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Review

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

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A R T I C L E I N F O

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A B S T R A C T

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. Randlkofer 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 extend, 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

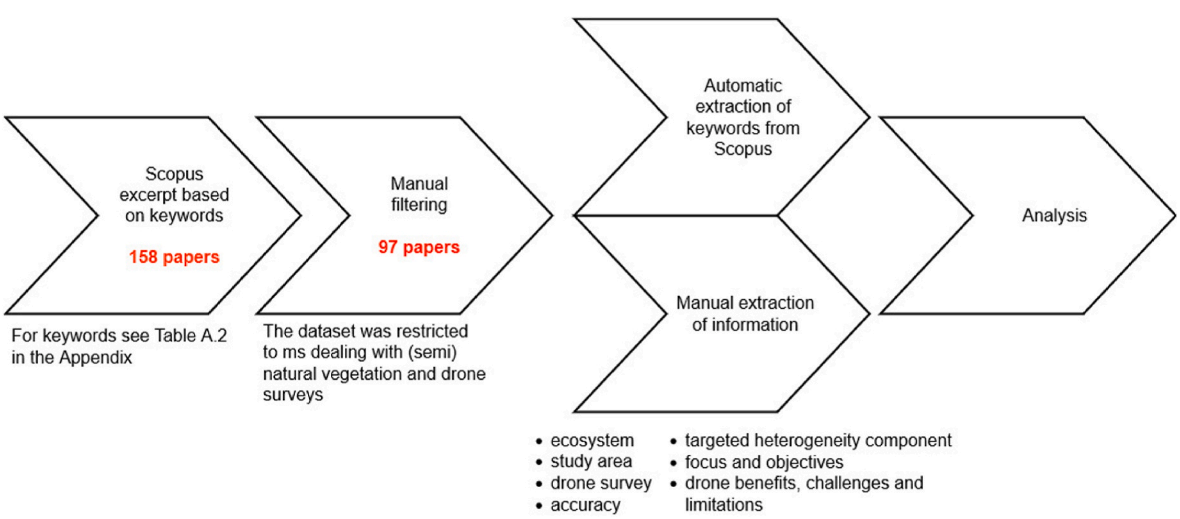

Fig. 1. Processing workflow of the meta-analysis.

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

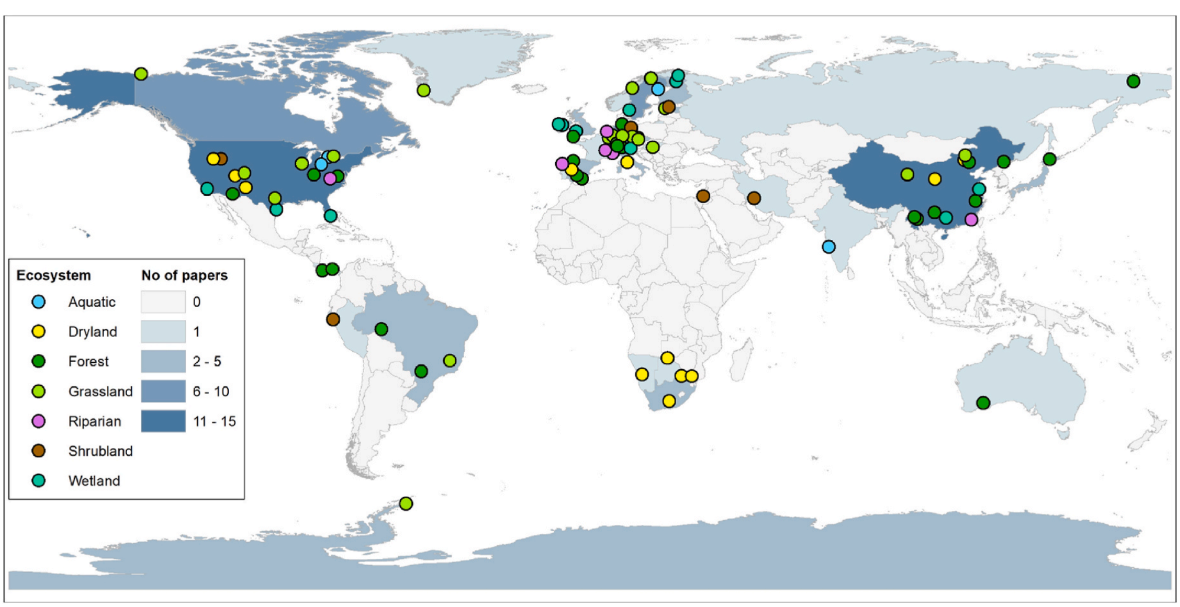

Fig. 2. Spatial distributions of the ecosystems investigated in the studies reviewed herein addressing vegetation heterogeneity using drones (referenced in Table A.2 in the Appendix). Case studies are divided according to the ecosystem/vegetation type.

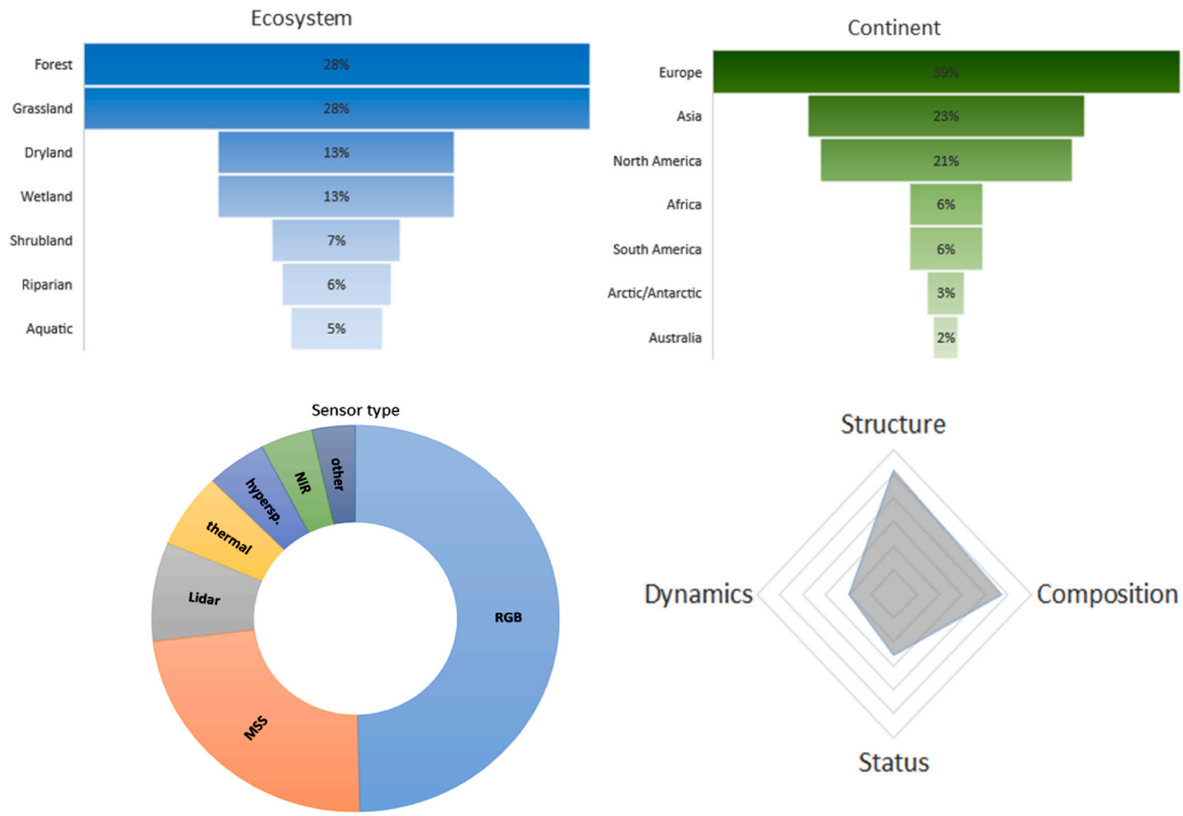

Fig. 3. An overview of drone studies divided according to the ecosystem type, continent, sensor and component of complexity addressed (for references see Table A.2 in the Appendix).

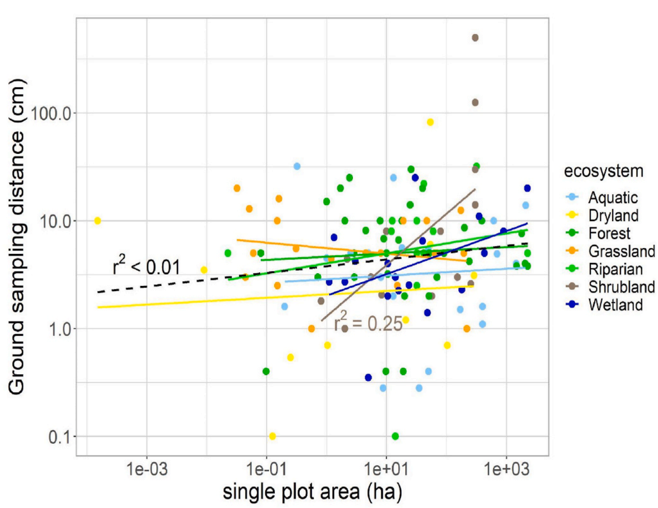

Fig. 4. Regression between the surveyed area and spatial resolution expressed by ground sampling distance according to the ecosystem/vegetation type (excerpted from the list of references given in Table A.2 of the Appendix). The data show no significant linear relationship ($r^2 < 0.01$), except for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

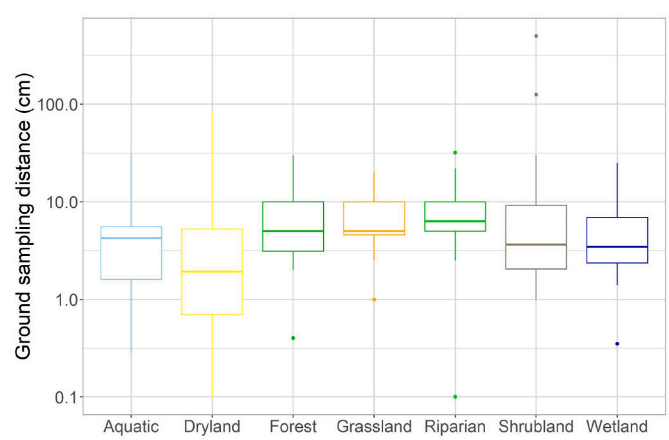

Fig. 5. Relationship between ecosystem type and ground sample distance (GSD). Boxplot shows median, upper and lower quartiles (upper and lower hinges), values as high as 1.5 times the quartiles (upper and lower whisker) and outliers (dots). The Y axis is in logarithmic scale. No significant differences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

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., 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,

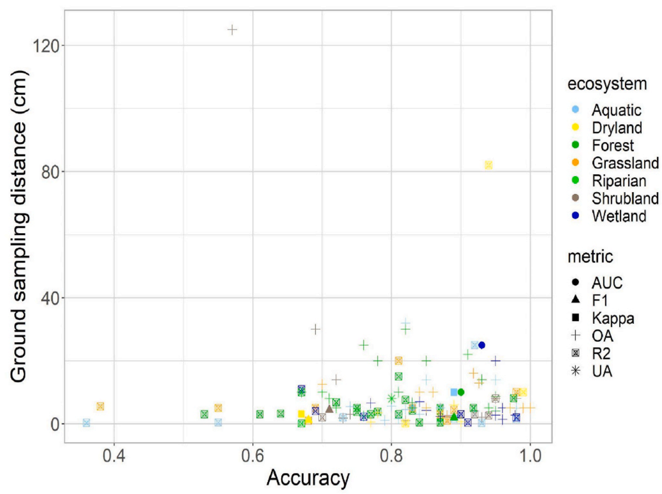

Fig. 6. Relationship between the spatial resolution and the classification accuracy excerpted from the literature (Table A.2 in the Appendix). Studies were divided according to the ecosystem/vegetation type, and the accuracy metric: AUC (area under the curve), F1 score, Kappa, OA (overall accuracy),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

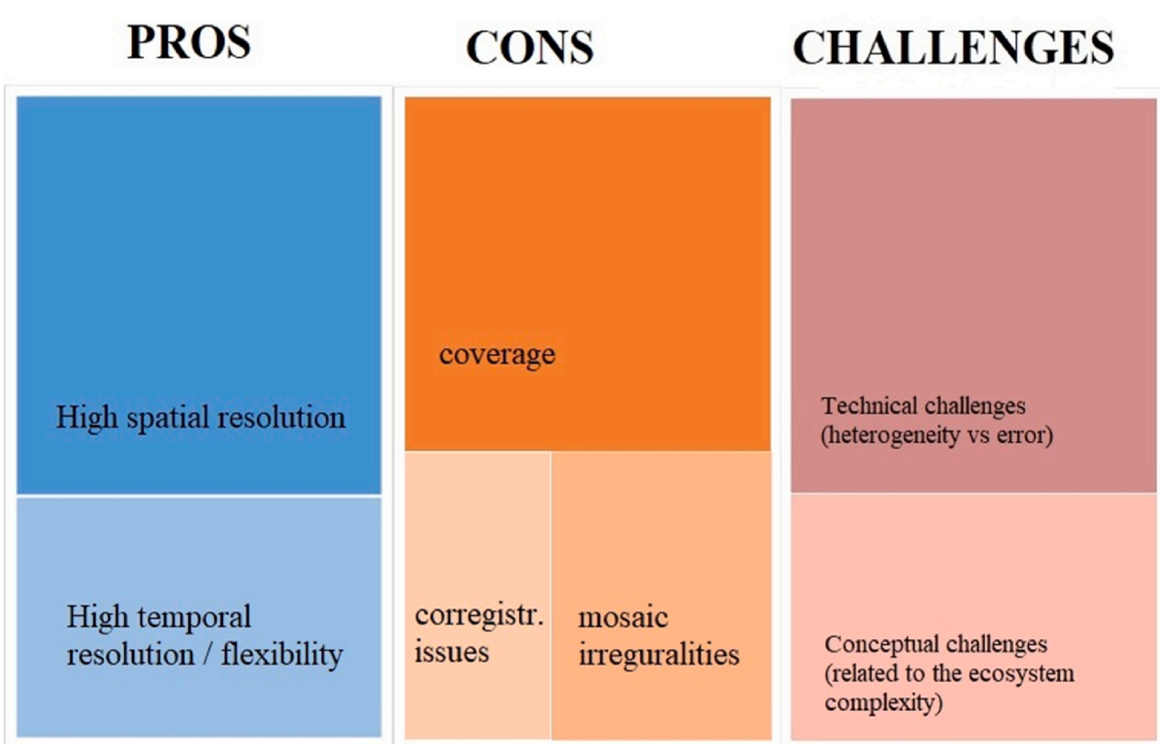

Fig. 7. The most mentioned advantages (pros), limitations (cons) and challenges related to the use of drones in ecosystem complexity assessment. Size of the box corresponds to the frequency of mention in our meta-analysis.

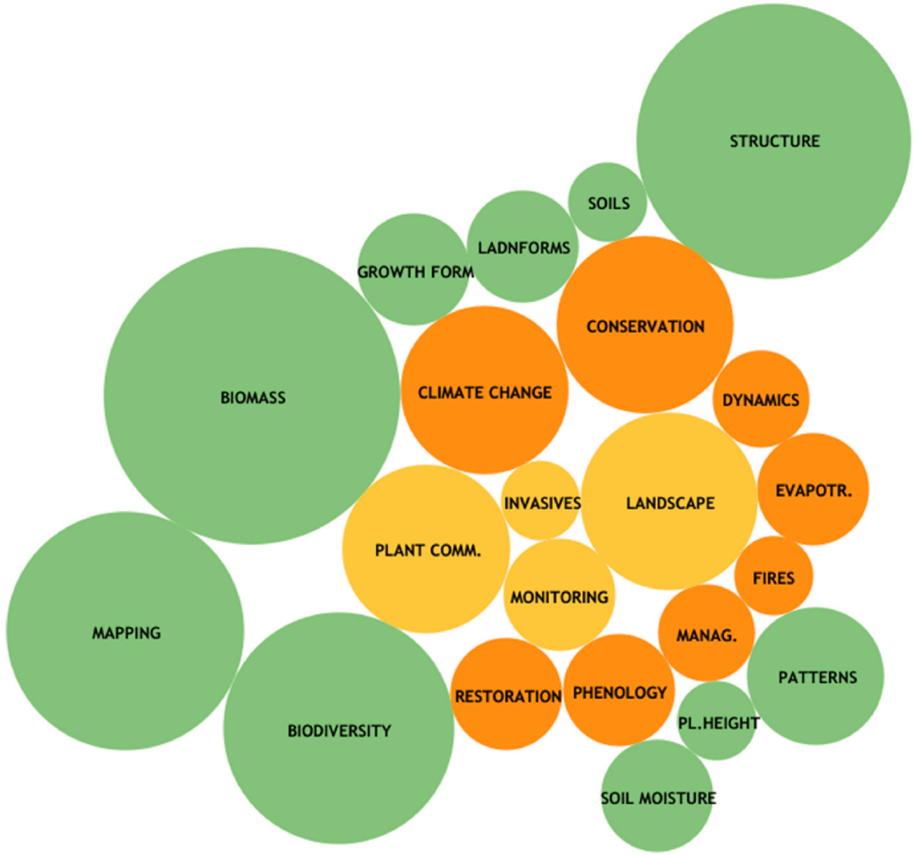

Fig. 8. Bubble plot of keywords from reviewed papers. The keywords retrieved from Scopus (both Authors and Index keywords) were manually assigned as objectives, and divided into the following groups: patterns (ecosystem state and structure) in green, and processes (ecosystem status and dynamics) in orange. 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,

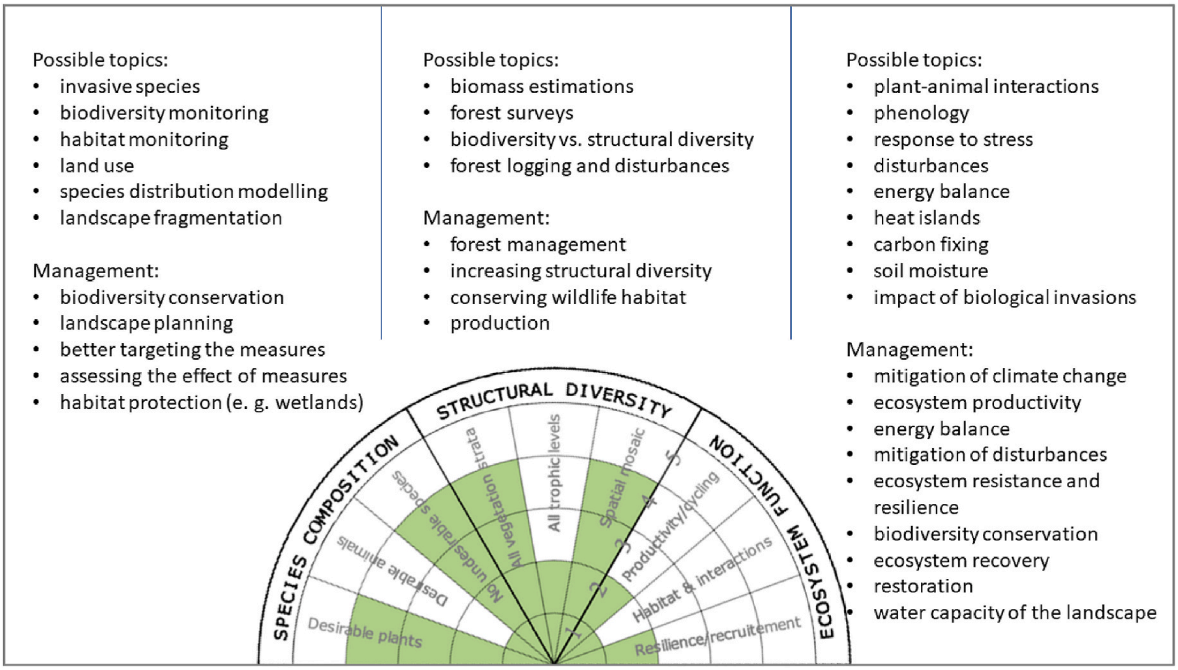

Fig. 9. Potential of drone surveys for practice in relation to the ecosystem complexity. Green fields indicate the current input of drone technology. Based on Recovery wheel (McDonald et al., 2016).

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 humper 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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