively, pathogens may have evolved a stronger virulence over time, reducing thus the hogweed density. A similar negative plant–soil feedback was demonstrated for *Sapium sebiferum*, a successful woody invader in southeastern USA, that showed less survival and biomass in soil collected near con- than heterospecifics (Nijjer *et al.* 2007). Nijjer *et al.* (2007) assume that this negative feedback may decrease *Sapium* persistence in invaded communities by limiting self-replacement, but unlike in our study, the authors do not provide a temporal framework of the expected invader's decline.

We hypothesise that the increasing hogweed dieback in soil with a long invasion history is a key for native species recovery. This process is likely to be further strengthened by decreasing competitive effects of hogweed, as native plants grown with the invader increased in soil occupied for a longer time. In this case, however, soil abiotic rather than biotic components drove the relationship as the variation in hogweed competitiveness was detected for sterile inocula only. These soil abiotic effects persisted in the pots fertilised by Hoagland solution, a treatment that we applied to control for chemical differences among different soil inocula as well as for side effects of soil sterilization (Troelstra *et al.* 2001). Still, soil chemical differences influenced the results, probably due to the relatively high ratio of soil inocula to sterile sand. The use of sterile field soil would probably be more appropriate in this case. There were also side effects of activated carbon intended to control for possible allelopathic effects (e.g. Callaway *et al.* 2005) that were previously documented for hogweed (Junttila 1975). We did not detect phytotoxicity in our study but the activated carbon reduced hogweed survival and modified the effect of soil inocula on the survival. It is possible, although not proved yet that increased

hogweed mortality in pots with carbon was due to reduced infection with arbuscular mycorrhiza as reported for *Senecio inaequidens* (Weißhuhn & Prati 2009). These authors also found substantial changes in soil chemistry after carbon addition. These changes could also have direct negative effects on hogweed survival. Altered soil chemistry could also outweigh the invasion history-dependent effects of soil microbiota on hogweed performance. Therefore, these possible confounding effects of experimental treatments must be born in mind when interpreting the results of the common garden study.

Our results constitute a rare empirical demonstration that a negative plant–soil feedback (Bever *et al.* 1997), as an example of a stabilising process (Chesson 2000; MacDougall *et al.* 2009), can reverse the initial negative impact of an aggressive invader on native resident species, resulting in their coexistence later on (Flory & Clay 2013). These results provide more sophisticated guidance to prioritise populations for control than recommendations based simply on invader's cover or population size; sites with a shorter invasion history should be prioritised in hogweed management. This should not be taken as an incentive for a 'do-nothing' strategy in invasive plant management, based on the argument that sites with a longer invasion history would recover spontaneously. First, even less vigorous, older hogweed populations represent obstacles for landscape management since after 50 years they still reach rather high cover, and serve as a seed source for invasions of intact sites (Nehrbass *et al.* 2007). Second, given the coupled oscillatory population dynamics of plants and their pests (Olff *et al.* 2000; Van der Putten 2003), the ongoing decline in hogweed cover may be followed by pest retreat, which, in turn, may allow hogweed population recovery. Therefore, dynamic processes regulating hogweed populations can rather be utilised as a complementary tool in informing large-scale systematic management, but not a management approach to avoid persistent ecological damage.

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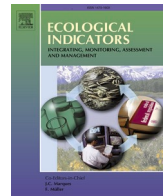
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Appendix 13.

PAPER 13. **Müllerová, J., Šíffel, E.** (2025). Cooling the Land Surface: Ecosystem Health and Water Availability Drive the Landscape Capacity to Mitigate Climate Change. *Ecol Indicators* 172: 113265.
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Cooling the land surface: Ecosystem health and water availability drive the landscape capacity to mitigate climate change

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ABSTRACT

Land surface temperature (LST) is profoundly interlinked with the landscape state, settings and functioning, with the connections being very complex. Although the role of wetlands and (semi)natural habitats, in mitigating climate extremes is generally understood, the mechanisms explaining the thermal patterns in complex landscapes remain unclear. We address this knowledge gap, investigating a link between the dynamics of LST and characteristics of a diverse sandstone landscape, focusing on the role of water features and forest health in alleviating temperature extremes. For our study, we used a model example of a sandstone protected area in the north of the Czech Republic that underwent significant changes during the last decade due to a bark beetle infestation and a consequent forest die-off and wildfire. LST data were obtained from MODIS and Landsat 8 sensors in a cloud-based Google Earth Engine platform. Machine learning regression model enabled us to assess complex multi-variable relationships and increase the LST spatial resolution. The results suggest the significant effect of both water availability and ecosystem health on LST, with vegetation indices, land cover and elevation being the main factors. The correlation of the satellite-based LST and in situ measured temperature depended on the canopy cover. The study indicates that in complex landscapes, LST data of high spatial and temporal resolution is necessary to disentangle local patterns and environmental drivers. Satellite data can serve as a reliable means to understand the mechanisms and prepare adaptive management measures to make the landscape more resistant to climate change related threats.

1. Introduction

Land surface temperature (LST) is one of the major factors affecting environmental conditions, as it plays a key role in heat flows and heat balance. Changes in LST can lead to alterations in physical and biochemical processes, as well as ecosystem functioning (Parain et al., 2019). The IPCC report indicates that the Earth's surface temperature has risen by an average of 1.59 °C since the end of the 19th century. The rate of increase in the last fifty years has been the fastest in the last 2000 years. By the end of the 21st century, it is expected to rise by 1.4 to 4.4 °C (Lee et al., 2023). In 2016, the World Meteorological Organization included LST among the essential climate variables (Belward et al., 2016).

Studies agree on the strong influence of soil moisture, water bodies, vegetation and topography on LST (Pablos et al., 2016; Entezari et al., 2019; Gupta et al., 2019; Guha and Govil, 2021). Vegetation indices, such as the Normalized Difference Vegetation Index (NDVI), can be used as indicators of both ecosystem health (Meneses-Tovar, 2011) and the

cooling effect of vegetation caused by shielding and evapotranspiration (Hanamean et al., 2003). However, the ability of vegetation to absorb radiation is also dependent on soil water content (Carlson et al., 1994). This means that LST, NDVI and water content are highly interlinked, and their relationship is very complex, especially in vegetated areas. Among topographical factors significantly affecting LST are elevation and slope, followed by topographic shading and direct insolation (Peng et al., 2022).

LST can be measured by ground measuring stations, however, such data are discontinuous and their quality is determined by the density of the measurements. In this regard, satellite data available for the entire globe at regular intervals provide a significant improvement. The most common source of high spatial resolution LST is Landsat 8 (L8) satellite, in orbit since 2013 with a 16-day cycle and a resolution of 30 m (visible and infrared bands), 15 m (panchromatic band), and 100 m (thermal bands of the TIRS sensor, García-Santos et al., 2018). The thermal data is further interpolated by cubic convolution and made publicly available at the 30 m resolution. As of 2014, the USGS does not recommend using

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data from band 11 due to stray light that adds to the calibration uncertainty, and thus, most studies use only the thermal band 10 (USGS, 2019). The Moderate Resolution Imaging Spectroradiometer (MODIS) provides high temporal resolution LST. This pair of sensors on board the satellites Terra (since 1999) and Aqua (since 2002) delivers 1 km LST every 1–2 days (Justice et al., 2002). Among other available thermal satellite sources are ASTER, published as a Global Emissivity Dataset (GED, 90 m resolution, 16 days cycle; Hulley et al., 2015), SLSTR on board the Sentinel-3 (since 2016, 1 km resolution; Coppo et al., 2010), VIIRS (since 2010, twice a day, 375 m resolution; Islam et al., 2016), IRS onboard Chinese mini-satellite HJ-1B (since 2008, 300 m resolution; Wang et al., 2010), and a new thermal mission ECOSTRESS onboard ISS (since 2018, resolution 39 x 68 m, 4–5 days cycle; Fisher et al., 2020; Silvestri et al., 2020).

Deriving LST from satellite data is inherently affected by measurement error caused by the distance of the sensor from the Earth's surface (Li et al., 2023). Algorithms recalculating the temperature measured at the satellite sensor to the surface temperature try to minimize this error using in situ measurements. It is also necessary to consider that passive sensors measure the temperature of the closest surface, and thus, the radiation reflected by the surface covered by dense vegetation expresses the temperature of the canopy surface (i.e. mesoclimate) rather than that of the earth's surface (i.e. microclimate). The difference between the two depends largely on the canopy openness and vegetation structure. In more closed and structurally complex ecosystems, such as forests, the difference between canopy surface temperature and forest microclimate can be significant (Kašpar et al., 2021). This difference is also influenced by other factors such as the type and health status of the vegetation cover, air temperature, humidity and the intensity of the incoming solar radiation, and can be critical for biodiversity, providing a range of environmental niches for a variety of species (Zellweger et al., 2019). To evaluate the degree of accuracy of satellite-derived LST, precise in situ measurements in various conditions are required. Such in situ data of the surface temperature are limited and scattered, but see, e.g., SURFRAD (Surface Radiation Budget Network; Augustine et al., 2000), BSRN (Baseline Surface Radiation Network; Driemel et al., 2018), ISMN Database (Dorigo et al., 2021) or SoilTemp (Lembrechts et al., 2020).

As already mentioned, LST is deeply interlinked with landscape settings and functioning. Consequences of climate change related to the increase in temperature and the decrease of amount and/or irregularity of precipitation are coupled with landscape change. The growing awareness of these threats draw attention to the amendment of landscape stability and ecosystem services, specifically to the role of wetlands and (semi)natural habitats, such as forests, in cooling the landscape and increasing its water retention capacity (An and Verhoeven, 2019; Stefanakis, 2019).

The Czech Republic is particularly sensitive to this issue due to the fact that it does not host any large rivers, and so maintaining and improving landscape functions such as water retention and temperature modulation under climate change is extremely important. The Central European region underwent significant landscape change during the last century (Kupková et al., 2016). Many problems of the Czech landscape can be attributed to the legacy of its communist past (historical disrespect to natural processes) that still causes a poor state of landscape, poor health of ecosystems and inappropriate management practices (Tickle and Clarke, 2000). This consequently causes disruption of many important ecosystem services, and the loss of landscape stability and biodiversity (Bochniarz and Cohen, 2022). The main causes for the Czech landscape malfunctioning can be summarized as: (i) agriculture – unsuitable practices, large blocks of fields, as well as low presence of hedgerows, small woody features and permanent grasslands; (ii) soil – consequent poor soil conditions at arable fields, suffering from soil compaction, erosion, low retention capacity and poor health of soil fauna; (iii) water – extensive channelizing and pipe-lining of rivers and streams in the past, low presence of wetlands and functioning alluviums;

(iv) forests – poor forest health related to the inappropriate past management, specifically extensive Norway spruce plantations suffering from drought and subsequent insect outbreaks, often followed by extensive clear cuts and destructive logging techniques disturbing the forest surface and hampering the potential regeneration (Petřík et al., 2015; Sušník et al., 2022). Long series of satellite data can bring insights into these processes and enable adopting appropriate measures mitigating the mentioned threats.

In this study, we investigated the link between the dynamics of LST and landscape characteristics, specifically the availability of water in the landscape and forest health, using a model example of a sandstone protected area in the north of Czech Republic. The unique settings of massive forest die-off during the study period coupled with dense network of in situ temperature measurements allowed us to study factors influencing LST patterns and dynamics, and to test the following hypotheses:

- We hypothesize that besides topography and land cover, LST is strongly influenced by water availability in the landscape as well as the state of ecosystems.
- We also expect that the relationship between satellite derived and in situ measured LST will change in relation to ecosystem health.
- We further explore LST dynamics at different scales, aiming to define appropriate spatial and temporal resolution that can be related to the landscape patterns and change. We hypothesize that for complex landscapes, LST at higher spatial and temporal scales is necessary, and test the possibility of refining LST resolution using environmental variables as a proxy in machine learning modeling.

We are also interested in the way the findings can support adaptive landscape management in the context of climate change (ref. EU Biodiversity strategy for 2030).

2. Methodology

2.1. Study area

This study focuses on the sandstone landscape in the north of the Czech Republic, bordering Germany (Fig. 1). The area is protected as the Bohemian Switzerland National Park, established in 2000 and covering nearly 80 km², and the Elbe Sandstone Protected Landscape Area established in 1972 and covering 243 km². It is connected to the Sächsische Schweiz NP established in 1990 on the German side of the border.

The area is characterized by a mosaic of dry and sun-exposed

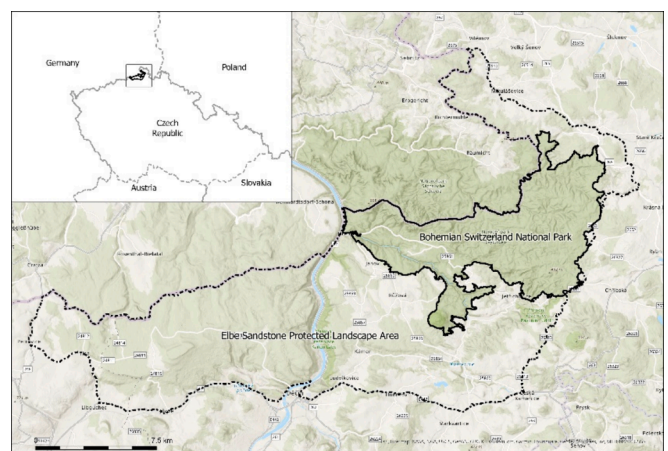


Fig. 1. Study area.

sandstone towers and cool shady deep canyons and valleys. Thanks to this dramatic geomorphology, large differences can be found in microclimatic conditions, such as climatic inversion valleys, and therefore, there is a pronounced gradient of different habitats (Härtel et al., 2012). The area is mostly forested, with prevailing N. spruce, mostly planted in the past and native only in aforementioned inversion valleys, Scots pine on sandy towers and rock outcrops, and remnants on originally common deciduous forests, mainly dominated by European beech. In the last decade of warm and dry years, aging N. spruce forests suffered by massive bark beetle outbreak followed by the forest die-off, and recently by an extensive wildfire (2022).

2.2. Datasets

For the study, we combined several datasets, such as satellite data (Landsat 8, L8, and MODIS), land cover raster/vector layers, and digital elevation model (Table 1).

LST was derived from L8 and MODIS satellite data from a period of 2016 to 2022. The data were restricted to the growing season (1 April to 31 October) to limit the effect of snow cover and sparse coverage due to high cloud cover during the winter. After filtering for high quality imagery, the final collection comprised 30 to 66 images (L8) and 518 to 618 images (MODIS), depending on the position within the study area.

For L8, USGS Collection 2 at Google Earth Engine (GEE) catalog provided a temperature layer derived from band 10 using a single channel algorithm at 30 m spatial resolution every 16 days. We also used several other bands, such as red and near-infra for NDVI, and QA band to mask out radiometrically saturated and cloudy pixels.

For MODIS, the already available collection Terra Land Surface Temperature and Emissivity Daily Global 1 km with daily frequency was capitalized on.

Several other sources were used to describe environmental conditions, such as vegetation health (NDVI from the same satellite data collections), land cover change (Dynamic World dataset; Brown et al., 2022), water availability in the landscape (water features in vector dataset DIBAVOD, Digital Base of Water Management Data; DIBAVOD, 2023; and wetland habitats selected from habitat mapping of Chytrý et al., 2010), and geomorphological characteristics derived from digital elevation model DMR5G (ČÚZK, 2023), such as elevation, aspect, Topographic Position Index (TPI) expressing the position of a pixel relative to its surroundings, and Topographic Wetness Index (TWI) determining the potential to accumulate rainwater derived solely from topography, irrespective of the absorptive capacity, settings of the landscape, presence of water sources or rainfall conditions (Maxwell and

Table 1
Overview of the used datasets. Abbreviations: USGS (United States Geological Survey), Landsat 8 (L8), MODIS (Moderate Resolution Imaging Spectroradiometer), LST (Land surface temperature), NDVI (Normalized Difference Vegetation Index), TPI (Topographic Position Index), TWI (Topographic Wetness Index).

Data source	Derived layers	Reference
Landsat 8 – USGS Collection 2	LST L8, NDVI	
MODIS – Terra Land Surface Temperature and Emissivity Daily Global 1 km	LST MODIS	
Dynamic World	land cover change	Brown et al. (2022)
DIBAVOD (Digital Base of Water Management Data)	water features	DIBAVOD (2023)
Habitat catalogue of the Czech Republic	wetland habitats	Chytrý et al. (2010)
Digital Elevation Model DMR5G	elevation, aspect, TWI, TPI	ČÚZK (2023), Maxwell and Shobe (2022)
Atlas of forest microclimate in the national parks Bohemian and Saxon Switzerland, version 1.0	in situ microclimatic measurements	Man et al. (2022)

Shobe, 2022).

Predicted values were compared to interpolated in situ forest microclimate measurements from over 200 sites within Bohemian Switzerland National Park, measuring nine microclimatic variables from 2018 to 2021 (Man et al., 2022). For the comparison, we used the 95th percentile of aggregated maximum atmospheric temperature measured at 15 cm above the surface (T_max95p_air_15cm) for the same site and time to avoid the seasonal effect.

2.3. Workflow

The research workflow is shown in Fig. 2. Available satellite datasets were compiled, filtered and analyzed using GEE. Derived LST products were aggregated to the average and maximum LST values (using the Reducer function in GEE). Changes in LST were exploited using the linearRegression function in GEE, where the slope determines the average annual temperature change in a given pixel.

In ArcGIS Pro, the detected LST patterns were related to ancillary datasets, as listed in section 2.2, to identify the main environmental drivers of LTS and its dynamics. Water features and vegetation health were of specific focus. To predict LST in greater detail and further explore the role of different variables, a regression model was built in ArcGIS Pro using the machine learning Random Forest (RF) method. Specifically, we used a Forest based Classification and Regression tool that supports both raster and vector explanatory variables. Predicted values of high spatial resolution (30 m, as for L8) and high temporal resolution (daily frequency, as for MODIS) were compared to the aforementioned in situ measurements (Man et al., 2022). Statistical analyses were done using ArcGIS and Python.

3. Results

3.1. Predicted and observed LST patterns

Predictive model of LST using regression RF model (Fig. 3) was able to predict daily LST at 30 m resolution, despite the fact that the input layer came from the MODIS sensor with 1 km resolution, and some of the explanatory variables also had course resolution. The coefficient of determination of the model was 0.84, and the average deviation of the modeled LST from the control values derived from the L8 sensor was 0.55 °C as compared to 1.11 °C deviation of the original MODIS LST.

The average LST observed from satellite data for the growing season 2016 to 2022 (April to October) was 20.3 °C, ranging from 18 to 32 °C. The maximum values ranged from 28 to 52 °C, averaging 34.4 °C (Fig. S1 in the Supplement). The MODIS sensor, with the course spatial resolution of 1 km, averaged the data, thus smoothing out the temperature extremes, while the more detailed data from the L8 sensor enabled capturing local LST differences.

Interannual variability of average LST observed from satellite data did not show any trend, likely due to the complex geomorphology and heterogeneity of the area (Fig. 4). As expected, data from the MODIS sensor show less variability due to the higher number of records and the smoothing effect of the coarser spatial resolution. However, from individual pixel LST changes, we can observe marked differences and distinct patterns, especially in case of the more detailed L8 sensor (Fig. 5). The average annual change ranges from −0.9 °C to + 1.5 °C for L8 and from −0.4 °C to + 0.4 °C for MODIS.

3.2. Effects of environmental variables on predicted LST

The predicted LST patterns were related to various environmental variables. Pearson correlation test (Table 1) showed a negative correlation of LST for vegetation health (expressed by NDVI) and elevation, and a positive correlation for aspect and the potential of the landscape to accumulate water (expressed by TWI). TPI showed no significant relationship with LST. These findings partly agree with the importance of

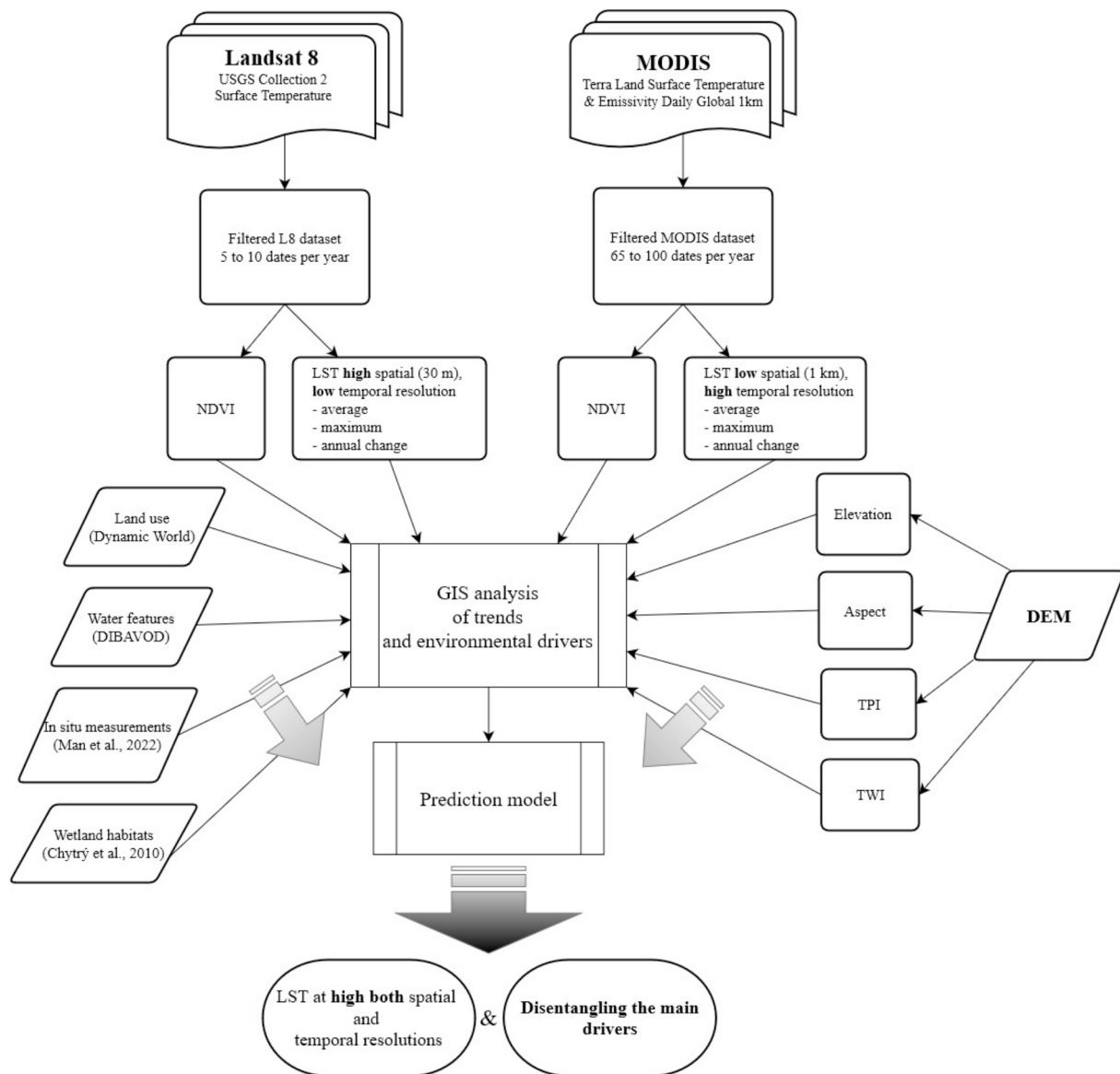


Fig. 2. The research workflow. Satellite-derived datasets were prepared in GEE (upper part of the flowchart), GIS analyses and machine learning predictive modeling were carried in ArcGIS Pro (lower part of the flowchart). Abbreviations: USGS (United States Geological Survey), Earth observation satellites – Landsat (L8), MODIS (Moderate Resolution Imaging Spectroradiometer), NDVI (Normalized Difference Vegetation Index), LST (Land surface temperature), DIBAVOD (Digital Base of Water Management Data), GIS (Geographical Information System), TPI (Topographic Position Index), TWI (Topographic Wetness Index), DEM (Digital Elevation Model).

variables in the prediction model (for the model description, see [section 3.1](#)), where NDVI and elevation were also identified as the most important explanatory variables ([Table 3](#)). To further explore the interactions among variables, we used variance partitioning ([Fig. 6](#)). The test confirmed the driving role of NDVI, and its interconnection with elevation and TWI.

The predicted patterns were related to the vegetation activity, expressed by Landsat-derived NDVI. Analysis of interannual changes in NDVI during the growing season showed that the maximum increase in LST (up to 9 °C for the study period) corresponded to sites affected by the bark beetle infestation, often followed by salvage logging, or by the wildfire in 2022 ([Fig. 7](#)). LST and NDVI were negatively correlated ([Table 2](#)) and NDVI was the third most important explanatory variable for predicting LST in the regression RF model ([Table 3](#)).

The LST patterns could also be related to the change in land cover, as derived from the Dynamic World dataset. This was actually the most important parameter for the RF model ([Table 3](#)), where water bodies

and forests were among the coldest land cover types, and grasslands showed temperatures similar to crops and urban areas ([Fig. 8](#)). Most of the differences were significant ([Table S1 and S2](#) in the Supplement), except the differences in mean LST among forest and water land cover types.

Due to the rugged geomorphology of the sandstone area, its strong influence on the temperature patterns could be superimposed. Correlation with LST was strongly positive for aspect and strongly negative for elevation ([Table 2](#)), with elevation being the third most important variable for the RF model ([Table 3](#)). Surprisingly, TWI showed a strong positive correlation. However, when further broken down into land cover types, the positive correlation was only valid for flat areas used for agriculture and urban areas, not for forested areas.

To test the influence of water availability, the layers of wetlands and water features were replaced by zero raster to simulate their complete absence. This manipulation increased modeled LST by 1 to 3 °C in case of the river Elbe, and less markedly in case of smaller water bodies

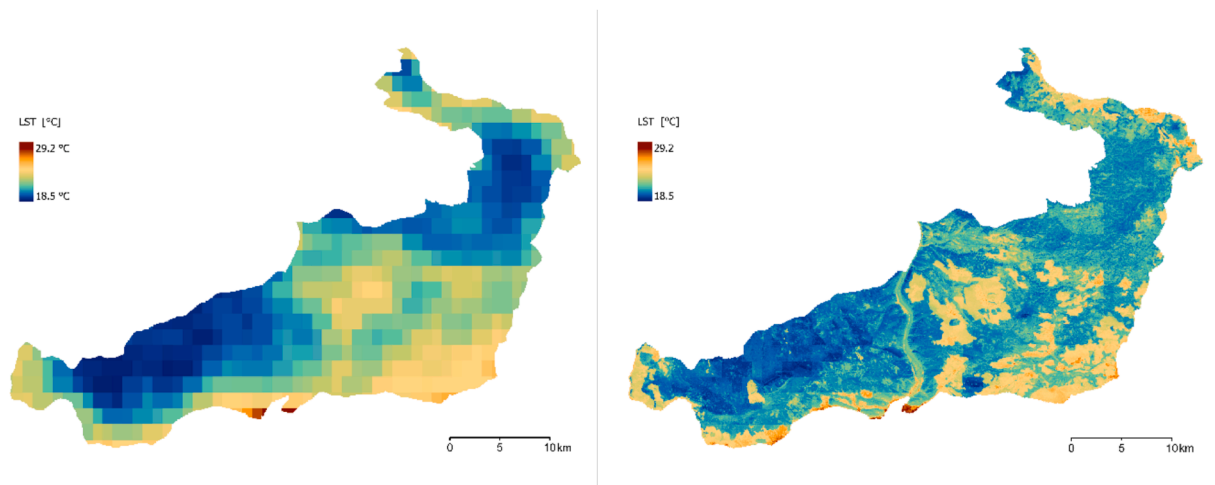


Fig. 3. Input MODIS Land surface temperature (LST) layer (left) and output predicted LST using regression Random Forest (RF) model (right).

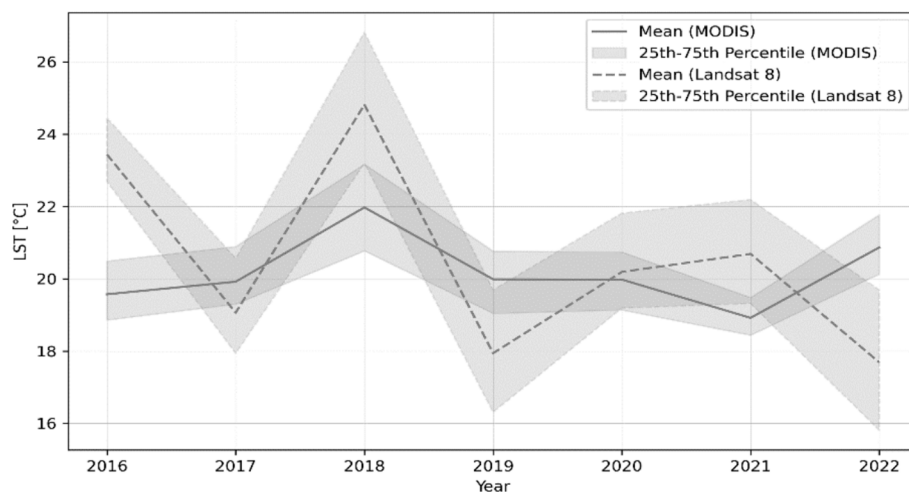


Fig. 4. Interannual dynamics of average Land surface temperature (LST) for growing season. Median and interquartile ranges show the degree of variability within the two datasets. Data from Landsat 8 were normalized so that their average value over the entire area corresponds to the MODIS.

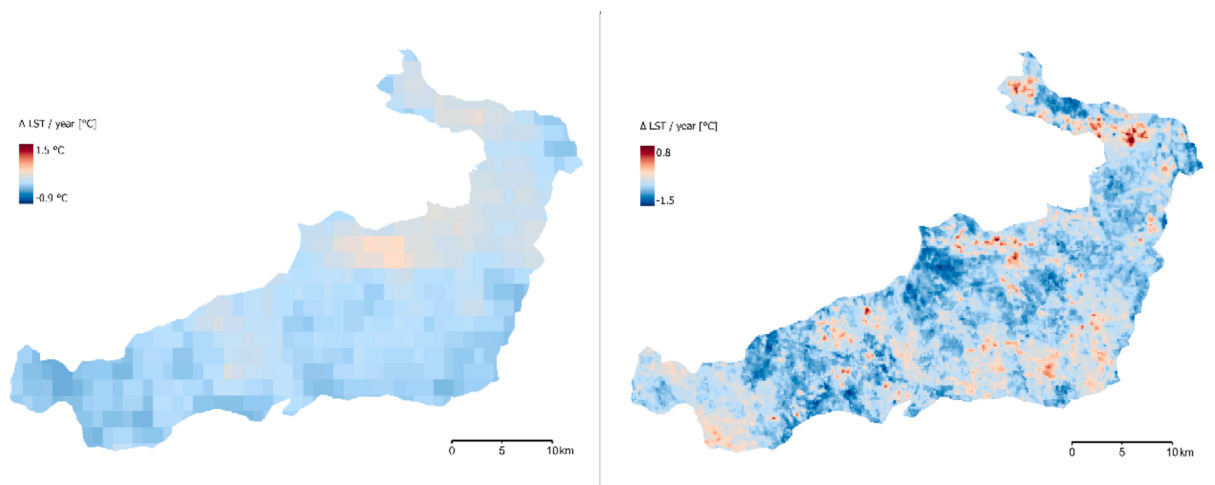


Fig. 5. Interannual change in average LST for the growing seasons of 2016 to 2022 as derived from MODIS (left) and L8 (right).

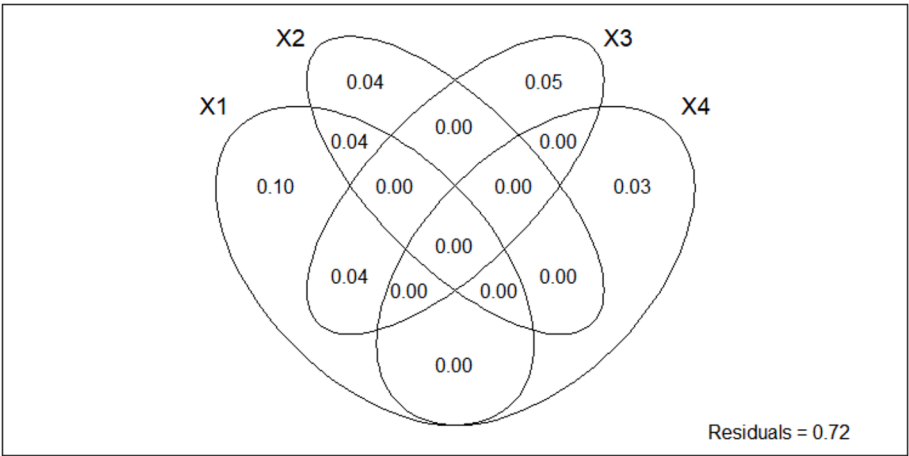


Fig. 6. Explained variance of selected variables analyzed using variance partitioning. X1 – Normalized Difference Vegetation Index, X2 – elevation, X3 – Topographic Wetness Index, X4 – aspect.

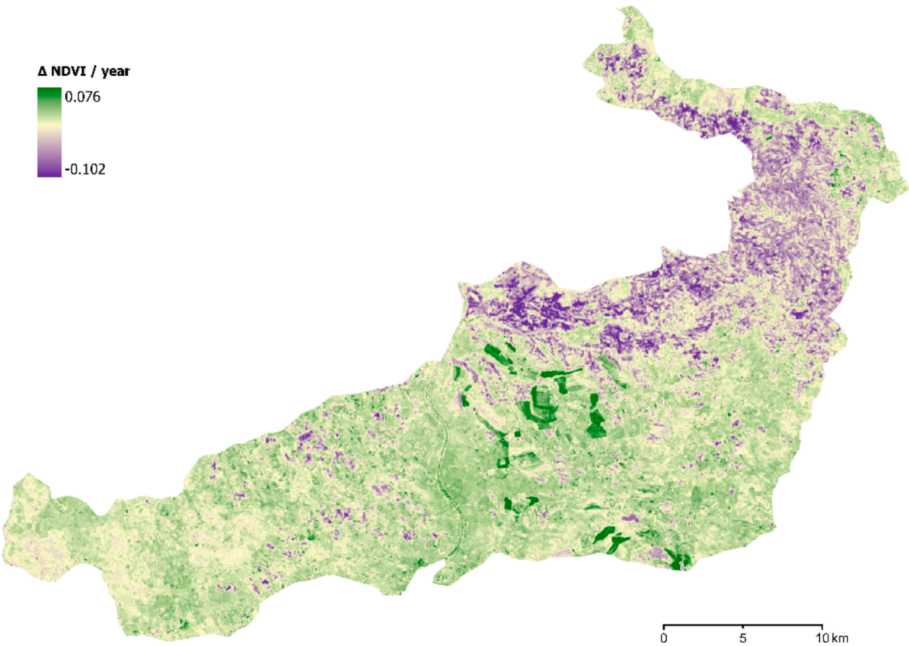


Fig. 7. Interannual change in Normalized Difference Vegetation Index (NDVI) for the growing seasons of 2016 to 2022 as derived from Landsat 8.

Table 2
Pearson correlation coefficients for average and maximum Land surface temperature (LST). Abbreviations: L8 (Landsat 8), TWI (Topographic Wetness Index), TPI (Topographic Position Index).

Variable	LST Avg	p-value	LST Max	p-value
NDVI L8	−0.41	< 0.001	−0.32	< 0.001
Elevation	−0.24	< 0.001	−0.34	< 0.001
TWI	0.26	< 0.001	0.2	< 0.001
Aspect	0.18	< 0.001	0.08	< 0.001
TPI	−0.01	0.316	0	0.977
Wetland habitats	−0.01	0.924	−0.03	< 0.001
Water features	−0.03	< 0.001	−0.06	< 0.001

(Fig. 9). Changes in predicted LST were significantly dependent on the proportion of removed water features (Fig. 10) but did not show any trend for wetland habitats.

Table 3
Variable importance for the prediction model (for the model description see section 3.1). Abbreviations: LST (Land surface temperature), L8 (Landsat 8), MODIS (Moderate Resolution Imaging Spectroradiometer), NDVI (Normalized Difference Vegetation Index), TWI (Topographic Wetness Index), TPI (Topographic Position Index).

Variable	Importance
Land cover 2017	31 %
LST MODIS	20 %
Land cover 2022	14 %
NDVI L8	11 %
Elevation	9 %
TWI	5 %
Aspect	4 %
TPI	2 %
Wetland habitats	2 %
Water features	1 %

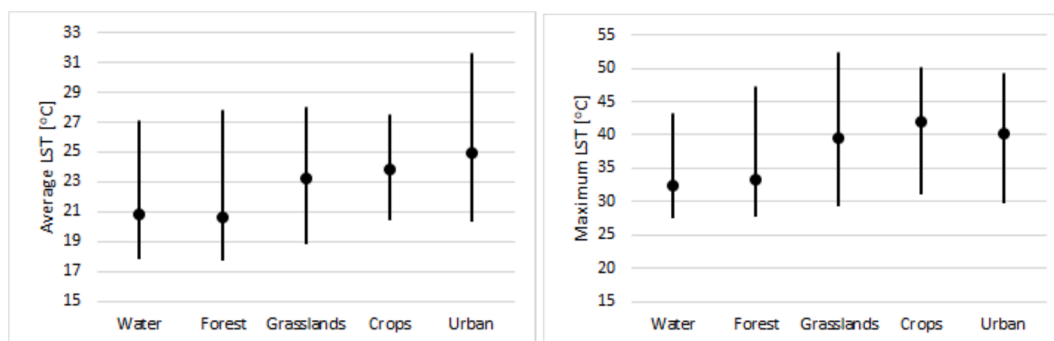


Fig. 8. Average (left) and maximum Land surface temperature (LST, right) according to the land cover type (Dynamic World dataset).

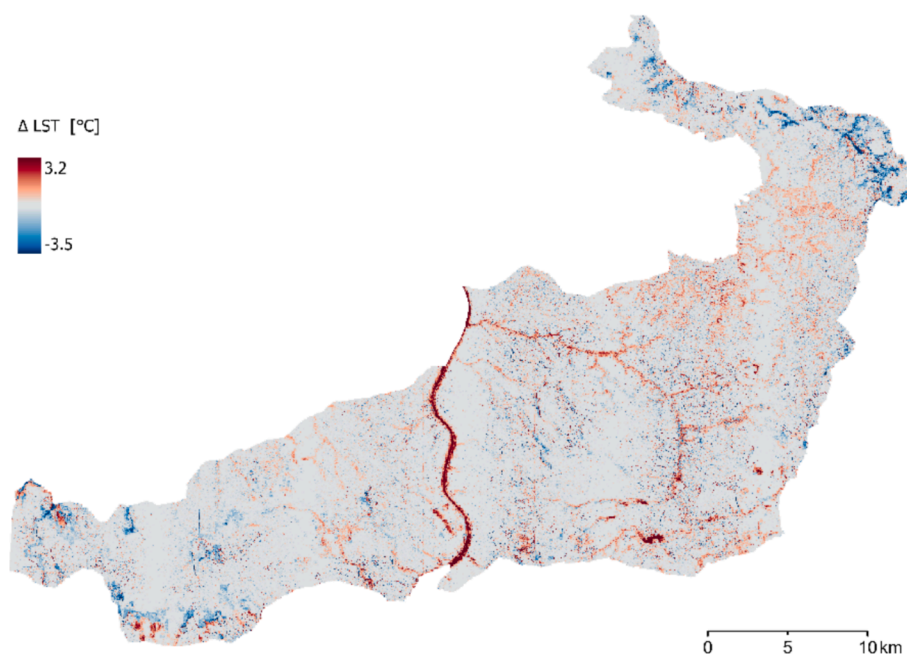


Fig. 9. Changes in predicted Land surface temperature (LST) due to simulated absence of water features and wetlands.

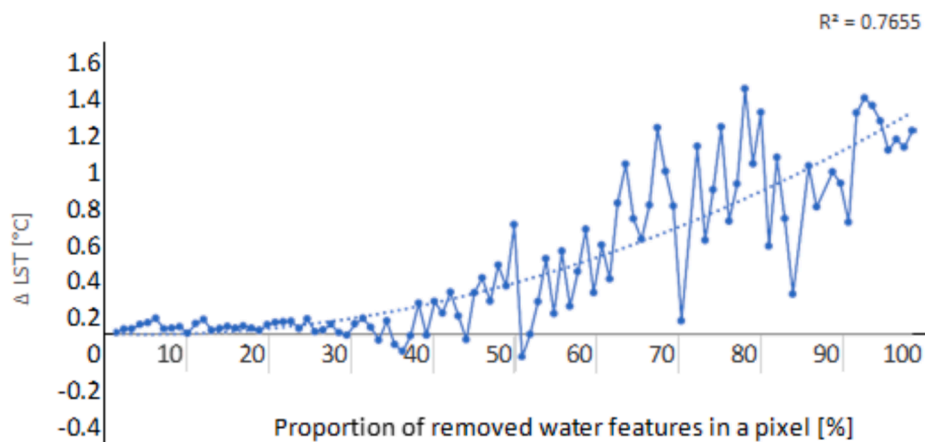


Fig. 10. Changes in predicted Land surface temperature (LST) caused by removing water features from the model.

3.3. Comparison to in situ measurements

The L8-derived LST values for the National Park were compared to

the in situ measurements of atmospheric temperature at 15 cm above the forest surface from 2018 to 2021 (Man et al., 2022). The differences between satellite- and in situ-derived maximum temperatures at the

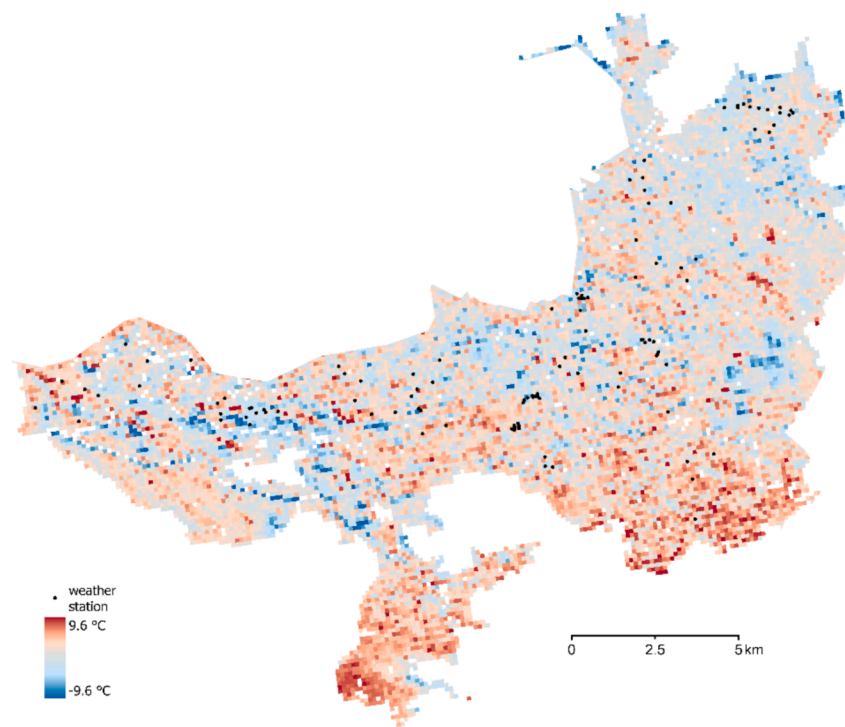


Fig. 11. Differences between Landsat 8 derived maximum Land surface temperature (LST, 95p) and in situ temperature measurements in 15 cm above the surface ($T_{\max 95p_air_15cm}$; Man et al., 2022).

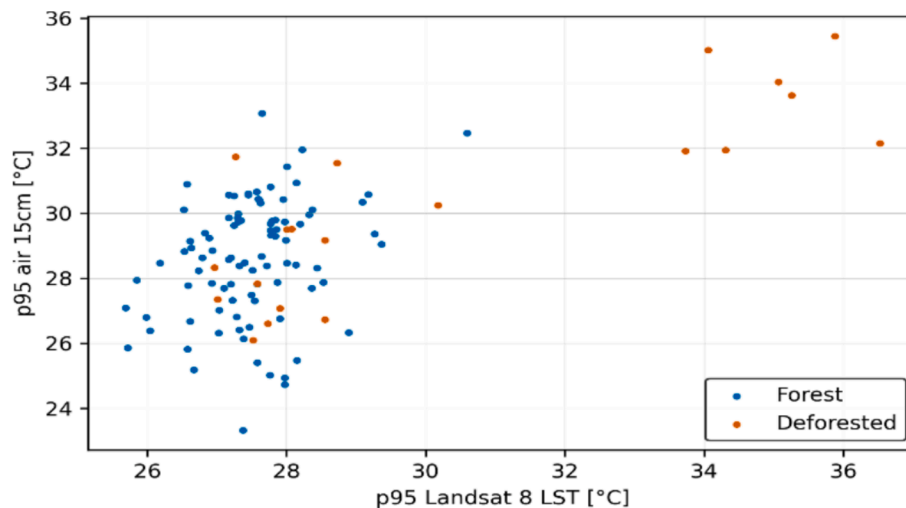


Fig. 12. Relationship between 95p temperatures derived from Landsat 8 and in situ measurements ($T_{\max 95p_air_15cm}$, Man et al., 2022). The stations deforested during the study period are marked in red.

location of the measuring stations were 2.2 °C on average and 5.6 °C at maximum (Fig. 11). The borders of the study area are the most distant from the in situ measuring stations, and the interpolation error could therefore be higher there (up to 10 °C). The coefficient of determination from the regression analysis was 0.36 (Fig. 12).

In case we restricted our analysis only to stations experiencing forest die-off during the study period due to the bark beetle, the coefficient of determination doubled to 0.69. On the contrary, for the stations that remained forested for the entire study period, the coefficient of determination dropped to only 0.09, even though there were no outliers caused by L8 data variability. The outliers apparent from the Fig. 12 can be attributed to the microclimate stations placed within the same large clearcut after the bark beetle outbreak, expressing the lowest NDVI

values. Normally, dead spruce forests were left standing dry within the National Park, but this particular part was clear-cut and later experienced the wildfire (in 2022, not included in the in situ measurements).

4. Discussion

Our study investigated the dynamics of LST and its relationship with landscape patterns in the protected sandstone area in the northern Czech Republic. We exploited two satellite datasets of different spatial and temporal resolution available from the GEE data catalog (MODIS and L8), along with in situ measurements collected during the growing seasons of 2016 to 2022.

The change in LST over the study period expressed high local

variation which can be attributed to various environmental factors. Generally recognized factors include geomorphology (elevation, slope, aspect, TWI, and TPI) and land cover type (Good et al., 2017). While the cooling effect of water features has already been demonstrated (Gohr et al., 2021), most research has focused on urban environments (Cai et al., 2018; Wang et al., 2019). Studies on topographically complex and forested landscapes are relatively sparse.

Our study confirmed that even in diverse natural areas, the influence of land cover on the LST is significant. Specifically, forest ecosystems and water features exhibited summer temperatures approximately 3 °C lower compared to other land cover types. The effect was particularly pronounced for water features and wetlands, that showed slight but consistent cooling effect on LST, especially in modulating the maximum summer temperatures. Their simulated absence in the regression RF model revealed local relationships and confirmed their significant cooling effect on the surrounding landscape. These findings align with the study of Gupta et al. (2019), even though the water features were not particularly abundant or large in our study area. This suggests that water features can mitigate excessive summer temperatures, even in the case of small-scale water bodies and wetlands.

Our study further confirmed strong positive effects of ecosystem health on alleviating the temperature extremes (cf. Koetz et al., 2018; Bowler et al., 2010; Rahman et al., 2020; Guha and Govil, 2021). In fact, most of the temperature increases in our study area occurred in spruce stands affected by insect outbreaks, followed by massive forest die-off, or by the forest fire. Despite natural recovery, forest die-off had a similar effect on LST as logging (Prevedello et al., 2019) or climate-driven shrub encroachment in semi-arid grasslands (Duman et al., 2021). Thus, we confirmed our hypothesis that the landscape's ability to mitigate the negative effects of global warming (extreme summer temperatures in this case) is hindered by landscape dysfunction and compromised ecosystem services. However, it is important to note that LST calculations from satellite data incorporate emissivity, which is commonly calculated using information on ecosystem health (NDVI, Guha and Govil, 2021).

Our results confirm that forest microclimate significantly mitigates the effect of insulation and strongly affects the accuracy of satellite-derived LST. The overall deviation of satellite-derived LST from in situ-measured atmospheric temperature at 15 cm above the surface was relatively high compared to other studies (Awais et al., 2022; Ermida et al., 2020; Käfer et al., 2019). It can be partly attributed to the aggregation of in situ data, as temperatures for a specific day could be compared within an aggregated dataset. Detailed spatial analysis revealed the strong effect of vegetation on the LST/in situ relationship, with dense canopies modulating the forest microclimate (cf. Zellweger et al., 2019). In forested areas, LST showed no correlation with in situ measurements, whereas at sites experiencing forest die-off during the study period, the correlation was high. This confirms our hypothesis that the relationship between the satellite-derived LST and the in situ-measured atmospheric temperature is impacted by forest ecosystem health. Future research could investigate the correlation of LST with other in situ-measured temperatures available in Man et al. (2022), such as temperatures from 2 m above and 8 cm below the surface.

Our research indicates that higher resolution is beneficial for capturing phenomenon in greater detail to unravel underlying ecological processes and spatial dependencies. While numerous thermal satellite data sources are available, meeting current scientific requirements often necessitates a compromise between temporal and spatial resolution. Available datasets with sufficient temporal resolution have a low spatial resolution (MODIS/VIIRS), and vice versa, the sources of high spatial resolution (Landsat) have a 16-days delay (Fisher et al., 2017), which, combined with frequent cloud cover, does not allow for continuous sensing. New thermal sensors, such as recently available ECOSTRESS (Anderson et al., 2021) or microwave data from Planet Labs (Planet Labs, 2024), offer high spatial and temporal resolution (frequency) but, due to their recent launch, are limited in terms of time

series analyses.

By analyzing the LST data of high temporal resolution (MODIS) and high spatial resolution (L8), we confirmed that neither dataset alone is sufficient to explain the landscape temperature patterns in detail appropriate for such diverse landscapes. While L8 could explain the patterns better due to its considerably higher spatial resolution, its low data acquisition frequency and high cloud cover limit its ability to capture the effects of certain environmental variables, such as water features. Various techniques exist to augment the quality of datasets, such as data fusion, pansharpening and modeling. We demonstrated that machine learning modeling can predict LST dynamics and change at both high spatial and temporal resolutions with sufficient accuracy. By using environment variables as proxies, it is possible to prepare data at scales relevant even for complex and diverse landscapes, allowing to explain local differences in temperature patterns, and relate the temperature changes to the landscape processes.

In the near future, planned missions will meet the spatial, temporal and spectral resolution requirements to investigate and monitor temperature conditions and changes at unprecedented scales. Notable governmental projects in the pipeline are the India (ISRO) – France (CNES) TRISHNA project (50 m, 3 days, planned for 2025; Lagouarde et al., 2019), the European (ESA) LSTM project (50 m, daily, from 2029; Koetz et al., 2018), and the NASA SBG project (60 m, 5 days, from 2027; Lee et al., 2022). These collaborative efforts will result in thermal imaging at a resolution of 50 to 60 m every three days in four thermal bands. However, in case of heterogeneous urban, complex mountainous or highly vegetated landscapes, even such advancement in thermal data resolution might not be sufficient (Granero-Belinchon et al., 2019; Michel et al., 2019). Besides the aforementioned governmental initiatives, private companies are already offering or planning to provide such very high resolution thermal data. Planet Labs microwave mission (unaffected by clouds, 100 m, twice a day; Planet Labs, 2024), Constellr (part of the HiVE project, 50 m, 2 days; Spengler et al., 2024) and SatVu (Lin et al., 2024) are already in orbit, and we can expect a surge in private thermal missions in the coming years.

These currently realized visions have the potential to revolutionize established workflows and open new possibilities and applications, whether we have in mind space agencies targeting large and long-planned missions and publicly available data, or the flexible private companies focusing on user-friendly solutions and high specialization for a specific purpose like precision agriculture or rapid fire response.

Our findings suggest that well-functioning landscapes with maintained ecosystem services can mitigate the negative effect of global warming to a certain extent. The revealed mechanisms of how landscape change and configuration impacts the surface temperature can further affect climate as well as biogeochemical cycles and biophysical and ecological processes (Blankinship et al., 2011; Finzi et al., 2011; Lawrence et al., 2022). These findings thus have important practical implications for adaptive landscape management in the context of climate change. To enhance landscape resilience and prevent further climate induced forest die-off and associated negative consequences, society should reconsider the traditional narrative of prioritizing forests as a source of timber irrespective of other important ecosystem services they provide. Our study highlights the need for adaptive management in Central Europe and elsewhere to cope with summer heat waves and precipitation shortages. This includes improving water retention capacity and shifting forest composition towards more drought-tolerant species, while respecting their natural distribution and requirements (Temperli et al., 2012).

5. Conclusions

The Central European landscape suffers from degradation and malfunctioning of important ecosystem services due to both historical policies and disrespect for natural processes. The growing interest in landscape retention capacity, forest health, and mitigation of weather

extremes related to climate change necessitates a need for a fundamental shift in land management. Our study on satellite-derived land surface temperature contributes to the ongoing discussion about potential shifts in land management narratives, indicating that satellite data are a reliable source of information for understanding the processes and environmental drivers behind environmental change. It can also serve as a foundation for developing adaptive management measures aimed at making the landscape more resilient to the both current and expected threats. Our results contribute to filling the major knowledge gap in explaining the thermal patterns in complex landscapes and disentangling individual drivers, highlighting the role of landscape state and ecosystem health in mitigating the negative consequences of global warming.

Authors contribution

Both authors contributed to the conceptualization, methodology and writing of original draft, ES to data curation and analysis, JM to supervision, funding acquisition and writing – review and editing.

CRedit authorship contribution statement

Jana Müllerová: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization. **Erik Šíffel:** Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.113265>.

Data availability

We have shared the link to the code repository

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