

Reviewing the Spectral Variation Hypothesis: Twenty years in the tumultuous sea of biodiversity estimation by remote sensing

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ARTICLE INFO

Keywords:

Biodiversity
Environmental heterogeneity
Mapping
Remote sensing
Review
Spectral heterogeneity
Spectral variation hypothesis

ABSTRACT

Twenty years ago, the Spectral Variation Hypothesis (SVH) was formulated as a means to link between different aspects of biodiversity and spatial patterns of spectral data (e.g. reflectance) measured from optical remote sensing. This hypothesis initially assumed a positive correlation between spatial variations computed from raster data and spatial variations in the environment, which would in turn correlate with species richness: following SVH, areas characterized by high spectral heterogeneity (SH) should be related to a higher number of available ecological niches, more likely to host a higher number of species when combined. The past decade has witnessed major evolution and progress both in terms of remotely sensed data available, techniques to analyze them, and ecological questions to be addressed. SVH has been tested in many contexts with a variety of remote sensing data, and this recent corpus highlighted potentials and pitfalls. The aim of this paper is to review and discuss recent methodological developments based on SVH, leading progress in ecological knowledge as well as conceptual uncertainties and limitations for the application of SVH to estimate different dimensions of biodiversity. In particular, we systematically review more than 130 publications and provide an overview of ecosystems, the different remote sensing data characteristics (i.e., spatial, spectral and temporal resolution), metrics, tools, and applications for which the SVH was tested and the strength of the association between SH and biodiversity metrics reported by each study. In conclusion, this paper serves as a guideline for researchers navigating the complexities of applying the SVH, offering insights into the current state of knowledge and future research possibilities in the field of biodiversity estimation by remote sensing data.

1. Introduction

The preservation of the Earth's biodiversity and the sustainable use of the planet's natural resources are key objectives in a range of global environmental initiatives such as the Kunming-Montreal Agreement (Obura et al., 2023) and the Sustainable Development Goals (SDGs)

adopted by the United Nations (Griggs et al., 2013; Opoku, 2019). The ratification of the 2030 agenda for Sustainable Development which defined seventeen SDGs is one of the biggest actions towards the conservation and preservation of environmental conditions on Earth for future generations, aiming at addressing the challenges currently faced by society (Lee et al., 2016; Schultz et al., 2016). In particular, goal 15 of the

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<https://doi.org/10.1016/j.ecoinf.2024.102702>

Received 11 April 2024; Received in revised form 28 May 2024; Accepted 22 June 2024

Available online 3 July 2024

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SDGs aims to “protect, restore and develop sustainable use of terrestrial ecosystems, to promote sustainable forest management, combat desertification, and halt and reverse land degradation and halt biodiversity loss” (Opoku, 2019). As stressed by Sayer et al. (2019) in order to attain these objectives, a robust emphasis on integration, widespread political and public engagement, and heightened responsiveness to local needs is imperative.

Biodiversity, broadly defined as the variety of life on Earth, supports multiple ecosystem services that are necessary for human well being and crucial for economic activities (Opoku, 2019). Biodiversity-oriented management, while holding the potential to mitigate the loss of ecosystem functions and services, faces a pressing reality. Projections indicate that by 2050, these losses are anticipated to incur a substantial cost, accounting for 7% of the world’s gross domestic product (Braat et al., 2008; Mace et al., 2018). It is, therefore, fundamental to acquire exhaustive information on the distribution of the different species, as well as knowledge on changes in distribution with time (Nagendra, 2001; Torresani et al., 2023a; Rocchini et al., 2023a). The definition of relevant ecological proxies informing on the situation and dynamics of biodiversity is, therefore, crucial to develop monitoring strategies feeding efficient planning strategies and conservation policies over the variety of land and water ecosystems, from local to national to global scale (Rocchini et al., 2010; Sandifer et al., 2015; Van Jaarsveld et al., 1998). It is imperative, however, to recognize the necessity of balancing trade-offs between biodiversity conservation and mitigation targets, particularly at the landscape scale. Implementing monitoring systems of this nature would not only facilitate the measurement of the effectiveness of interventions and implemented policies but also contribute to the nuanced management of such trade-offs.

Historically, estimates of species diversity were mainly based on field inventories performed by scientific experts such as trained ecologists and botanists. This approach usually provides accurate information, but turns out to be time-consuming and costly, and shows limitations due to a possible bias of the operator and standardized replication of protocols for inventories (Rocchini et al., 2019). At regional and national levels, biodiversity monitoring strategies differ widely among countries, resulting in non-standardized datasets and these are often further limited by the absence of a data sharing policy (Conti et al., 2021). In recent decades, Earth observation appeared to be an innovative and robust instrument for monitoring ecosystem biodiversity, allowing the collection of uniform, periodic and economically sustainable data (Cavender-Bares et al., 2020; Foody and Cutler, 2003; Skidmore et al., 2021). Recent progresses in sensor technology and changes in data access policy now often allow free and open access to fine spatial resolution imagery with global coverage and high revisit frequency. The free and open data access policy of acquisitions from various remote sensing platforms, combined with increased capacity for data processing make Earth observation data and processing possible and economically acceptable for biodiversity monitoring (Nagendra, 2001; Rocchini et al., 2010; Pettorelli et al., 2014).

In the past, different remote sensing datasets have been used to estimate various components of biodiversity in distinct ecosystems through numerous methodologies (Kacic and Kuenzer, 2022; Nagendra, 2001; Torresani et al., 2019). Optical information acquired with passive sensors such as digital aerial photographs, airborne imaging spectroscopy, multispectral imagery from unoccupied aerial vehicle (UAV), airborne and satellite platforms have also been widely used to assess biodiversity in various ecosystems (Laurin et al., 2014; Dandois et al., 2015; Lassau et al., 2005; Rocchini, 2007; Torresani et al., 2019; Asner, 2015). LiDAR (Light Detection and Ranging) and radar data have shown considerable potential for the estimation of vegetation structure metrics (Bergen et al., 2009; Kacic et al., 2023; Moudry et al., 2023; Simonson et al., 2012; Torresani et al., 2020) and related biodiversity (Moudry et al., 2021).

Various methodologies have been developed to take advantage of these different types of data in order to estimate indicators or metrics of

biodiversity in various ecosystems (Kacic and Kuenzer, 2022; Wang and Gamon, 2019a). Some approaches aim to directly map specific targets (e.g. single species or populations) from fine spatial or spectral resolution data and supervised classification (Immitzer et al., 2012; Sheeren et al., 2016). Other approaches estimate the functional component of biodiversity through plant functional traits and their diversity in space (such as leaf area index, pigment content, leaf nitrogen content, water content, tree crown diameter, canopy shape index) (Durán et al., 2019; Rossi et al., 2020; Hauser et al., 2021a) or through the mapping of the habitats, using information related to climate, geology, topography and derived land cover types (Foody, 2008; Stein et al., 2014; Wang and Gamon, 2019b; Sun et al., 2021). Another family of methodologies investigates the relationship between the in-situ biodiversity and changes in reflectance captured from optical images (Turner et al., 2003; White et al., 2010; Nagendra, 2001; Gillespie et al., 2008; Palmer et al., 2002). The Spectral Variation Hypothesis (SVH) represents a typical example of this group of approaches, which often extends beyond image-based methods to incorporate spectral data for robust testing and analysis.

The SVH assumes that variability in the spectral response captured by optical sensors serves as a proxy for assessing taxonomic information (Palmer et al., 2002). This hypothesis suggests that areas exhibiting high spectral heterogeneity (SH) in remotely sensed images correspond to a greater diversity of ecological niches capable of supporting higher species richness compared to areas with low SH (Rocchini et al., 2004). While initially focused on differences between pixels in an image, particularly in terms of heterogeneity, the fundamental concept of the SVH revolves also around spectral differences rather and not only on pixel-based variation alone. This distinction is significant as not all assessments of the SVH directly pertain to individual pixels; rather, the central concept and terminology of “spectral variation” emphasize the examination of spectra rather than pixel-level attributes. Hence, analogous constructs like ‘optical diversity’ (Ustin and Gamon, 2010), ‘spectranomics’ (Asner and Martin, 2009), ‘spectral species’ (Féret and Asner, 2014), and ‘spectral diversity’ (Cavender-Bares et al., 2020), contribute to a more comprehensive framework for elucidating the SVH and its associated principles.

The SVH has been extensively tested in diverse conditions over the past decade, encompassing various ecosystems, remote sensing optical images, and a range of SH indices. While this approach provides rapid estimates of spatial patterns that may relate to biodiversity, ecological diversity, and environmental heterogeneity, at different scales, it is crucial to acknowledge that its effectiveness may vary across different conditions and ecosystems (Gamon et al., 2020; Fassnacht et al., 2022). Numerous investigations, particularly the comprehensive study by Gamon et al. (2020), have underscored the non-universal applicability of the SVH, illustrating its context-dependent nature. This body of work highlights the imperative for adopting methodologies that are attuned to the scale of analysis (Schmidtlein and Fassnacht, 2017; Möckel et al., 2016; Rossi et al., 2022; Perrone et al., 2023; Hauser et al., 2021b; Fassnacht et al., 2022). Such an approach is crucial for enhancing the efficacy of SVH in biodiversity monitoring, ensuring that the scale of observation matches the ecological phenomena being studied. Exploring the conditions and limitations under which the SVH is applicable, including sensor choice, optical data characteristics, image pre-processing, heterogeneity indices, and field information, is a central objective of this study. By investigating where and under which circumstances the SVH is valid, our study aims to contribute to the refinement and targeted application of the SVH as a potential guide for field sampling and an indicator of spatial changes over time.

In this review, we acknowledge the multifaceted nature of biodiversity, which can be broadly defined as the variety and variability of life on Earth, encompassing different levels of organization, from genes to species to ecosystems. The studies included in our analysis employ a wide range of biodiversity definitions and metrics, reflecting the diverse aspects of biodiversity. These include species richness (the number of different species present in an area), diversity indices such as Shannon’s

H index or Simpson's D index, as well as measures of functional and phylogenetic diversity. This diversity of definitions underscores the complexity of the concept of biodiversity and highlights the challenges in using remote sensing data to capture its different dimensions. Furthermore, it's essential to consider that biodiversity is not limited to the species composition within a single habitat (alpha diversity) but also extends to beta and gamma diversity, which represent the diversity between habitats and the overall diversity within a landscape or region, respectively. These different dimensions of biodiversity are crucial for understanding the ecological and evolutionary processes that shape natural communities. To clarify these concepts, Table 1 provides definitions of alpha, beta, and gamma diversity.

Due to the majority of papers focusing on the use of the SVH for assessing alpha diversity, this review predominantly addresses alpha diversity. Given the fewer papers addressing beta and gamma diversity directly, we have dedicated a separate subsection (5.4 Beyond alpha: harnessing spectral heterogeneity for comprehensive biodiversity assessment) to discuss these aspects in greater detail, aiming to highlight their significance and explore their less represented dimensions in SVH studies.

The effectiveness of the SVH can vary significantly based on the specific aspect of biodiversity being assessed (e.g., taxonomic vs. functional diversity), the spatial scale of analysis (alpha, beta, or gamma diversity), and the ecological context of the study area. Thus, when evaluating the SVH across the diverse studies included in this review, it is crucial to consider the specific definitions and metrics of biodiversity employed, as they influence the interpretation of the relationship between spectral and biological diversity. This consideration is vital for a fair and nuanced evaluation of the SVH's applicability across different ecosystems and for advancing our understanding of how remote sensing can be effectively utilized in biodiversity monitoring and conservation.

A full review of the application of the SVH for species diversity monitoring was proposed more than ten years ago by Rocchini et al. (2010). This field of research was very productive in the past decade, and different aspects of the SVH were tested, highlighting advantages and pitfalls of the hypothesis. The aim of this paper is to give an updated overview of the advances and uncertainties related to the application of SVH as a proxy for different aspects of biodiversity. The paper is structured in eight sections: i) an introduction section providing an updated definition of SVH considering recent advances in remote sensing, ii) a material and method section defining the literature search, filtering process with a summary of the selected studies, iii) a review of the ecosystems for which the SVH was tested, iv) the different remote sensing data characteristics used to test the SVH, v) a comprehensive analysis of metrics, tools, and applications within the SVH, vi) the uncertainties related to the SVH, vii) the future perspective and viii) a conclusion section.

Finally, we report a table where all the studies reviewed in this work are summarized by area of study, remote sensing data used, goal of the study, main outcome, used heterogeneity indices, used field diversity measure and standardized goodness.

Table 1
Definitions of Alpha, Beta, and Gamma Diversity.

Diversity Type	Definition
Alpha Diversity	The variety of species within a specific habitat or ecosystem. It measures the local diversity and can include metrics such as species richness, Shannon's H index, and Simpson's D index.
Beta Diversity	The change in species composition across habitats within a landscape. It quantifies the difference between communities, reflecting the rate of turnover of species from one habitat to another.
Gamma Diversity	The total species diversity within a large region or landscape, encompassing multiple habitats.

2. Systematic literature review and overview

2.1. Literature review methodology

A systematic literature review on the SVH has been carried out using the platform Web of Science. To initiate the selection process for studies focusing on the SVH, we utilized the following search string (our analysis encompassed papers published until December 2023) within the Advanced Search Query Builder of Web of Science: $((TS = ("spectral\ variation\ hypothesis" OR "spectral\ variability\ hypothesis" OR "spectral\ heterogeneity" OR "spectral\ species" OR "spectranomics" OR "spectral\ diversity" OR "optical\ diversity")) AND TS = ("remote\ sensing" OR "earth\ observation" OR "satellite")) AND LA = (English) AND DT = (Article)$. The search parameters "TS" stands for topic (restricting to title, abstract, and keywords), "LA" for language, and "DT" for document type. The literature review was completed using the same approach in Scopus.

After skimming through the papers retrieved from the initial search, a total of 131 relevant papers were identified for further analysis. These articles were then examined thoroughly, and details related to 'ecosystem/area of study', 'remote sensing data used', 'goal of the study', 'main outcome', 'heterogeneity index used' and 'field diversity index' were extracted from each study.

Quantitative measures such as R^2 (transformed to R), R, Kendall's tau and Spearman's Rho were extracted to evaluate the association between SH and biodiversity metrics in each article. To achieve consistency and comparability across various metrics, we opted for selecting the highest values in each study. Subsequently, the articles were categorized into three distinct classes based on their level of goodness. It is important to note that this classification is not intended to evaluate the overall quality or merit of the papers, rather, it was created as a means to objectively classify papers concerning the SVH based on specific quantitative measures. Class one ("l") represented articles with low goodness, characterized by R, Spearman's rho, accuracy, and Kendall's tau values ranging from 0 to 0.5. Class two ("m") encompassed articles with medium goodness, featuring values ranging from 0.51 to 0.65. Lastly, class three ("h") included articles with high goodness, displaying values ranging from 0.66 to 1. This systematic approach allowed for a standardized and rigorous assessment of the reviewed articles' quality and provided insights into their relative performance within the selected measures of goodness. It is worth noting that this kind of selection, while deemed the best option to standardize the diverse range of studies employing numerous quantitative measures, may be considered a limitation of the study.

2.2. Summary of findings

In our literature review, we ascertained a total of 131 publications. The yearly publication count demonstrates a steady upward trajectory in the overall number of publications from 2000 to 2023 (Fig. 1). Notably, there was a peak of publications in 2021 and 2022, indicating the growing interest in utilizing SH as a remote sensing indicator for assessing biodiversity. It is widely believed that the initial experimentation of the SVH occurred in 2002, when Palmer et al., (2002) formulated the hypothesis that variability in remotely sensed signal captured by optical images could be a relevant proxy to assess the biodiversity of vascular plants in the Tallgrass Prairie preserve (Oklahoma, USA) using aerial panchromatic photography. In this seminal work, the authors correlated different SH metrics with three biodiversity indices (species richness, rarity and number of infrequent species) at different scales, evidencing positive correlations between SH expressed as standard deviation of reflectance and both rarity index and number of infrequent species. However, during our systematic literature review, we recalled that the SVH was previously conceptualized by Palmer et al. (1999) and first tested by Gould (2000) in 2000. In his paper, Gould unveiled that the variability of the Normalized Vegetation Index - NDVI - (using the standard deviation as heterogeneity index) obtained from Landsat TM

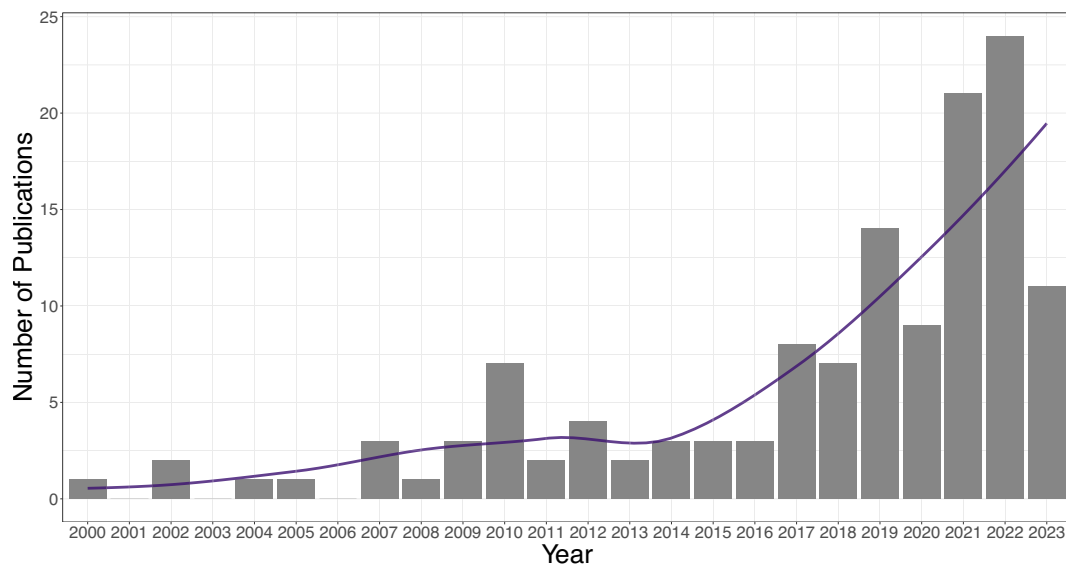


Fig. 1. Temporal distribution of publications testing the Spectral Variation Hypothesis between 2000 and 2022. The purple trend line shows the constant increase of SVH-related publications over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

images could be considered a good indicator of landscape heterogeneity and it correlated well to the plant species richness in the Arctic ecosystem of Hood River Region, Canada. The study demonstrated that by synergistically incorporating information on vegetation types alongside NDVI variability values, a more precise estimation of the plant species diversity within a specific area could be obtained.

In total, the SVH has been tested in 35 different countries included in this review (Fig. 2). The United States emerged as the country with the highest number of study areas, with 21 publications, closely followed by Italy with 20 publications. India and China followed with 8 publications, Switzerland and Portugal with 5. Additionally, when considering countries with a single publication from their study area, a total of 16 countries were identified. These findings highlight the diverse international application of the SVH within the reviewed articles. It is important to note that certain publications examining the SVH in simulated ecosystems, utilizing synthetic data, or focusing on theoretical aspects were not included in this map. When considering the continental distribution of publications, Europe accounted for 41%, North America for 23%, Africa for 16%, Asia for 18%, and South America for 3% of the total publications.

3. An ecosystem-oriented review of the application of SVH

The review of the SVH encompasses studies conducted in various ecosystem types (Fig. 3). Forest ecosystems represented the largest proportion (28%) of the studies analyzed concerning the SVH. Grassland studies accounted for a significant portion (25%) followed by mixed types (22%), where the SVH was tested over large areas covering different ecosystems. Wetlands (7%), coastal regions (5%), Savannah (5%), agricultural areas (3%), agro-forests (2%), Arctic regions (1%), marine ecosystems (1%), and soil habitats (1%) also contributed to the overall body of research.

Notably, a considerable fraction of the studies (approximately 10%) did not focus on any specific ecosystem but were either reviews, theoretical articles discussing the SVH in general terms, or studies investigating certain aspects of the SVH without testing it in real-world ecosystems.

These percentages reflect the relative distribution of studies across different ecosystems, highlighting the diverse range of environments that have been explored in the context of the SVH. Focusing on the forest ecosystems, the SVH has been studied in various habitats worldwide, including: tropical forests (Badourdine et al., 2023; Chraibi et al., 2022;

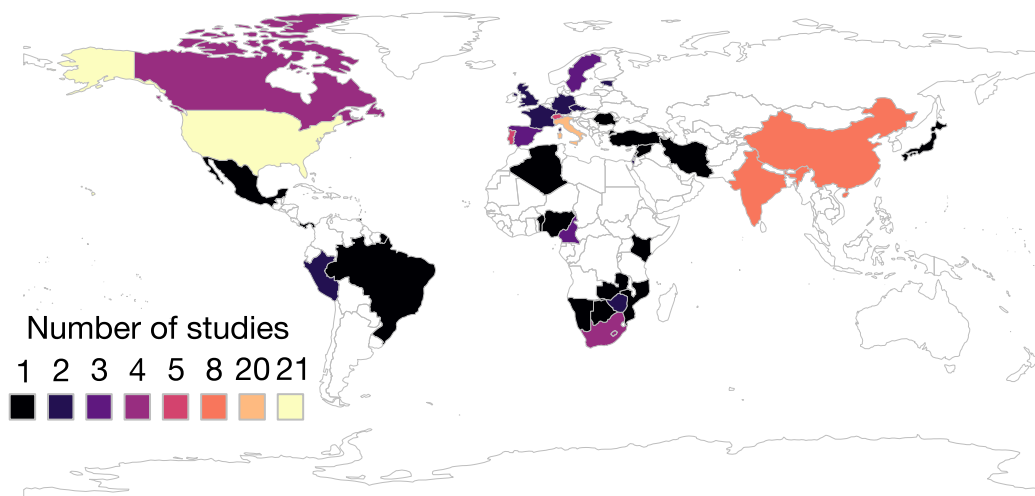


Fig. 2. Spatial distribution map showcasing the test locations where the Spectral Variation Hypothesis was tested.

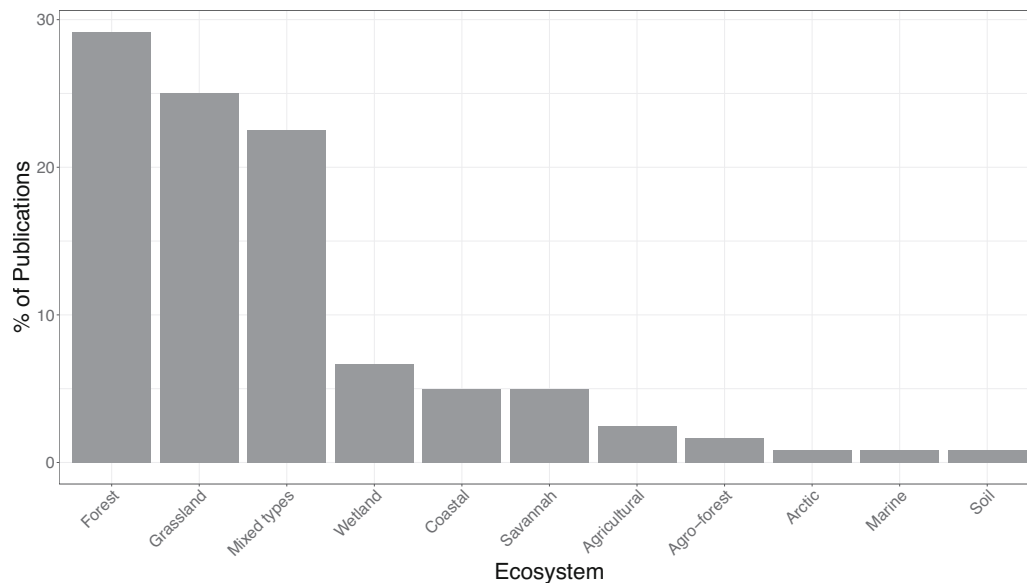


Fig. 3. Percentage of studies testing the Spectral Variation Hypothesis across different ecosystems.

Gillespie, 2005; Féret and Asner, 2014; Nagendra et al., 2010; Hernández-Stefanoni et al., 2012; Somers et al., 2015; Asner and Martin, 2011), Mediterranean forests (Levin et al., 2007; Pacheco-Labrador et al., 2022), urban forests (Sun et al., 2021), mountain and alpine forests (Torresani et al., 2018; Torresani et al., 2019; Torresani et al., 2021; Chitale et al., 2019; Louail et al., 2022; Torresani et al., 2022; Pangtey et al., 2023), temperate forests (Tagliabue et al., 2020), mangrove forest (Wang et al., 2022a) and mixed forests (Chitale et al., 2019; Chaurasia et al., 2020; Khare et al., 2018; Khare et al., 2019; Khare et al., 2021). In grassland ecosystems the approach has been tested in prairies (Gholizadeh et al., 2022; Gholizadeh et al., 2018; Palmer et al., 2002; Schweiger et al., 2018; Wang et al., 2022b; Wang et al., 2018b; Wang et al., 2016; Wang et al., 2018a), restored (Gholizadeh et al., 2019; Gholizadeh et al., 2020), semi-natural (Hall et al., 2012; Hall et al., 2010), mountain/alpine (Rossi et al., 2021; Rossi et al., 2022; Monteiro et al., 2022; Mohapatra et al., 2019; Sakowska et al., 2019; Imran et al., 2021), mesic/semi-arid (Zhao et al., 2021; Conti et al., 2021; Polley et al., 2019) grasslands and also from a world database on protected areas that encompass different grassland types (Peng et al., 2022). The category of 'mixed types' habitat encompassed all investigations that examined the SVH not within a single ecosystem, but across various ecosystems, this concerns studies where the approach was tested over different habitats (Hauser et al., 2021b; Dahlin, 2016; Pafumi et al., 2023), regions (Frye et al., 2021; Liccari et al., 2022; Rocchini and Vannini, 2010; Shahtahmassebi et al., 2017; Warren et al., 2014; Rocchini et al., 2008; Schmidtlein and Fassnacht, 2017; Paz-Kagan et al., 2021), countries (Da Re et al., 2019; Oindo and Skidmore, 2002; Perrone et al., 2023; Rocchini et al., 2011) and over different states (Mpakairi et al., 2022; Rocchini et al., 2014; Schweiger and Laliberté, 2022; Jung, 2022). In coastal regions, the SVH has been examined in dune landscapes (Malavasi et al., 2021; Marzioletti et al., 2021; Marzioletti et al., 2020), as well as in various other ecosystems present within coastal areas (Tassi and Gil, 2020; Onyia et al., 2019; Villoslada et al., 2020; White et al., 2010). In wetland areas the hypothesis has been tested in different areas located in Italy (Rocchini et al., 2004; Rocchini, 2007), in the USA (Taddeo et al., 2019; Taddeo et al., 2021) and in China (Tan et al., 2023; Tan et al., 2022). Focusing on agricultural areas, different authors tested the SVH in regions with both high (Tassi et al., 2022) and low (Rugani and Rocchini, 2017) abundance and diversity of agricultural lands, as well as in abandoned agricultural fields (Anece et al., 2017). Similarly, the approach has been tested also in agro-forestry systems (Chraibi et al., 2021; Rocchini et al., 2018), and in pulpwood

and oil-palm plantations (Hauser et al., 2022). In the Savannah ecosystem, the hypothesis has been tested only in the African continent, in particular in Cameroon (Ploton et al., 2022) and in the southern countries (Namibia, Zimbabwe, South Africa, Zambia) (Madonsela et al., 2017; Mutowo and Murwira, 2012; Oldeland et al., 2010; Mapfumo et al., 2016). Within the soil ecosystems we refer to a study by Blanco-Sacristán et al. (2019), where different SH indices derived from very high spatial resolution hyperspectral images were utilized as a reproducible method to monitor changes in the diversity of lichen-dominated biocrust communities. Other authors tested the SVH in other ecosystems such as arctic (Gould, 2000), marine (Herkül et al., 2013), and virtual areas (Heumann et al., 2015; Pacheco-Labrador et al., 2023). Finally, many studies analyzed different theoretical or methodological aspects of the SVH without testing them over real ecosystems (Rocchini, 2009; Fassnacht et al., 2022; Rocchini and Neteler, 2012b; Rocchini et al., 2010; Rocchini et al., 2022a).

Although originally conceived for assessing vegetation diversity, the SVH has garnered attention in recent studies, extending its application to the assessment of animal diversity, in particular of ticks (Da Re et al., 2019), mammals (Oindo and Skidmore, 2002) benthic invertebrates (Herkül et al., 2013) and birds (Anderle et al., 2023). This became achievable due to the correlation between SH and environmental heterogeneity, which, in turn, intricately intertwines with species diversity.

Fig. 4 provides a comprehensive overview of the application of the SVH across various ecosystems, with each ecosystem associated with the level of correlation assessed between remotely sensed variables and in-situ measured biodiversity metrics. Notably, forest ecosystems have been extensively studied, and the majority of these studies reported high goodness, indicating a consistent and robust performance of SVH in forested environments, while a few studies presented medium or low goodness. Grassland ecosystems have also been a focal point for SVH examination; however, with a wide range of relationships, suggesting that the applicability of SVH in grasslands may present a unique set of challenges hampering the assessment of biodiversity using remote sensing. Agricultural and agro-forestry systems have been explored in only a limited number of studies, yielding diverse outcomes. The former consistently demonstrated high reliability, whereas the latter exhibited lower accuracy, indicating potential challenges in applying SVH within these particular contexts. Savannah ecosystems, despite fewer studies, consistently showed good results, suggesting promising applications. The reliability of SVH in soil and arctic ecosystems was indicated by high accuracy ratings, although the limited number of studies highlights the

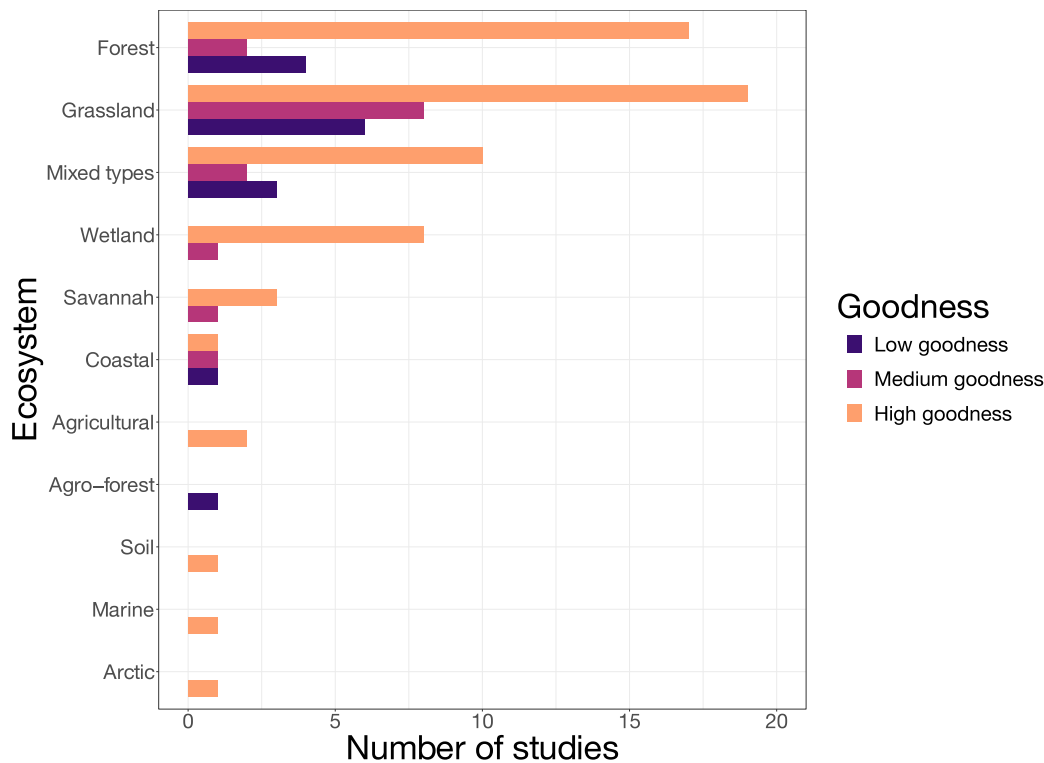


Fig. 4. Number of studies testing the Spectral Variation Hypothesis divided by goodness results. This is based on the highest correlation coefficient found in a study (R, Spearman’s rho, accuracy, and Kendall’s tau values). Ranging from 0 to 0.5 = Low goodness. From 0.51 to 0.65 = Medium goodness. From 0.66 to 1 = High goodness.

need for additional research to strengthen reliability. Wetland ecosystems, with a wide range of studies, consistently reported medium to high goodness, indicating potential effectiveness. Marine ecosystems consistently exhibit good results; however, due to the limited number of studies, further exploration in these environments is needed. Finally, the mixed types ecosystem exhibited both high and low accuracy instances, emphasizing the need for additional research to draw comprehensive conclusions.

In the elucidation of results across diverse ecosystems, it becomes apparent that their interpretation is intricately shaped not solely by inherent ecosystem characteristics but also by a confluence of factors, including the optical data employed, the heterogeneity index applied, and the specifics of field data acquisition. The nuanced interplay of these multifaceted elements will be comprehensively examined and discussed in detail in the subsequent sections, contributing to a more thorough understanding of the intricacies involved in the application of the SVH.

4. Remote sensing data used to test the SVH

4.1. Optical data characteristics

In this section, we go into a more detailed examination of the optical data characteristics employed in assessing SH, aiming to elucidate key factors influencing the outcomes of biodiversity analyses.

To enhance clarity in our discussion on optical characteristics and their impact on biodiversity studies, Table 2 provides definitions for spatial, temporal, spectral, and radiometric scales. This reference helps navigate the complex relationships between remote sensing data, biodiversity metrics, and the SVH, offering a concise framework for understanding how these scales affect biodiversity monitoring through optical imagery.

Over the past 50 years, numerous Earth observation platforms have been developed and launched to collect images of the Earth’s surface,

Table 2 Definitions of Spatial, Temporal, Spectral and Radiometric Scales.	
Scale Type	Definition
Spatial Scale	The grain and extent of spatial data, affecting how spatial patterns and processes are observed and interpreted.
Temporal Scale	Refers to the timing and frequency of data acquisition, influencing the observation of temporal dynamics.
Spectral Scale	The sampling interval, resolution and range of spectral data, impacting the differentiation and analysis of surface features.
Radiometric Scale	Pertains to the sensor’s sensitivity to measure the brightness of surface objects, affecting data quality.

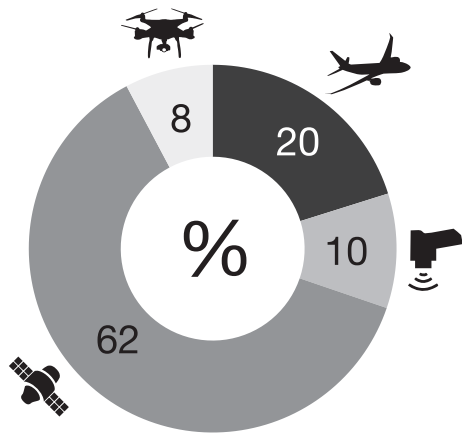


Fig. 5. Percentage of publications across remote sensing platforms (satellite, UAV, airplane and field).

with sensors exhibiting various spatial and spectral properties and the ability to capture repeated acquisitions over time (Crowley and Cardille, 2020; Wulder et al., 2022). According to our analysis (Fig. 5), the distribution of platforms employed in testing the SVH reveals notable variations in their prevalence. Satellite-based platforms constitute the dominant platform, with 62% of studies harnessing their capabilities to assess the SH. Airborne platforms, encompassing various aerial sensing methods, contribute significantly with 20% while field data, representing ground-based measurements, contribute to 10% of the studies. In contrast, UAVs contribute to a comparatively modest 8% of the studies, indicating a relatively limited but emerging use of UAVs in SVH research. The prevalence of the satellite platforms in SVH studies is attributed to its widespread utilization, facilitated by the accessibility of free and open-source data (Rocchini and Neteler, 2012a). Satellite data, being a cost-effective and readily available remote sensing solution, enable researchers to engage in biodiversity analysis (Turner et al., 2003). In contrast, airborne acquisitions, which have played a crucial role in remote sensing analysis, particularly through the utilization of high spatial resolution orthoimages for conceptualization and testing of SVH (Waser et al., 2004; Rocchini et al., 2004; Palmer et al., 2002), require substantial funding for data acquisition and processing. Field analyses, demanding extensive time and resources, present additional challenges. The relatively limited representation of the UAV platform in SVH studies can be attributed to its emerging status in ecological studies, with just over a decade of development. However, the emergence of UAVs equipped with specialized sensors and analysis methods has significantly advanced the field of very high spatial resolution image analysis for biodiversity monitoring, with SVH proving to be valuable despite the challenges associated with highly detailed data (Rossi et al., 2022; Malavasi et al., 2021; Conti et al., 2021; Jackson et al., 2022). As UAV capabilities continue to advance (Rossi and Wiesmann, 2024; Torresani et al., 2023a), we will likely witness an increase in their integration into biodiversity research, fostering a more comprehensive understanding of SVH and its implications for biodiversity analysis.

Upon in-depth analysis of studies assessing the SVH across diverse platforms and sensors, clear patterns in accuracy emerge (Fig. 6). Spaceborne multispectral studies dominate, reporting generally good results in testing the SVH across diverse ecosystems (Madonsela et al.,

2017; Torresani et al., 2021; Mapfumo et al., 2016; Gillespie, 2005; Rocchini, 2007). However, some studies within this subset exhibit medium and low goodness of fit, introducing variability in performance (Rossi et al., 2021; Pacheco-Labrador et al., 2022; Hauser et al., 2021b; Schmidlein and Fassnacht, 2017; Monteiro et al., 2022; Fassnacht et al., 2022). Additionally, studies using hyperspectral spaceborne data contribute, adding further variability in goodness ratings (Pacheco-Labrador et al., 2022; Gholizadeh et al., 2022). Airborne platforms with hyperspectral sensors, though fewer, typically exhibit high goodness ratings, indicating their effectiveness in SVH testing (Oldeland et al., 2010; Schweiger and Laliberté, 2022; Wang et al., 2016; Gholizadeh et al., 2020; Paz-Kagan et al., 2021; Van Cleemput et al., 2023). However, some studies report instances of low accuracy within this configuration (Möckel et al., 2016; Herkül et al., 2013). Fewer studies focus on using multispectral and panchromatic sensors within airborne platforms (Rocchini et al., 2022a; Palmer et al., 2002). Field-based studies, especially those employing hyperspectral sensors at the leaf level, consistently report high accuracy, emphasizing the reliability of field hyperspectral data in close-range SVH applications (Schweiger et al., 2018; Thornley et al., 2022). UAV-based studies with hyperspectral sensors predominantly report good results, showcasing the effectiveness of UAV platforms in SVH investigations. However, the limited number of studies using UAV configurations, particularly with multispectral sensors (Tan et al., 2023; Tan et al., 2022; Villoslada et al., 2020; Conti et al., 2021; Jackson et al., 2022; Malavasi et al., 2021), results in varied goodness ratings, emphasizing the need for additional research in this domain. Additionally, it is noteworthy that hyperspectral (imaging spectroscopy) sensors from UAVs often exhibit suboptimal performance, possibly due to factors such as poor signal-to-noise ratio and platform instability.

Among all the used sensors, Landsat has the highest representation with 31 studies of the total publications (Taddeo et al., 2021; Rugani and Rocchini, 2017; Perrone et al., 2023; Levin et al., 2007; Madonsela et al., 2017) (Fig. 7). The total sum of sensors exceeds the total number of analyzed studies because individual studies often tested different sensors. The series of Landsat satellites represent the longest-running program (since 1972) for the acquisition of satellite imagery of the Earth and the Landsat data archive is still underutilized for such

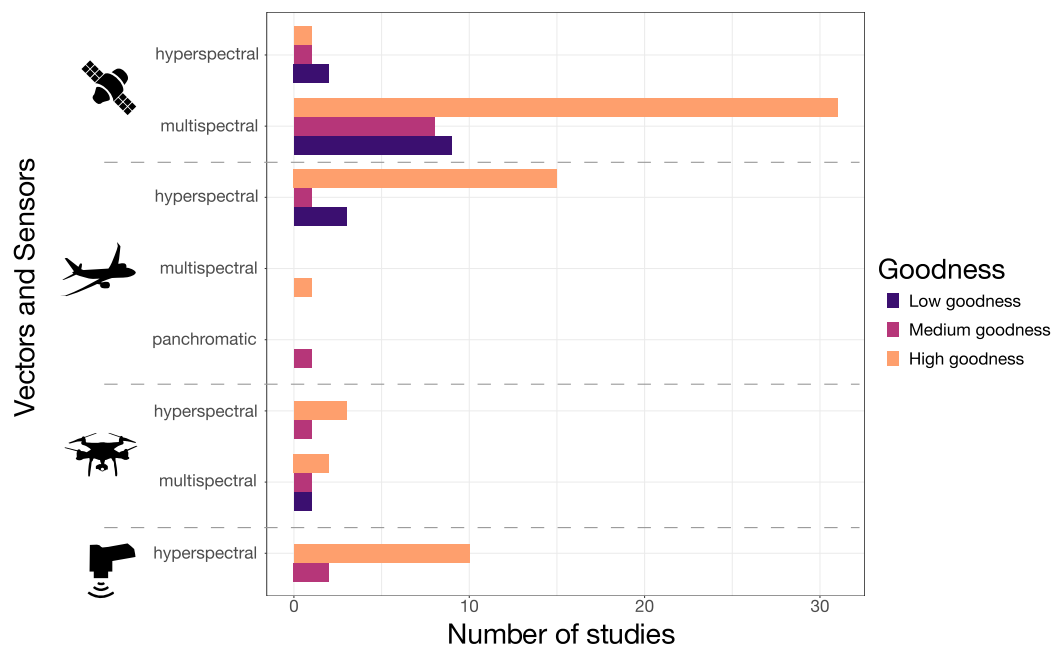


Fig. 6. Number of studies testing the Spectral Variation Hypothesis divided by levels of goodness across different platforms (satellite, airplane, unoccupied aerial vehicle, field) and sensors. The goodness is based on the highest correlation coefficient found in a study (R, Spearman's rho, accuracy, and Kendall's tau values). Ranging from 0 to 0.5 = Low goodness. From 0.51 to 0.65 = Medium goodness. From 0.66 to 1 = High goodness.

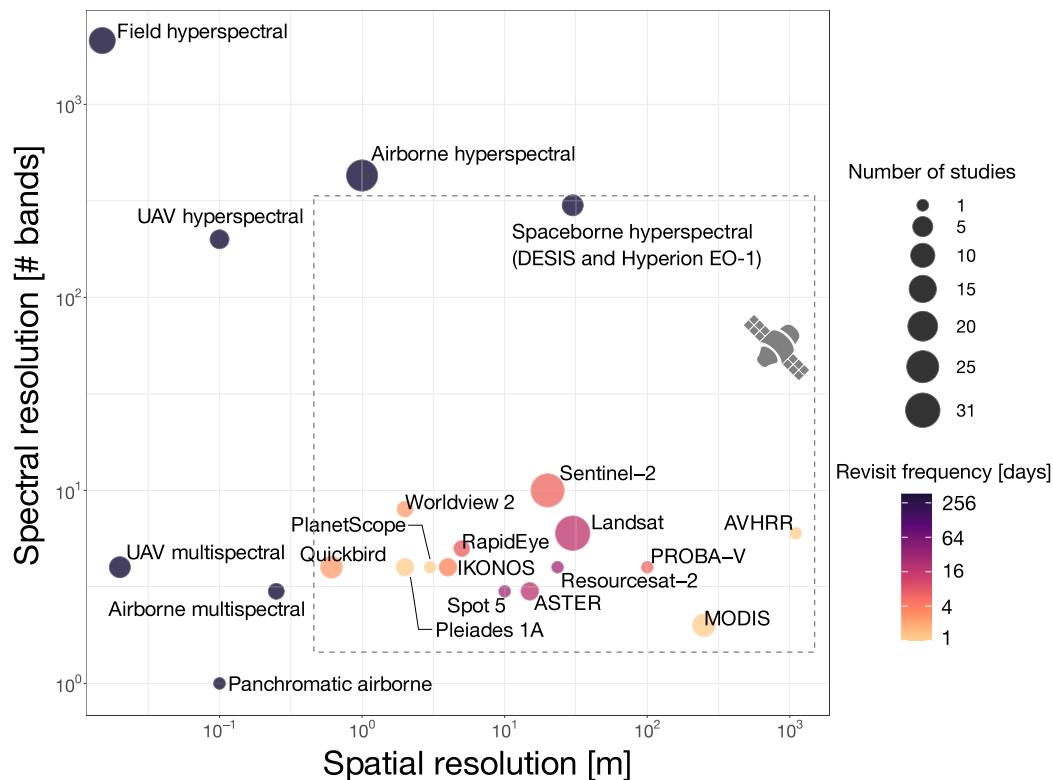


Fig. 7. Distribution of publications across remote sensing platforms (satellite, airplane, unoccupied aerial vehicle, field) with their spectral sampling, spatial resolution and revisit frequency. Satellite sensors are featured within the grey dotted box.

applications, despite the potential of such data for biodiversity and natural retrospective ecosystems monitoring. It is followed by Sentinel-2 (Licari et al., 2022; Hoffmann et al., 2019; Hauser et al., 2021b; Torresani et al., 2021) with 28 studies. (Da Re et al., 2019; Rocchini et al., 2014; Schmidtlein and Fassnacht, 2017). The Sentinel-2 twin constellation is a relatively newer mission (since 2015) with advanced capabilities, including higher spatial resolution and improved spectral coverage compared to Landsat. At the time of writing this review, it is gaining popularity and recognition among researchers, but it has not yet surpassed the extensive usage and familiarity of Landsat in the field of the SVH. Hyperspectral field (Thornley et al., 2022; Blanco-Sacristán et al., 2019; Badourdine et al., 2023) and hyperspectral airborne (Tagliabue et al., 2020; Somers et al., 2015; Schweiger and Laliberté, 2022; Gholizadeh et al., 2019) sensors accounted for 13 and 24 publications, respectively. Other satellite sensors such as MODIS (Da Re et al., 2019; Rocchini et al., 2014; Schmidtlein and Fassnacht, 2017), QuickBird (Hall et al., 2010; Levin et al., 2007; Rocchini et al., 2004), ASTER (Laurin et al., 2014; Mutowo and Murwira, 2012), Pleiades (Khare et al., 2018; Khare et al., 2019), IKONOS (Nagendra et al., 2010; Végh and Tsuyuzaki, 2021), RapidEye (Khare et al., 2018), AVHRR (Oindo and Skidmore, 2002), CORONA (Shahtahmassebi et al., 2017), DESIS (Pacheco-Labrador et al., 2023), PlanetScope (Marzioletti et al., 2021), PROBA-V (Thouverai et al., 2021), SPOT (Lopes et al., 2017) and Worldview 2 (Mapfumo et al., 2016), together with hyperspectral and multispectral UAV (Malavasi et al., 2021; Polley et al., 2019; Xu et al., 2022; Zhao et al., 2021) have less than 10 publications.

Future use of hyperspectral data is anticipated to increase with new satellites like EnMAP (Environmental Mapping and Analysis Program, launched in 2022 by the German Space Agency (Guanter et al., 2015)) and PRISMA (Precursore IperSpettrale della Missione Applicativa, launched in 2019 by the Italian Space Agency (Guanter et al., 2015; Loizzo et al., 2018)). Though these missions lack global coverage for comprehensive biodiversity monitoring, they pave the way for future global hyperspectral missions, such as NASA's SBG (Cawse-Nicholson

et al., 2021) and ESA's CHIME (Nieke and Rast, 2018), expected in the late 2020s helping on improving biodiversity estimation worldwide.

The availability of optical images measuring surface reflectance in the visible and infrared domains, with medium to fine spatial resolution at both local and global coverage, has facilitated the development of applications that exploit Earth observation data for research purposes and its transition into operational applications (Crowley and Cardille, 2020). However, using optical remote sensing images for biodiversity assessment presents several challenges, as highlighted in different SVH related studies (Rocchini et al., 2010; Fassnacht et al., 2022). These challenges encompass limited funding and support from public organizations, which may result in heightened dependence on private sector involvement for data acquisition and the limitations imposed by inadequate temporal, spatial and spectral resolutions. Overcoming these obstacles becomes crucial for fully unlocking the potential of optical data in biodiversity studies and gaining deeper insights into ecological dynamics. In light of these considerations, this section aims to delve into the spatial, spectral and temporal characteristics of remote sensing data within the context of the SVH. By exploring the interplay between these data characteristics and the SVH, we can gain a deeper understanding of their implications for biodiversity assessment and monitoring.

Notably, the goodness of fit is not solely dictated by the optical data characteristics but is intricately tied to the specific ecosystems under scrutiny. As we transition from the discussion on the prevalence of different remote sensing platforms and sensors (Fig. 6) and the distribution of studies across these configurations, our analysis further goes into the nuanced patterns of goodness of fit ratings. This examination, illustrated in Fig. 8, uncovers ecosystem-dependent variations in the effectiveness of the SVH for biodiversity assessments.

The Figure shows distinctive patterns across ecosystems, underlining the impact of the optical characteristics on the SVH and biodiversity assessments. In forests, there is a prevalent reliance on spaceborne multispectral studies, showcasing the potential of coarser spatial resolution data in such ecosystems (Torresani et al., 2019; Gillespie, 2005).

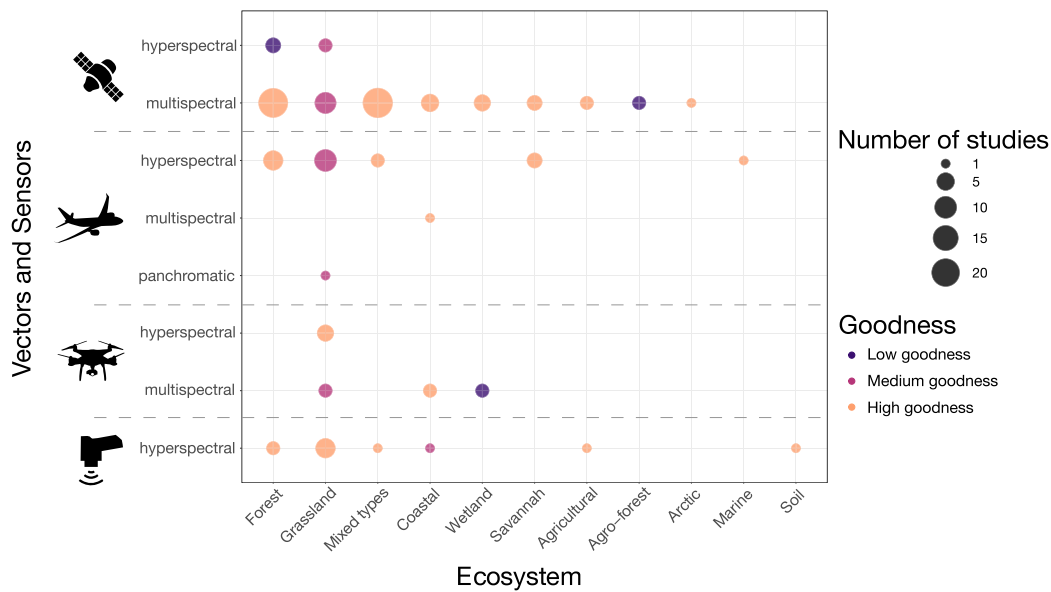


Fig. 8. Number of studies testing the Spectral Variation Hypothesis across different ecosystems using different platforms and sensors and levels of goodness (in this case the average value of all the studies per ecosystem). This was based on the highest correlation coefficient found in a study (R, Spearman's rho, accuracy, and Kendall's tau values). Ranging from 0 to 0.5 = Low goodness of fit. From 0.51 to 0.65 = Medium goodness of fit. From 0.66 to 1 = High goodness of fit.

Notably, while airborne hyperspectral studies show a robust correlation (Chaurasia et al., 2020; Wallis et al., 2023), they are less abundant compared to spaceborne multispectral studies. Field hyperspectral studies, though less frequent, consistently exhibit strong correlation and high goodness (Schweiger et al., 2018) across all the ecosystems. In grassland ecosystems, airborne and spaceborne studies, show low to medium goodness (Möckel et al., 2016; Monteiro et al., 2022), remarking the importance of high spatial resolution data for a successful application of the SVH (Wang et al., 2018a). Conversely, studies utilizing UAV (Polley et al., 2019; Wang et al., 2018a) and field optical data (Gholizadeh et al., 2018; Thornley et al., 2022), which benefit from higher spatial resolution, tend to report higher accuracy. While UAV technology holds great potential for enhancing our understanding of spectral diversity, further advancements are necessary to ensure its consistent and reliable application in biodiversity assessments. An interesting aspect, particularly within grassland studies, is the crucial role of spectral information, more specifically the number of spectral features sampled. Sole reliance on multispectral and panchromatic datasets, despite possessing high spatial resolution, tends to yield only moderate accuracy (Palmer et al., 2002). These findings highlight that both spatial and spectral characteristics are critical in remotely estimating plant diversity in grassland ecosystems. The work of Gamon et al., (2020) highlight the complexity of these scale interactions, suggesting that the interplay between spatial and spectral scales can significantly influence biodiversity assessment outcomes. This nuanced understanding underscores the importance of a scale-informed approach, integrating both dimensions to effectively capture the diversity within these ecosystems.

4.2. Spatial resolution

With spatial resolution, we refer to the spatial grain (pixel size) of the optical data used to assess the SH. The choice of the appropriate spatial resolution for remote sensing information should be discussed specifically in light of the objectives of any type of ecological application (Moudry et al., 2023; Rocchini et al., 2023b). As highlighted by Nagendra and Rocchini (2008), finer spatial resolution does not systematically benefit remote sensing applications. The need for spatially detailed images is indeed, in many cases, a double-edged sword, particularly when focusing on complex and heterogeneous systems. In

the specific context of SVH, the choice of an appropriate spatial resolution is legitimately a core uncertainties to address, as it is the main driver of spatial heterogeneity of spectral information. Images with coarse spatial resolution result in a mixed signal at pixel scale, integrating the spectral signature of different surfaces (e.g. vegetation, soil, water bodies), homogenizing the signal and causing difficulties in clearly identifying boundaries between spatial entities (individuals, vegetation types, ecosystem types) (Rocchini et al., 2010; Nagendra et al., 2010; Feilhauer et al., 2021). Fine spatial resolution may lead to a level of details within spatial entities causing strong heterogeneity, for example when pixels allow distinction between branches and leaves: when the dimensions of individuals of interest from an observed system (e.g. trees from a forest) are larger than pixel size, the variability between neighboring pixels increases along with spectral entropy “by increasing the level of intra-class variation and introducing spatial heterogeneity resulting from in-shadow pixels” (Rocchini et al., 2010).

Drawing from Gamon et al. (2020), it's critical to recognize that the interplay of spatial, temporal, spectral, and angular resolutions in remote sensing data profoundly affects our ability to detect and interpret biodiversity. The alignment of these scaled dimensions with the biological scales of diversity necessitates a sophisticated understanding beyond mere resolution enhancement. Segmentation methods may provide a promising avenue to exploit high spatial resolution imagery to match and box-average the area (e.g. canopy in forest ecosystem) of interest (Zheng et al., 2022). However, the overarching complexity suggests that while high spatial resolution can enrich texture metrics and take advantage of modern analytical techniques, such as convolutional neural networks (Schiefer et al., 2020), or enhance impure pixel masking (Gholizadeh et al., 2018), its efficacy is inherently linked to a comprehensive, scale-aware approach in biodiversity monitoring.

4.2.1. SVH across different spatial resolution

Various studies investigated the influence of the spatial resolution on the relationship between SH and biodiversity, in order to provide recommendations and identify limitations of available remote sensing data when studying specific ecosystems (Gamon et al., 2020; Rocchini, 2007; Khare et al., 2019; Wang et al., 2018a). However, it is worth noting that these studies have reported contrasting results, highlighting the complex role of spatial resolution in the assessment of the SVH. For instance, some research (Torresani et al., 2019; Rossi et al., 2022; Torresani et al.,

2018; Wang et al., 2018a) has indicated that optical data with medium to high spatial resolutions, like those obtained from Sentinel-2 or UAVs, outperform data from sensors with coarser resolutions, such as Landsat 8, in correlating SH with biodiversity metrics. Conversely, other studies (Khare et al., 2018; Rocchini, 2007) have presented a case for the utility of lower spatial resolution data in certain contexts. However, the challenge for deriving such conclusions is that differences between sensors happen at multiple dimensions, spatial resolutions will differ but at the same time the spectral layout differs. Some attempts have been made to isolate the impact of spatial resolution on functional diversity patterns. For example, Helfenstein et al. (2022) used both Sentinel-2 and APEX data, with the latter spectrally convolved to match Sentinel-2 but at its native spatial resolution. The study concluded that the spectral properties of Sentinel-2 data allow for physiological trait derivation, and that spatial resolution has a profound impact on diversity metrics (Helfenstein et al., 2022). The diversity of findings reveals the significance of understanding the underlying factors contributing to these disparities. In some cases, as previously stated and showed in Fig. 8, medium-high spatial resolution optical data have proven effective for capturing SH and assessing biodiversity. This preference often arises when researchers focus on ecosystems (e.g. forests), where such spatial resolutions align with the unique SH characteristics of these environments. On the contrary, in other contexts, when the SH is estimated at broader scale (e.g. over different ecosystems), coarser spatial resolution data is favored. Additionally, as also shown in Fig. 8, very high spatial resolution data has been commonly applied especially in ecosystems like grasslands, where finer spatial details are necessary for a comprehensive assessment of the SH (Wang et al., 2018a). This variability of finding underscores a deeper complexity in how spatial resolution impacts the assessment of the SVH, highlighting the importance of matching the scale of remote sensing data with the biological scales of diversity under investigation. Thus, the 'optimal' spatial resolution is contingent upon specific study goals, the ecological context of the targeted ecosystem, and the methodological approach employed. This perspective aligns with the broader understanding that the selection of spatial resolution in remote sensing studies is not merely a technical decision but a fundamental consideration that requires careful alignment with the ecological phenomena being studied and the specific objectives of the research.

4.2.2. Sampling design: The effect of plot size in the SVH

Another important aspect of spatial scale that influence the relationship SH-biodiversity is related to the plot size, often referred to as the 'grain effect'. This topic represents an often-overlooked aspect that affect the assessments of different aspect of biodiversity (Gholizadeh et al., 2022). Most of the studies that tested this topic (Gholizadeh et al., 2022; Oldeland et al., 2010; Rossi and Gholizadeh, 2023; Robertson et al., 2023; Hauser et al., 2021a) within the SVH for the assessment of vegetation diversity, showed that a stronger relationship between SH and plant diversity was observed for larger sampling plots, likely attributed to broader ranges in species and SH values across larger areas. The determination of plot size, or more broadly, the field sampling design, in remote sensing studies of plant diversity, is frequently established and concluded before planning remote sensing data collection or is conducted independently, often addressing goals unrelated to the objectives of the remote sensing study. In this light, as highlighted by Gholizadeh et al. (2022), the disconnect between remote sensing and field sampling design is considered a missed opportunity. Remote sensing is probably the only feasible means to provide globally continuous spatial estimates of biodiversity, extending beyond small plots. Consequently, it is crucial to pay specific attention to field data collection to better match field observations to the pixel size (Végh and Tsuyuzaki, 2021) of remote sensing data and develop standardized field protocols (Pacheco-Labrador et al., 2022).

4.3. Spectral resolution

4.3.1. Spectrum considerations in the SVH

Spectral characteristics include the spectral range, which encompasses the wavelengths covered by the sensor, the number of spectral bands (or the sampling interval for hyperspectral sensors), and the spectral resolution. As an example, hyperspectral images combine a high number of contiguous spectral bands and high spectral resolution, allowing for the measurement of continuous surface reflectance properties and the characterization of multiple vegetation traits (Feilhauer et al., 2018). Increasing spectral sampling and/or spectral resolution may enhance the capacity to distinguish and discriminate among species or communities with different spectral signatures, influenced by a complex combination of biophysical properties such as leaf chemistry and canopy structure (Rocchini et al., 2010). However, the number of bands alone is not necessarily an indicator of improved performance. Properly positioned bands can capture specific spectral features relevant to the targeted vegetation or environmental parameters, optimizing the sensor's sensitivity to key signals and minimizing spectral redundancy. Therefore, careful consideration of band placement is essential for maximizing the effectiveness of spectral data acquisition and analysis in remote sensing applications (Rocchini, 2007).

While the choice of spectral characteristics, such as the number and placement of spectral bands, is critical for analyzing SH and biodiversity through the SVH, it's essential to balance between ecosystem-specific adaptations and the need for methodological standardization. Different methodologies have been adopted in different SVH studies giving back different results about the spectral resolution of the data. Some studies focused on identifying optimal spectral regions when estimating biodiversity metrics using a spectral diversity, Gholizadeh et al. (2018) found that spectral bands near 680 nm—associated with chlorophyll absorption—played a significant role in distinguishing areas of varying vegetation diversity in prairie ecosystems, suggesting that targeted spectral analyses may offer enhanced discriminative power. However, at coarser spatial resolutions, the NIR region (700–914 nm) became more informative, indicating that the choice of spectral range and resolution can greatly affect the accuracy of biodiversity estimates. Similarly, Wang et al. (2018b) observed that the use of full-range hyperspectral data over the entire spectrum (400 to 1000 nm) did not necessarily confer additional benefits for plant diversity assessment, indicating that the thoughtful selection of spectral bands could be more critical than the sheer quantity of spectral information. They also found that the most informative spectral regions for estimating species richness varied with spatial resolution, highlighting the importance of selecting appropriate spectral bands tailored to the spatial scale of the study.

Other studies focused on the employment of conventional ordination techniques like PCA (Da Re et al., 2019; Rocchini et al., 2004; Herkül et al., 2013). Some others focused on the use of vegetation indices, such as the NDVI which have demonstrated the capacity to capture subtle variations in reflectance associated with specific leaf traits of different species (Torresani et al., 2019; Oindo and Skidmore, 2002; Helfenstein et al., 2022). Others have used regression or physically-based models to derive 'optical traits' as ecologically measurable intermediates before calculating diversity metrics (Durán et al., 2019; Torresani et al., 2021; Hauser et al., 2021a; Hauser et al., 2022). All these methods underscores the adaptability of SVH analyses to different ecological contexts and spectral data characteristics. However, this adaptability raises concerns regarding the comparability of results across studies, emphasizing the challenge of achieving a standardized approach that can be uniformly applied while still accounting for the unique spectral signatures of different ecosystems. To reconcile this, a dual approach is recommended where methodological flexibility is maintained for ecosystem-specific investigations, allowing researchers to tailor their spectral analysis to the particular traits and conditions of their study area. Simultaneously, efforts should be made to develop and agree upon a set of core spectral metrics and methodological standards that can facilitate cross-study

comparisons and aggregate analyses. This approach would involve the establishment of benchmark spectral characteristics and analysis procedures that are broadly applicable across diverse ecosystems, thus providing a common framework for evaluating the SVH. By doing so, we can enhance the utility of SVH analyses in biodiversity research, enabling more consistent and comparable insights into the relationships between SH and species diversity across different ecological contexts.

In most of the cited studies, it turned out that spatial, rather than spectral, resolution was the limiting factor in their analyses. Rossi et al. (2022) proposed two primary explanations for the relatively lower significance of high spectral resolution compared to high spatial resolution. First, spectral bands are highly correlated and spectral metrics condense the spectral information making the full information highly redundant and biased towards some spectral features. The second explanation, which is partially discussed in Section 6 ('Uncertainties related to the SVH'), focuses on the influence of canopy structure on the relationship between SH and species diversity. Reflectance measurements taken over vegetation patterns encompass information about leaf traits, canopy structure, and their interactions. For instance, specific regions of the electromagnetic spectrum (e.g., visible and near-infrared) exhibit strong correlations with grassland canopy variables (e.g., total biomass), allowing the capture of most spectral variance between plants through the reflectance of a few bands within this spectral region.

4.4. Temporal resolution

When estimating biodiversity using remote sensing data within the SVH, it is crucial to consider the temporal dimension, as the temporal resolution of optical remote sensing data plays a significant role in capturing dynamic changes in ecosystems and providing valuable insights into the temporal patterns of species and communities. With temporal resolution here we do refer to the frequency at which data are collected over the same area and the specific timing of these acquisitions, including considerations of daily and seasonal variations. This definition underscores the importance of capturing both periodic changes in ecosystems, such as phenological shifts, and more abrupt ecological events, such as disturbances. Temporal resolution, therefore, not only dictates how often an ecosystem is observed but also when these observations occur, to ensure relevant biological phenomena are accurately represented in the data. The relationship between SH captured by optical images and field observations of biodiversity can exhibit significant seasonal fluctuations, influenced by factors such as phenological changes (Wang et al., 2023), structural variation (Dronova et al., 2021) and physical effects like shading (Lopatin et al., 2019). To establish a meaningful connection between spectral variations and taxonomic or functional diversity, it is important to select an acquisition period that maximizes the discrimination between different species or groups of species. Various studies (Torresani et al., 2019; Wang et al., 2022b; Pangtey et al., 2023; Rahmanian et al., 2023) explored the

impact of the seasonal variation of SH in the context of the SVH. Their findings underscore the necessity of analyzing complete time series of remote sensing data to take advantage of the temporal differences among species and communities effectively. This recurring pattern is ascribed to shifts in leaf phenological conditions, alterations in leaf chemistry, and changes in canopy structure. Recently Fassnacht et al. (2022) discussed this aspect in more depth, exploring the influence of daily, seasonal, and stochastic dynamics on Earth's ecosystems and the corresponding variations in optical traits captured by remote sensing sensors. The authors stated that the daily variations, such as changes in leaf orientation, can affect spectral signatures, especially in airborne data or with orbit shifts in polar-orbiting satellites. Seasonal variations pose challenges to SVH due to changes in optical traits like leaf area index and pigments, influenced by flowering events and phenology. Intraspecific variations, such as those due to health, growth form, environmental adaptations, and stress events, further complicate spectral variation analysis in larger spatial extents. As an example we elaborated in Fig. 9 the data of Feilhauer and Schmidtlein (2011) showing how grassland exhibit different spectral behaviors depending on their phenological state during a vegetating season, affecting spectral variation measures and potentially the SVH results.

In addition to the various stages of leaf development, farming practices (e.g. in managed ecosystems) play a significant role in shaping the SH and its relationship with species diversity (Rossi et al., 2021; Ghoulizadeh et al., 2020). Particularly, within grasslands, anthropogenic activities such as burning, grazing, mowing, fertilizing, and harvesting significantly alter SH. Such alteration, i.e., the temporal component of spectral diversity, can be an important predictor of plant diversity (Rossi et al., 2024). In the context of SVH research in forest ecosystems, most studies integrating remotely sensed spectral diversity solely made use of mono-temporal measurements from remote sensing and field data (Kacic and Kuenzer, 2022), thus only assessing the SVH at a single temporal snapshot and not investigating aforementioned temporal influences.

Concluding, the impact of daily and seasonal dynamics on optical traits and SH is very strong, emphasizing the significance of considering phenological behavior and natural and anthropogenic stressors when interpreting spectral variation metrics to ensure precise biodiversity assessments using optical data. Analyzing the complete time series of remote sensing data, instead of relying solely on single acquisitions, proves valuable in utilizing temporal differences among species and communities (Rossi et al., 2021; Rossi et al., 2024). Additionally, frequent revisits and acquisitions are crucial, particularly in regions with high cloud cover like tropical rainforests (Drusch et al., 2012). Statistical methods that partition variance into various factors (Wang et al., 2022b; Rossi et al., 2021), can help to explore these complex interactions between spatial, spectral, and temporal scales, offering a methodological framework for disentangling the influences of phenology and management influence on spectral diversity and improving the reliability of

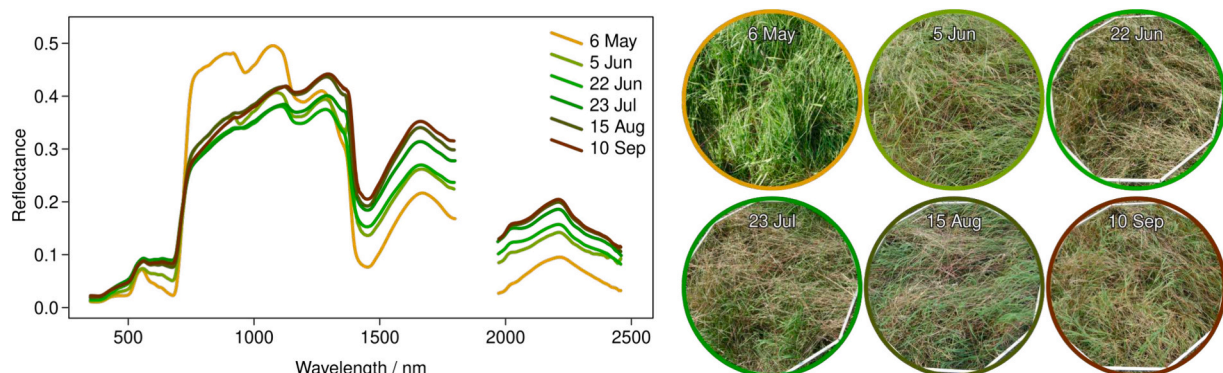


Fig. 9. Grassland seasonal development and related spectral signals of the canopy. Data are taken from Feilhauer and Schmidtlein (2011).

remote sensing as a tool for biodiversity monitoring.

5. A comprehensive analysis of metrics, tools, and applications in biodiversity studies

5.1. Assessing spectral heterogeneity: Metrics and the spectral species concept

The choice of a suitable metric for evaluating SH has proven to rely on the available remotely sensed data, the ecological goal, and the analytical approach employed to establish the relationship between SH and biodiversity. Some metrics have shown to be more appropriate for the assessment of diversity gradients over very large areas (e.g. global scale) while in other cases local diversity patterns may be of interest.

Fig. 10A shows the distribution of the reviewed studies across the spectral indices used to assess the SH. The coefficient of variation showed to be the most used index for the assessment of the SH accounting for approximately 16% of the publications. The substantial influence of the Rao's Q index, contributing around 13%, is particularly noteworthy given its relatively recent introduction to the field (Rocchini et al., 2017), this rapid adoption underscores its substantial influence in SVH

studies. Other metrics make smaller but still noteworthy contributions: the standard deviation and the Shannon index, the latter largely used in ecology as index for species diversity, make up approximately 9% and 7% of the publications, respectively. The mean euclidean distance and the convex hull area and volume are also noteworthy, with contributions of around 7% and 6%, respectively. Other metrics like spectral species (that encompass also the spectral richness and communities clustering), the spectral variance (that include the indices that measure the spectral divergence and distance) make smaller but still noteworthy contributions, each representing around 5–4% of the publications. Several other indices, including Simpson's D index, Renyi index, range, spectral alpha diversity index, spectral entropy, spectral evenness, spectral rarefaction, Berger-Parker index, spectral cumulative residual entropy, Hill and Pielou indices, contribute each approximately 1–2%, indicating their presence in the literature but with comparatively lower prominence. Another 16% of the publications are represented by other heterogeneity indices that have been used only once in the literature.

Some of the most used metrics, such as the Rao's Q index used with a single dimensional mode (Hauser et al., 2021b; Torresani et al., 2021; Pangtey et al., 2023) or the mean distance from centroid (Rocchini et al., 2004) (Table 3) are more appropriate when computed from low spectral

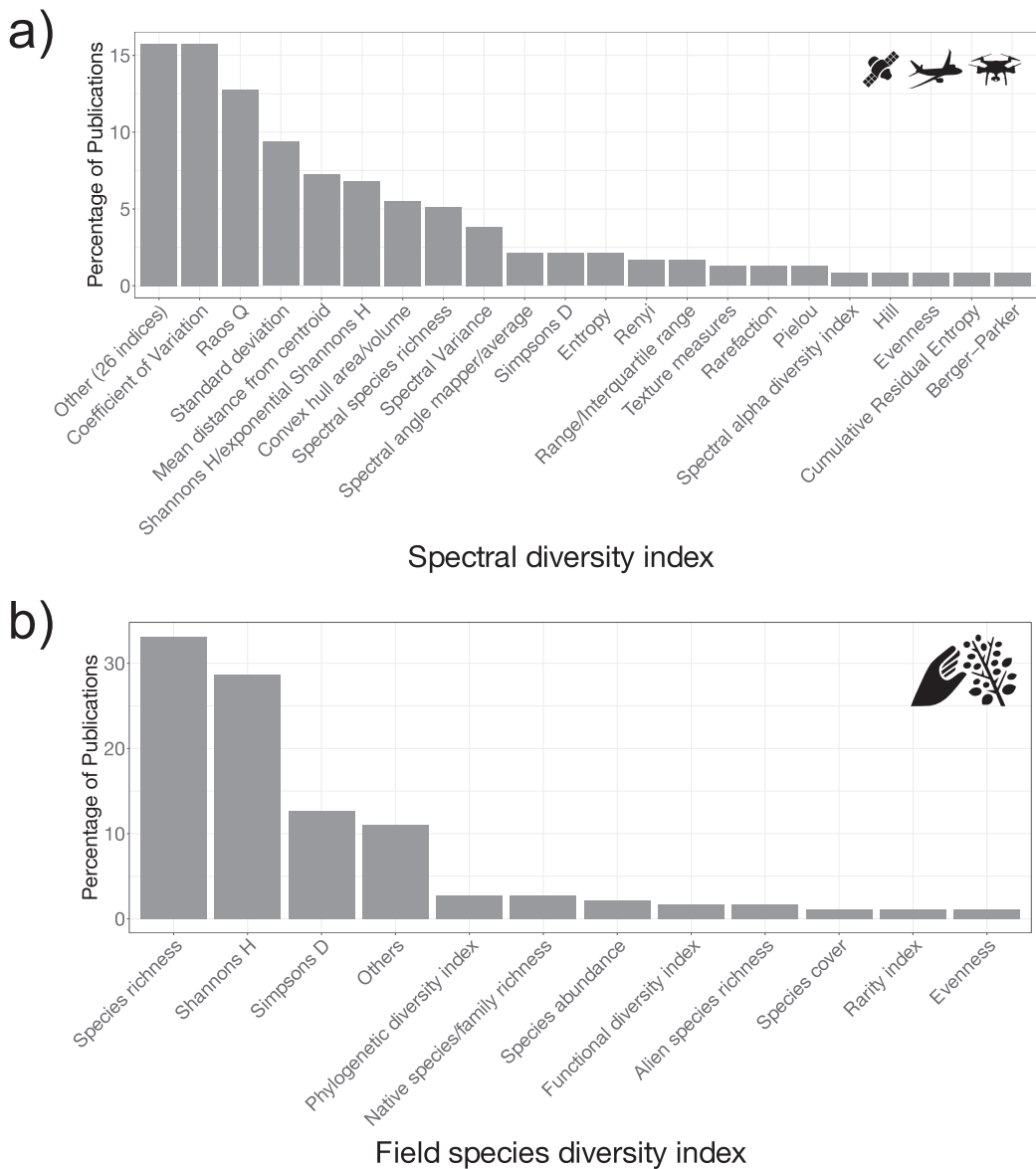


Fig. 10. Distribution of Publications across heterogeneity indices used to assess the Spectral Heterogeneity.

Table 3
Characteristics of the most used heterogeneity indices.

Heterogeneity index	Characteristics
Coefficient of variation	Measures relative variability; ratio of the standard deviation to the mean, expressed as a percentage
Rao's Q index	Combines abundance and pairwise dissimilarity of pixel values; captures diversity by considering pixel values proportional abundances and their differences
Standard deviation	Measures absolute variability in spectral values; captures the dispersion of pixel values around the mean; higher values indicate greater heterogeneity
Mean distance from centroid	Average distance of all pixel values in a dataset (e.g., raster) from the mean centroid value; assesses the compactness and spread of pixel values in a spectral space; higher values indicate more spread and heterogeneity
Shannon's H index	Quantifies pixel value diversity by considering richness and evenness; higher values indicate greater diversity; commonly used to measure entropy in ecological studies but also used in remote sensing
Convex hull/volume	Encompasses the smallest convex set containing all points in a dataset; measures the spatial extent and volume occupied by spectral points; larger volumes indicate greater spectral diversity and heterogeneity

dimension information such as panchromatic images, singular optical bands, spectral indices or individual layers resulting from feature selection or feature extraction applied on multispectral sensors (Rocchini et al., 2010; Torresani et al., 2019; Torresani et al., 2020). On the other hand, other metrics such as the spectral convex hull area/volume (Gholizadeh et al., 2018; Hauser et al., 2021b), the coefficient of variation (Lucas and Carter, 2008) and the spectral angle mapper/average (Gholizadeh et al., 2022) have been developed to harness the full spectral information available in multispectral and hyperspectral images (see Table 3 for a comprehensive description of these most used indices). These metrics are essential for preserving and exploiting the wealth of spectral data that might otherwise be lost when using unidimensional indices, especially in scenarios involving multispectral or hyperspectral sensors.

According to our analysis, 41% of the studies explored diverse heterogeneity metrics, showcasing a nuanced approach to assessing SH. In contrast, 59% of the studies focused on a single metric, indicating a preference for simplicity or a targeted investigation into specific aspects of SH. This diversity in the approach to metric selection underscores the complexity of SH assessments and suggests that researchers adopt varied strategies based on their goals and the available remotely sensed data.

As suggested by Fassnacht et al. (2022), an essential consideration concerning heterogeneity indices pertains to the careful selection of appropriate spectral metrics for evaluating biodiversity. This choice holds significant importance because certain metrics can exhibit heightened sensitivity to extreme spectral values stemming from diverse sources, including spectral noise, bare ground reflectance, and illumination factors (Gholizadeh et al., 2018). As noted by Rossi et al. (2022), metrics such as convex hull volume and to a lesser extent, the coefficient of variation exhibit pronounced susceptibility to extreme values and, for this reason, must be used judiciously, as they may lead to an overestimation of SH due to the presence of deceased biomass, soil and shadows. Conversely, alternative metrics like the spectral species richness demonstrate reduced sensitivity to extreme values (Perrone et al., 2023, 2024), offering a more pragmatic approach to biodiversity analysis.

Complementing these metrics, the spectral species richness, based on the spectral species concept stands out as a noteworthy method for assessing biodiversity. This concept, developed by Féret and Asner (2014) is based on the idea that the continuous nature of spectral information can be transformed into discrete spectral species through unsupervised clustering methods (Féret and Asner, 2014). Hence, the spectral space is divided into distinct clusters, with each cluster representing a spectral species. The goal is to assign each pixel to a specific

cluster, essentially treating each pixel as an individual or a member of a spectral species. This discretization allows for the computation of various diversity metrics, similar to plant diversity metrics. As emphasized by Rocchini et al. (2022a), the initial theory behind the spectral species concept defines a species by its unique spectral signature (resulting in a 'pure pixel'), making it detectable within the pixels of a spectral image. However, in practice, the presence of multiple species (or habitats (Rocchini et al., 2021a)) within a single pixel (mixed pixel), due to varying spatial resolutions, complicates the assignment of spectral information to specific species, bringing a level of uncertainties to the approach. Rossi and Gholizadeh (2023) addressed this issue by combining the spectral species concept with spectral unmixing, thus considering the spectral signature of each pixel as the mixture of multiple spectral species. The approach suffers from other conceptual limitations for operational applications. The clustering algorithm and the number of clusters needs to be arbitrarily set by users, this suggests that the number of clusters should be adjusted based on an expected overall diversity expected from an area/landscape, if comparing outputs of the method produced independently from various landscapes. Furthermore, the approach may introduce bias, especially in highly diverse ecosystems since the fixed definition of spectral species can lead to overestimation in sites with low taxonomic diversity. Researchers, such as Lopes et al. (2017) and Rocchini et al. (2021a), explored spectral species for assessing species diversity in grasslands and mapping "spectral communities" across Europe, respectively. Gholizadeh et al. (2020) applied hyperspectral clustering to estimate alpha diversity, incorporating a "virtual dimensionality" approach to estimate the number of spectral species. These efforts demonstrate the utility of spectral species in diverse ecosystems and spatial scales.

5.2. Open-source tools for spectral heterogeneity assessment

Recently, various authors have developed open-source packages facilitating the estimation of diverse heterogeneity indices (Table 4). These accessible solutions not only streamline the process of SH assessment but also contribute to the widespread adoption of SVH in biodiversity studies. This accessibility fosters a collaborative and inclusive approach, empowering researchers with user-friendly tools to delve into the intricate dynamics of SH across diverse ecosystems. Rocchini et al. (2021b) developed the R *rasterdiv* package designed for computing heterogeneity indices (BergerParker, copNDVI, CRE, Hill, paRao, Pielou, Rao, RaoAUC (Thouverai et al., 2022), Renyi, Shannon's H) using remotely sensed data. The *rasterdiv* is supported by firmly grounded in information theory, utilizing reproducible open-source algorithms (Thouverai et al., 2021). Additionally, Tassi et al. (2022) developed an open-source Python application, *spectralrao-monitoring*,

Table 4
Open-source tools for spectral heterogeneity assessment in biodiversity studies.

Package Name	Language	Key Features	Source	Reference
<i>rasterdiv</i>	R	Computes various heterogeneity indices from raster datasets	CRAN	(Rocchini et al., 2021b)
<i>spectralrao-monitoring</i>	Python	Calculates the Rao's Q diversity index from raster datasets	GitHub	(Tassi et al., 2022)
<i>biodivMapR</i>	R	Computes alpha and beta diversity from raster datasets	GitHub	(Féret and de Boissieu, 2020)
<i>stdiversity</i>	R	Calculates spectral diversity over time from optical information	GitHub	(Rossi et al., 2021)
<i>unmix</i>	R	Assesses spectral diversity at subpixel level from optical information	GitHub	(Rossi and Gholizadeh, 2023)

with the intention of harnessing the faster computational power offered by Python for the calculation of the Rao’s Q diversity index. [Féret and de Boissieu \(2020\)](#) developed the R *biodivMapR* package, largely tested in different studies ([Pafumi et al., 2023](#); [Robertson et al., 2023](#); [Ploton et al., 2022](#); [Zhang et al., 2023](#)) and designed for computing alpha (using the Shannon’s H and Simpson’s D indices) and beta diversity (using the Bray–Curtis dissimilarity) under the scope of the SVH based on the spectral species concept. Finally, other R packages are available on GitHub, for example tools for calculating the spectral diversity over time and at the subpixel level (<https://github.com/RossiBz/stdiversity> and <https://github.com/RossiBz/unmix>).

Table 5 illustrates the diversity of open-source tools available for biodiversity assessment, focusing on packages that offer advanced methods for exploring diversity through traits and facilitating the estimation of alpha and beta diversity. *Vegan*, a comprehensive package for community ecology, enables the computation of various diversity indices, *FD* focuses on measuring functional diversity from traits data, highlighting the importance of trait-based approaches in understanding biodiversity patterns, *picante* offers tools for integrating phylogenetic and trait diversity into ecological research while *gdm* facilitates Generalized Dissimilarity Modeling to analyze and model spatial patterns of biodiversity, taking into account ecological distance and environmental gradients. These packages significantly enhance the analytical capacity of researchers, allowing for a deeper exploration of the ecological and evolutionary underpinnings of biodiversity. Through their extensive features, these tools aid in uncovering the multifaceted nature of biodiversity and its critical role in ecosystem health and resilience, underlining the necessity of incorporating diverse methodological approaches in biodiversity studies.

5.3. Field diversity data

A comprehensive review of field species diversity indices reveals a diverse landscape of metrics employed in biodiversity studies (Fig. 10 B). Among these, species richness stands out as the most frequently utilized, accounting for around 32% of the indices surveyed. Following closely behind is Shannon’s H, representing around 28%, emphasizing the significance of information entropy in capturing species diversity patterns. Simpson’s D contributes to around 12% of the diversity indices, offering insights into community dominance. A notable 11% is dedicated to various other indices (such as infrequent species index, Pielou’s J, Species rarefaction), reflecting the richness of approaches in assessing biodiversity. The consideration of native species, families, and richness collectively contributes around 3%, underscoring the importance of understanding the composition of ecosystems. Also species abundance and phylogenetic diversity/index occupy 3%, highlighting the attention given to both population sizes and evolutionary relationships. Alien species richness, species cover, rarity index, functional diversity index, and evenness collectively contribute to the remaining 8%, showcasing the breadth of ecological dimensions covered in SVH-related studies.

While species richness emerges as the most frequently utilized metric in the comprehensive review of field species diversity indices, it is noteworthy to acknowledge different research findings that challenge the conventional emphasis on this metric. Different studies ([Oldeland et al., 2010](#); [Torresani et al., 2019](#); [Xu et al., 2022](#); [Wang et al., 2018b](#))

suggest that abundance-based measures, exemplified by the Shannon’s H Index, demonstrate a stronger relationship with SH than for example species richness alone. These indices appear to align with vegetation structure, considered a subset of environmental heterogeneity, providing a nuanced reflection of SH nuances ([Oldeland et al., 2010](#); [Foody and Cutler, 2003](#)). This perspective further supported by the work of [Madonsela et al. \(2017\)](#), underscore the idea that SH tends to be more strongly correlated with dominant or more abundant species, which play a pivotal role in shaping the landscape, compared to rare and occasional species that are only partially captured by richness metrics.

5.4. Beyond alpha: Harnessing spectral heterogeneity for comprehensive biodiversity assessment

Beyond its foundational role in estimating within-community diversity (alpha), the SVH has evolved to encompass a broader spectrum, with around 15% of our review studies extending its application to assess beta and or gamma diversity, as well as venturing in different ecological areas. Beta diversity, representing the turnover of species composition between different communities or localities, plays a crucial role in understanding ecological transitions and landscape heterogeneity. The application of SVH to beta diversity estimation involves assessing variations in spectral signatures across landscapes ([Rocchini et al., 2019](#); [Schweiger and Laliberté, 2022](#)). Different habitats, characterized by distinct species compositions, are expected to exhibit higher SH. This approach allows researchers to quantify and visualize the turnover of species as reflected in the diversity of spectral patterns. The majority of research exploring beta diversity within the context of the SVH primarily focuses on forest ecosystems ([Arekhi et al., 2017](#); [Chraibi et al., 2022](#); [Féret and Asner, 2014](#); [Hernández-Stefanoni et al., 2012](#); [Khare et al., 2019](#); [Laliberté et al., 2020](#); [Robertson et al., 2023](#)), with subsequent studies expanding into grasslands ([Rossi et al., 2021](#); [Polley et al., 2019](#); [Gholizadeh et al., 2020](#)) and over mixed types of habitat ([Hoffmann et al., 2019](#); [Liccari et al., 2022](#); [Pafumi et al., 2023](#); [Schweiger and Laliberté, 2022](#)).

To assess beta diversity in various ecosystems, studies have utilized different types of remote sensing data, including Landsat ([Arekhi et al., 2017](#); [Hernández-Stefanoni et al., 2012](#); [Khare et al., 2019](#)), Sentinel-2 ([Chraibi et al., 2021](#); [Hoffmann et al., 2019](#); [Liccari et al., 2022](#); [Pafumi et al., 2023](#); [Rossi et al., 2021](#)), airborne hyperspectral ([Schweiger and Laliberté, 2022](#); [Robertson et al., 2023](#); [Laliberté et al., 2020](#); [Gholizadeh et al., 2020](#)) and UAV hyperspectral imagery ([Polley et al., 2019](#)). These tools have proven effective in capturing vegetation physiological changes, species turnover, and habitat diversity by analyzing spectral variables and heterogeneity. Particularly, coarse satellite data suggest that single pixels might represent plant communities, emphasizing beta diversity estimations based on pixel differences rather than within-pixel diversity ([Khare et al., 2021](#); [Khare et al., 2019](#); [Hoffmann et al., 2019](#)).

[Rocchini et al. \(2018\)](#) discussed the methods for estimating beta diversity from remote sensing data, including different approaches. The first incorporate multivariate statistical analyses and ecological distances like the Bray-Curtis dissimilarity, largely used in different studies ([Baldeck and Asner, 2013](#); [Chraibi et al., 2021](#); [Chraibi et al., 2022](#); [Rossi et al., 2021](#); [Rocchini et al., 2022b](#)), the Jaccard distance that measures species overlap between habitats, emphasizing presence-absence data

Table 5
Open-source tools for assessing diversity via traits and methods for alpha and beta diversity estimation.

Package Name	Language	Key Features	Reference
<i>vegan</i>	R	Community ecology package, diversity indices	(Oksanen, 2015)
<i>FD</i>	R	Functional diversity metrics from traits	(Laliberté et al., 2014)
<i>picante</i>	R	Phylogenetic and trait diversity	(Kembel et al., 2010)
<i>gdm</i>	R	Generalized Dissimilarity Modeling	(Mokany et al., 2022)

(Gholizadeh et al., 2020; Arekhi et al., 2017), and the Hellinger distance (Liccari et al., 2022; Schweiger and Laliberté, 2022), more sensitive to rare species. Another similar approach based on a detrended correspondence analysis was tested by Hernández-Stefanoni et al. (2012)) that visually represents species turnover across gradients, contributing to understanding spatial biodiversity variation. Rocchini et al. (2018) highlight also the spectral species concept (discussed in section 5.1) as another approach for assessing beta diversity, crucial for identifying distinct ecological communities through remote sensing. Féret and de Boissieu (2020) describe how the spectral species concept, useful for beta diversity assessment, is operationalized through the *biodivmapR* R package, effectively utilized in various research studies to analyze beta diversity from remote sensing data (Pafumi et al., 2023; Robertson et al., 2023). Lastly also the Rao's Q index, largely used to assess alpha diversity has been used to assess beta diversity (Khare et al., 2019; Rocchini et al., 2019). In this context Khare et al. (2019) demonstrated that, across various spatial resolutions and scales, the Rao's Q index offers superior accuracy over the conventional Shannon's H index for estimating beta diversity in complex forest settings. Adding to the comprehensive discussion on SH's role in beta diversity assessment, Laliberté et al. (2020) discussed a novel approach that quantifies the spectral composition variation among communities within a region, emphasizing the unique contributions of each community and spectral feature to overall beta diversity.

About gamma diversity, Laliberté et al. (2020) described a method originally designed for partitioning the diversity in its spatial component (Legendre and De Cáceres, 2013) adapted to allow partitioning the spectral diversity into alpha, beta, and gamma components. They suggested that high spectral beta diversity may arise from turnover in plant species and/or functional trait composition across environmental gradients such as soil properties and hydrology. On the other hand, high spectral alpha diversity may be a result of local biotic interactions among co-occurring plants, including phenomena like resource partitioning and conspecific negative density dependence. Their approach allows for a more nuanced understanding of the factors contributing to spectral diversity in plant communities. Rossi et al. (2021) extended the approach to include temporal dissimilarities between pixels. The resulting beta spectral diversity accounts for the spectral variance between-community over space and time and their interaction, thus taking into account diverse phenology and farming practices among various plant communities when estimating plant diversity.

In contrast to the variance partitioning approach of Laliberté et al. (2020), Chao et al. (2024) propose a gamma decomposition framework for the analysis of multifunctionality based on Hill numbers. Due to its novelty, the sample-based approach has not yet been tested based on remote sensing imagery. Previous research by Chao et al. (2023) on standardized measurements and comparisons of beta diversity provides the statistical foundation for the multifunctionality decomposition approach.

Additionally, the SVH has been applied to assess functional diversity, which represents the variation in functional traits among species within a community. Functional traits are ecological characteristics that influence a species' interactions with its environment and other species. By measuring SH and relating it to functional traits, researchers can gain insights into the functional diversity of plant communities. Ma et al. (2019) demonstrated the potential of the SVH to capture functional diversity gradients in major European forest types, while Schneider et al. (2017) and Helfenstein et al. (2022) use vegetation indices as proxies of functional traits to explore its application to assess functional diversity in a forested mountain range. Other studies take an intermediate step and first derive biophysical traits from spectra through partial least squares regression (Durán et al., 2019; Schweiger et al., 2018) or radiative transfer model inversion (Hauser et al., 2021a; Rossi et al., 2020) to assess functional diversity. These studies highlight the versatility of the SVH in characterizing not only species diversity but also functional diversity in plant communities.

Recent studies have also unveiled the versatility of SVH for applications beyond its initial scope encompassing diverse domains. In the field of land cover change detection, SH proves instrumental in identifying alterations in land cover across various scales. Notably, Tassi and Gil (2020) utilized SH metrics from Sentinel-2 data to effectively detect and monitor coastal land cover changes with high spatial resolution. The sensitivity of SH metrics to changes in spectral reflectance becomes a crucial mechanism for capturing shifts induced by alterations in land cover. Similarly, in land cover classification, SH emerges as a catalyst for enhancing accuracy. As illustrated by Marzietti et al. (2020), SH metrics derived from multispectral imagery contribute to mapping coastal dune landscapes. The discriminative capabilities of SH metrics become apparent in distinguishing between land cover types that exhibit similar spectral signatures. The significant differences in spectrally derived diversity metrics across land use also become clear in Hauser et al. (2022) comparing between intact forest, logged forests, and plantations in Borneo. In the context of eco-geomorphological monitoring, SH serves as a valuable tool for assessing the integrity of ecosystems, such as coastal dunes. Malavasi et al. (2021) used SH metrics from UAV imagery to monitor the eco-geomorphological integrity of coastal dunes while Gastauer et al. (2022) assessed the environmental quality of mining waste piles based on SH from Sentinel-2 data. In the context of atmospheric carbon fluxes and greenhouse gas exchanges, no direct or indirect effects on carbon content were detected by testing the SVH in forest ecosystem (Wallis et al., 2023). On the other hand, SH showed to serve as a tool to assess environmental heterogeneity, validating the relationship between satellite emissivity indices and eddy covariance data across various ecosystems: in areas with large correlation, SH and related environmental heterogeneity was lower, while weaker correlations were associated with higher environmental heterogeneity (Torresani et al., 2022).

6. Uncertainties related to the SVH

In the preceding sections, we have explored the extensive body of research that highlights a compelling link between SH and species diversity. These studies collectively underscore the potential of SH as a valuable tool for assessing biodiversity in diverse ecosystems. However, as we delve deeper into the complexities of this relationship, it becomes evident that the path to fully harnessing the power of the SVH is not without its challenges and uncertainties due to its correlative nature. While the SVH has demonstrated promise in multiple studies, can not be considered the 'holy grail' for estimating biodiversity through remote sensing data; rather, it represents just one assumptive option among many, that needs to be applied with caution. The complexities of the factors that influence the SVH, potentially acting in a multivariate manner, still necessitate a more comprehensive exploration. Studies employing the SVH often follow diverse lines of reasoning, ranging from indicators of geo- or habitat diversity influencing species diversity to exploring trait and functional diversity linked to species diversity, ultimately driving spectral diversity (Hauser et al., 2021b). With a few rare exceptions (Ludwig et al., 2024) a systematic assessment of these drivers, considering their simultaneous and potentially ambiguous effects is needed. A more thorough investigation into these aspects will contribute to refining the theoretical underpinnings of the SVH and provide a more robust foundation for its application in assessing biodiversity through remote sensing data.

The large body of research shows that adapting SH metrics and methodologies to diverse ecological settings remains challenging, resulting in variability of the goodness-of-fit found between studies. The nuances and spectrally dominant features of ecosystems vary, while the choice of data sources, spectral platforms, field-based indices, and SH measures between studies simultaneously shape our perception of spatial features across ecosystems, thus confounding the quest for a universal 'one-size-fits-all' robust implementation of the SVH, which is unlikely to exist given the complexity.

It is worth noting that many of the studies showcased in the literature demonstrate high model performance, often achieving remarkable goodness-of-fit. As showed in Fig. 7 just few studies reported no or low correlation between SH and biodiversity (Schmidtlein and Fassnacht, 2017; Chraïbi et al., 2021; Conti et al., 2021; Lopes et al., 2017; Möckel et al., 2016; Monteiro et al., 2022; Villoslada et al., 2020; White et al., 2010; Ludwig et al., 2024). The apparent success of the SVH can be attributed, in part, to the iterative nature of scientific inquiry. Researchers frequently conduct multiple trials, experimenting with diverse field indices, optical data sources featuring various resolutions, and a range of heterogeneity metrics. The results that ultimately find their way into publications may understandably favor those that align with the SVH's premise. This inherent bias in reporting positive outcomes can potentially skew the broader understanding of the SVH's efficacy. Hence, it is crucial to approach SVH-related research with a discerning eye. Recognizing the challenges and potential uncertainties that accompany SVH investigations allows for a more balanced assessment of its applicability and limitations.

In the following paragraphs, we will briefly outline uncertainties, citing and referring to specific studies which delve into these issues with greater detail and analysis.

6.1. Optical image characteristics: Spectral, spatial, temporal resolution and atmospheric corrections

In exploring the relationship between SH and biodiversity, the optical characteristics of images, including spectral, radiometric, spatial and temporal resolution emerge as crucial. Since we explored all these characteristics in Section 4, we do not delve deeper here to avoid redundancy.

Atmospheric correction methods of optical images play another crucial role in the reflectance data, affecting the robustness of biodiversity metrics derived from SH. Recent investigations have revealed that the selection of atmospheric correction methods can significantly influence the temporal consistency of reflectance data and for this reason of SH, hindering the robustness of biodiversity metrics (Chraïbi et al., 2022). Utilizing vegetation indices like NDVI as inputs for SH calculations offers a method to mitigate atmospheric and environmental variations, enhancing the reliability of biodiversity assessments through a more consistent basis for SH (Kacic and Kuenzer, 2022; Chraïbi et al., 2022). In summary, these optical image characteristics significantly influence the application of the SVH in biodiversity monitoring. Understanding these complexities and uncertainties is critical for refining remote sensing methodologies for biodiversity assessment, emphasizing the necessity for ecosystem-specific approaches and the thoughtful integration of optical data characteristics (Torresani et al., 2019; Rocchini, 2007; Khare et al., 2019; Wang et al., 2018a; Rossi et al., 2022; Rocchini et al., 2017; Fassnacht et al., 2022; Gholizadeh et al., 2020; Kacic and Kuenzer, 2022; Chraïbi et al., 2022; Ludwig et al., 2024).

6.2. Spectral heterogeneity metrics

As already highlighted in section 5, the choice of SH metrics adds to the complexity of the relationship between SH and biodiversity. As stressed by Fassnacht et al. (2022), the indices used to assess the SH are subject to different technical considerations that include the choice of spectral regions and the radiometric resolution of the optical images. Heterogeneity indices are influenced by the characteristics of the optical images, in particular by the spectral coverage of the bands, by the radiometric resolution and by the sun-sensor geometry. As a result, the same metric calculated for different satellite sensors may yield different meanings and capture different processes related to spectral variation,

which can pose issues when comparing data from different sensors.

6.3. Vegetation complexity, biomass, density and soil

Vegetation height and vertical complexity as well as the variation of plant and leaf traits introduce uncertainties in SH-biodiversity correlations (Conti et al., 2021). The alignment of remote sensing spatial resolution with vegetation's physical structure impacts SH measurements. High vertical complexity within ecosystems may result in a uniform appearance in remote sensing data, reducing observed SH due to an 'occlusion effect' where taller vegetation obscures shorter plants and creates shadowed areas (Conti et al., 2021). Furthermore, the challenge of distinguishing species with similar spectral signatures is compounded by intraspecific variability and shared traits, though hyperspectral sensors offer improved discrimination by capturing a broader spectrum of spectral bands. Biomass plays a crucial role in influencing SH across landscapes (Rossi et al., 2022). Higher biomass levels within communities are associated with increased SH, although this relationship varies with vegetation characteristics, including functional traits and morphological features.

Also plant density, as stressed in different studies (Gillespie, 2005; Van Cleemput et al., 2023) plays a crucial role in shaping the intricate relationship between SH and species diversity. Higher plant density often signifies heightened resource competition, potentially leading to the dominance of a few species and reduced overall diversity (Connell, 1978). Additionally, it fosters intensified biotic interactions among species, impacting their survival and diversity. In contrast, varying plant densities within an ecosystem can create diverse microhabitats, supporting a wider array of species adapted to different conditions and thereby increasing both spectral and local species diversity. The importance of vegetation cover in influencing SH metrics was further highlighted by Hauser et al. (2021b), who investigated the constituents of SH metrics derived from Sentinel-2 over a mountainous Mediterranean semi-natural region, considering functional and species diversity, variation in landscape morphology and vegetation cover fraction in multivariate linear mixed-effect models. The study revealed that differences in vegetation cover contributed to two-thirds of the explained variance in the SH metrics, with species richness playing a significant but reserved role as a predictor. This underscores the need for closer examination of the drivers of SH, such as vegetation cover and soil properties, to better understand the mechanisms behind its effectiveness and robustness in different scenarios. Since the optical signal is mainly determined by leaf and plant traits, their variation across the species in a mixed stand drives the spectral variation in the canopy. Plant stands that feature species with converging traits, i.e. for example a similar pigmentation, water content or leaf area, hence show a lower spectral diversity despite a possibly high species diversity (Ludwig et al., 2024). This observation highlights the importance to consider ecological knowledge on plant properties in the application of the SVH.

In revisiting the role of soil within the context of SH and biodiversity, it becomes evident that soil characteristics contribute significantly to the SH observed in remote sensing data, extending beyond a mere backdrop to a dynamic influencer of spectral diversity (Rossi and Gholizadeh, 2023). The variability in soil reflectance, driven by factors such as moisture and texture, complicates the straightforward application of SH metrics by introducing an additional dimension of variability that must be accounted for. Advanced filtering and correction techniques, such as those outlined by Gholizadeh et al. (2018), offer pathways to mitigate soil's confounding effects, enhancing the reliability of SH metrics. However, these methodologies underscore the intricate balance required to accurately interpret spectral data, highlighting soil's dual role as both a challenge and an opportunity in the quest to link remote

sensing observations with biodiversity outcomes. Such a nuanced understanding reinforces the need for comprehensive strategies that encompass the full spectrum of environmental variables influencing spectral diversity, ensuring a robust framework for biodiversity assessment.

6.4. Habitat type

The type of habitat or vegetation appears to be as important, if not more so, than the sheer number of habitats (refer to Fasnacht et al., (2022) for a more in-depth analysis). This becomes evident when considering that some habitats, despite being rich in species diversity, exhibit low spectral variation when observed through the lens of typical satellite sensors. In such cases, the correlation between spectral variation and biodiversity becomes less straightforward (Perrone et al., 2023; Ludwig et al., 2024). Complications arise when comparing areas with varying numbers of habitats or with a patchy structure, challenging the boundary between-site and within-site. The relationship between habitat/patches count, SH, and species richness/diversity is intricate and can confound straightforward biodiversity assessments based solely on SH metrics.

6.5. Use of moving window approach

The choice of moving window size for calculating the SH had a significant impact on the relationship between SH and biodiversity. According to different studies (Conti et al., 2021; Tagliabue et al., 2020; Rocchini et al., 2004) there is no one-size-fits-all moving window size and the optimal size will vary depending on the specific ecosystem and study objectives. The selection of an appropriate moving window size should be carefully tailored to the characteristics of the ecosystem and the goals of the study, recognizing that it can significantly influence the outcomes of the SH-biodiversity relationship. As an example, Schmidt-lein and Fasnacht (2017) stated that a moving window approach could fail to estimate plant diversity in a heterogeneous human-dominated landscapes due to the complex spatial structure of the environment (with arrangement of field edges, roads, and fields) inflating the SH. Therefore, the parcel-based approach proposed by Rossi et al. (2024) should be preferred in agricultural landscapes. Furthermore, as highlighted by Laliberté et al. (2020), utilizing a moving window approach to evaluate spectral beta-diversity calculates this diversity separately for multiple small sub-regions, lacking an estimation of spectral beta-diversity for the entire region as a whole.

6.6. Field data, diversity indices and sampling design

The quality and quantity of field data can also have a significant impact on the results of biodiversity assessments based on SH. The collection of field data should adhere to a standardized sampling design to ensure reliability and comparability across different studies. Inconsistencies in sampling methods or biases in data collection can introduce significant uncertainties into the analysis.

The choice of diversity indices used in the analysis is another source of potential uncertainty. Different diversity indices, such as Simpson's D or species richness, offer distinct perspectives on biodiversity. Simpson's D, for instance, takes into account both species richness and evenness, placing more weight on dominant species (Oldeland et al., 2010). On the other hand, species richness solely quantifies the number of species giving the same weight to rare species that may only marginally influence the reflected light from plant communities. Furthermore, other facets of plant diversity such as functional and phylogenetic diversity may display a stronger relationship with spectral diversity compared to taxonomic diversity (Rossi and Gholizadeh, 2023; Ludwig et al., 2024),

given that phenotypic plant traits are directly associated with plant spectra (Kothari and Schweiger, 2022; Ollinger, 2011; Woolley, 1971). As a result, the choice of diversity indices and the dimension of plant diversity considered can lead to varying conclusions regarding the relationship between SH and biodiversity.

In consideration of the sampling design, often referred to as the 'grain effect,' it is evident that the plot size at which data is collected can introduce uncertainties in the SVH. Matching field data specifically designed to align with the on-ground pixel footprint of sensors presents significant challenges (Hauser et al., 2021a; Pacheco-Labrador et al., 2022). Despite challenges, studies conducted by Rocchini et al. (2004) and Oldeland et al. (2010) have demonstrated that as the spatial scale of analysis increases, a stronger correlation between SH and species richness emerges. Thus, the grain effect, as it is often referred to, becomes a significant source of uncertainty in the context of the SVH.

7. Future perspectives

In the context of our comprehensive review, it becomes evident that while numerous studies have highlighted the potential of SH as a proxy for biodiversity, a multitude of factors influence these metrics. These factors, as elaborated in section 6 of our review 'Uncertainties related to the SVH', introduce various uncertainties into the relationship between SH and biodiversity. To advance the understanding of this relationship and to move towards the development of a more robust methodological framework for biodiversity monitoring from optical remote sensing data, there is a pressing need for systematic investigations that encompass all these uncertainties. We propose that future research efforts focus on larger geographic regions that meticulously consider the inter-connectivity of factors contributing to uncertainty in the SVH. To facilitate a comprehensive analysis, it may be beneficial to initiate this research with virtual data that encapsulates the entire optical spectrum, subsequently, these experiments can be replicated using real field data. Furthermore, considering different sensors, spectral platforms, and data sources will contribute to a more comprehensive understanding of the complexities inherent in the SVH and its applicability as a biodiversity monitoring tool.

7.1. Trade-offs in the data resolutions for biodiversity estimations

Due to technical constraints, designing a sensor involves achieving a compromise among the resolution of the three dimensions of remote sensing data, i.e., spatial, spectral and temporal. Moreover, while our review has acknowledged the significance of the three different dimensions encompassing remote sensing data when testing the SVH, the questions remain: which dimension should be prioritized? And are there inherent trade-offs between the resolutions in estimating plant diversity via SH? Answering these questions remains speculative (Cawse-Nicholson et al., 2023); no study has comprehensively analyzed the trade-offs among resolutions of remote sensing data for biodiversity estimation. To the best of our knowledge, only Gamon et al. (2020) considered simultaneously the importance of spatial, spectral, and temporal resolution. The majority of the SVH studies have highlighted the relevance of spatial resolution for establishing a robust connection between plant diversity and the SH. At the same time, our review suggests that spectral resolution is less prominent compared to temporal and spatial dimensions. Nevertheless, innovative SH methodologies have emerged for estimating local diversity using coarse satellite data, holding promise in addressing the constraints of coarse spatial resolution of hyperspectral sensors by capitalizing on high spectral resolution (Rossi and Gholizadeh, 2023). Furthermore, finer spatial resolution does not systematically benefit remote sensing applications (section 4). Consequently, a critical avenue for future research involves investigating whether varying combinations

of resolutions could lead to similar results. Conducting a comprehensive study within the three-dimensional space of remote sensing data would hold significant importance for guiding the development of future sensors.

7.2. Spectral diversity: One piece of the puzzle

In addition to future directions in spectral diversity research, challenges stemming from space-related factors will persist (Hauser et al., 2021b). Addressing these ongoing limitations reveals that spectral diversity cannot function as a standalone predictor of plant diversity. Similarly, Cavender-Bares et al. (2022) argue that the promise of remote sensing data capabilities should be tempered by the recognition that the patterns of variation they reveal do not translate to processes and mechanisms without integration of knowledge of biological, biogeographic, and anthropogenic processes across spatial and temporal scales. Spectral diversity needs to be seen as one piece of the puzzle and using it alone to estimate plant diversity is reductive given the broad potential of spaceborne remote sensing (Lausch et al., 2016; Zellweger et al., 2019). Besides products derived from optical sensors, thermal, and structural diversity components of plant communities could also be crucial for their diversity estimations (Deák et al., 2021; Zellweger et al., 2019). Therefore, identifying and incorporating data products from imaging spectroscopy and other spaceborne sensors, like Light Detection and Ranging (LiDAR), Synthetic Aperture Radar and thermal sensors, into a single application to estimate plant diversity accurately is an exciting and challenging area for future research.

Particularly, the incorporation of data from LiDAR presents an interesting possibility for further investigation. The concept of integrating structural information has indeed been tested successfully. Different studies (Torresani et al., 2020; Tamburlin et al., 2021) explored, in various ecosystem (e.g. grassland, forest) the relationship between structural heterogeneity, derived from the variability of LiDAR data collected by airborne (Torresani et al., 2020) and spaceborne sources (e.g., GEDI instrument (Torresani et al., 2023b)) as well from photogrammetric UAV (Torresani et al., 2024), and species diversity, yielding positive results. This approach was subsequently termed the 'Height Variation Hypothesis' (HVV) stating that the higher the height heterogeneity HH of a considered ecosystem (e.g. forest ecosystem) derived from LiDAR data the higher the species diversity. This hypothesis is supported by various ecological studies (Guo et al., 2017; Lindenmayer et al., 2000; Moudry et al., 2023; Alvites et al., 2021; Kissling and Shi, 2023) that state that the more complex the vertical structure of a given ecosystem the higher the HH, which means that a higher number of potential habitats and niches can host a greater diversity of plant species, as well as animal species like birds. Furthermore, it is worth noting that topographic heterogeneity, derived from LiDAR-derived digital terrain models, can also serve as an indirect proxy to explain biodiversity (see the work on geodiversity from Record et al. (2020) and Cavender-Bares et al. (2020)). This concept finds support in various ecological studies (Badgley et al., 2017; Antonelli et al., 2018; Fjeldsø et al., 2012), emphasizing that complex topographic areas, such as mountain ecosystems, create diverse habitats where animal and vegetation species evolve and diversify.

7.3. Beyond plant diversity

From the challenges of plant diversity estimation, another more general question arises as to whether the SH should not be better used for biodiversity estimation beyond plant species. Spectral diversity excels in capturing the heterogeneity of different surfaces (water, soil, rock, non-photosynthetic vegetation, burned patches, and plant functional types), making it a potential tool for biodiversity beyond plant species. In particular, invertebrate diversity could be linked more than

plant diversity to habitat heterogeneity (Krauss et al., 2003; Kerr et al., 2001). The otherwise confounding effect of non-vegetated areas in remotely sensed plant diversity estimation could positively affect the estimation of insect diversity since many are commonly found in non-vegetated areas like ponds, bare soil, and rocks (Samways et al., 2020; Gobbi et al., 2021). This idea is consistent with the SVH, but studies testing the feasibility of SH to estimate insect diversity at different spatial scales remain sparse offering future research avenues.

Exploring SH beyond plant diversity unveils its potential for broader biodiversity estimates, including invertebrate diversity which correlates with habitat heterogeneity (Krauss et al., 2003; Kerr et al., 2001). This is crucial as spectral diversity captures varied surfaces (water, soil, rock, etc.), beneficial for assessing non-vegetated habitats where many invertebrates thrive (Samways et al., 2020; Gobbi et al., 2021). This aligns with the SVH and introduces 'surrogacy' in biodiversity estimation, where certain biodiversity components serve as proxies for others, a concept advanced by Magurran (2021) and further discussed in the context of geodiversity (Record et al., 2020; Cavender-Bares et al., 2020) offering a nuanced understanding of habitat complexity influencing biodiversity, yet literature on SH's applicability to insect diversity across scales is scant, presenting ripe avenues for future research.

8. Conclusions

The recent surge of interest within the research community in the SVH, which has developed over the last few decades, underscores its growing reputation as a potential approach for estimating biodiversity from various angles, particularly for quickly estimating biodiversity in remote and challenging-to-access areas or as a first-guide for field sampling. In this review, we highlighted the SVH characteristics studied in the last decade: the ecosystems where the SVH has been recently tested, the characteristics of the optical data used to test the SVH, the heterogeneity indices used to assess the SH, the field data characteristics and the new considered approaches. Additionally, the uncertainties, which give rise to potential drawbacks and pitfalls, were analyzed and should be carefully considered in the context of its application. Finally, we examined future perspectives that call for comprehensive and systematic studies, considering the interconnected factors such as ecosystems, optical data, field and heterogeneity indices, and various approaches to address the challenges associated with the application of the SVH.

The adoption of the SVH is closely linked to remote sensing programs like the Copernicus program (Aschbacher, 2017) and the active participation of esteemed space agencies such as ESA and NASA. However, it is crucial to underscore that, despite these commendable initiatives and various global efforts and environmental regulations aimed at biodiversity monitoring and protection, there is a pressing need for further action. Increased financial support from policymakers is imperative, as funding in this crucial area remains insufficient (Skidmore et al., 2021; Tranquilli et al., 2012). Moreover, while open data policies are increasingly expected for publication, especially in reputable journals, there remains a critical shortage of accessible venues or archives for openly publishing the extensive volumes of data associated with the complexity of this topic (Buchanan et al., 2018; Rocchini and Neteler, 2012a). Strengthening an 'open data source policy' that extends beyond data producers to include the research community is imperative. Furthermore, fostering stronger collaboration between ecologists and Earth observation experts is essential for advancing research in this field (Randin et al., 2020).

Data availability

Table

Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Aneece, IP; Epstein, H; Lerdaun, M (2017) Correlating species and spectral diversities using hyperspectral remote sensing in early-successional fields	Agricultural ecosystem (Abandoned agricultural fields, Blandy Experimental Farm, Shenandoah Valley, Clarke County Virginia, USA)	Field, hyperspectral data	Assess the relationship between vegetation species diversity and spectral diversity. Estimate how the relationship change by spectral region and by intraspecific and interspecific variabilities in pigments	Positive correlations in the visible regions using band depth data, positive correlations in the near-infrared region using first derivatives of spectra, and weak correlations in the red-edge region using the two spectral transformation techniques	Standard deviation	Shannon's H	h
Arekhi, M., Yilmaz, O. Y., Yilmaz, H., & Akyüz, Y. F. (2017). Can tree species diversity be assessed with Landsat data in a temperate forest?. Environmental monitoring and assessment, 189, 1-14.	Forest ecosystem (temperate forest in the Gönen dam watershed area, northeast part of the Kazdağı Mountain, Turkey)	Satellite, Landsat 8	To investigate the relationship between alpha diversity of trees and spectral variables derived from Landsat data in a temperate forest, along with exploring the connection between beta diversity and remotely sensed data using species composition and spectral distance similarity	NDVI and spectral variables are effective for assessing forest physiological changes and estimating plant diversity, with potential for habitat diversity analysis, while emphasizing the need to consider tree species differences in spectral patterns.	NDVI, greenness, DVI, EVI (alpha), Jaccard coefficient (beta)	Species richness, Shannon's H, Simpson's D	h
Asner, G. P. (2015). Organismic remote sensing for tropical forest ecology and conservation1, 2. Annals of the Missouri Botanical Garden, 100(3), 127-140.	NA	NA	Address the scientific challenges associated with understanding tropical forests, particularly in terms of monitoring forest cover, composition, carbon content, and biodiversity	NA	NA	NA	NA
Asner, G. P., & Martin, R. E. (2009). Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. Frontiers in Ecology and the Environment, 7(5), 269-276.	Forest ecosystem (lowland Hawaiian rainforests - USA)	Airborne, hyperspectral data	To introduce the concept of "spectranomics" and demonstrate the link between chemical, spectral, and taxonomic diversity in tropical forest canopies to facilitate more accurate and comprehensive biodiversity mapping.	Development of a conceptual framework and prototype airborne instrumentation, termed "spectranomics," which integrates high-resolution imaging spectroscopy and light detection and ranging (lidar) technologies to map tropical forest canopy diversity based on chemical and spectral signatures	NA	NA	NA
Asner, G. P., & Martin, R. E. (2011). Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest. New Phytologist, 189(4), 999-1012.	Forest ecosystem (lowland tropical forest - Peru)	Field, hyperspectral data	To integrate phylogenetic, chemical, and spectral properties of canopies to determine the degree of phylogenetic organization of canopy chemical traits across soil types and assess the quantitative linkage between chemical constituents and canopy spectroscopy, testing the "spectranomics" concept.	Canopy chemistry and spectroscopy reveal insights into tropical forest community assembly, with high variation in chemical traits among taxa, linking remote sensing to evolutionary and ecological processes.	Coefficient of Variation	NA	NA
Badourdine, C; Feret, JB; Pelissier, R; Vincent, G (2022) Exploring the link between spectral variance and upper	Tropical forest (French Guiana)	Field, hyperspectral data	Explore the relationship between spectral variance and taxonomic diversity in forest ecosystem	The correlation between total variance and taxonomic diversity was relatively weak, while the interspecies variance	Spectral Variance	Species richness, Shannon's H and Simpson's D	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
canopy taxonomic diversity in a tropical forest: influence of spectral processing and feature selection Baldeck, C. A., & Asner, G. P. (2013). Estimating vegetation beta diversity from airborne imaging spectroscopy and unsupervised clustering. <i>Remote Sensing</i> , 5(5), 2057-2071.	Savannah (Kruger National Park - South Africa)	Airborne, hyperspectral data	Develop a method for estimating beta diversity evaluating unsupervised methods for estimating species turnover, and comparing these with supervised species classification approaches	and taxonomic diversity were strongly correlated Unsupervised method based on k-means clustering of crown spectra can effectively estimate beta diversity among sites without the need for training data	Bray-Curtis	NA	NA
Blanco-Sacristán, J., Panigada, C., Tagliabue, G., Gentili, R., Colombo, R., Ladrón de Guevara, M., ... & Rossini, M. (2019). Spectral diversity successfully estimates the α -diversity of biocrust-forming lichens. <i>Remote Sensing</i> , 11(24), 2942.	Biocrust community, mixture of lichens and mosses (Aranjuez, central Spain)	Field, hyperspectral data	Assess alpha diversity of lichens in biocrust community	Positive correlations between spectral heterogeneity assessed through specific heterogeneity indices and species diversity indices of lichens (Simpson index correlate the better with spectral heterogeneity) The book enhances understanding of biodiversity via remote sensing across biology, ecology, and geography, aiming to detect plant diversity with different remote sensing data. It proposes a global biodiversity monitoring framework, addressing spectral detection, technical challenges, and scale integration.	Coefficient of variation, standard deviation	Species richness, Shannon's H, Simpson's D, Pielou	h
Cavender-Bares, J., Gamon, J. A., & Townsend, P. A. (2020). <i>Remote sensing of plant biodiversity</i> (p. 581). Springer Nature.	NA	NA	NA		NA	NA	NA
Chaurasia, A. N., Dave, M. G., Parmar, R. M., Bhattacharya, B., Marpu, P. R., Singh, A., & Krishnayya, N. S. R. (2020). Inferring species diversity and variability over climatic gradient with spectral diversity metrics. <i>Remote Sensing</i> , 12(13), 2130.	Forest (India)	Airborne, hyperspectral data	Assess alpha diversity (tree species diversity)	Positive relationship between spectral heterogeneity (calculated through Convex hull index) and tree species diversity	Convex hull	Species richness	h
Chitale, V. S., Behera, M. D., & Roy, P. S. (2019). Deciphering plant richness using satellite remote sensing: a study from three biodiversity hotspots. <i>Biodiversity and Conservation</i> , 28(8), 2183-2196.	Different habitats, mixed wet evergreen, dry evergreen, deciduous, and mountain forests (Himalaya, Indo-Burma, Western Ghats, India)	Satellite, Landsat TM	Assess vegetation species richness	The variance explained by different models varied according to the spectral index applied and the type of life-form considered. Adding physiographic indices such as altitude, slope, and aspect increased the variance explained by the models	NDVI, EVI, MSAVI2, NDWI	Species richness	h
Chraibi, E., Arnold, H., Luque, S., Deacon, A., Magurran, A.	Agro-forest ecosystem (Northern Range of	Satellite, Sentinel-2	Assess tree alpha and beta diversity	No direct correlations between diversity	Exponential Shannon's H (alpha). Bray-Curtis (beta)	Exponential Shannon's H (alpha). Bray-Curtis (beta)	l

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
E., & Féret, J. B. (2021). A remote sensing approach to understanding patterns of secondary succession in tropical forest. <i>Remote Sensing</i> , 13(11), 2148.	Trinidad and Tobago, West Indies)			indices based on field and RS data. However, RS-derived Bray-Curtis dissimilarity better captured the turnover in composition with age difference between sites, showing potential for the identification of a gradient of regeneration in abandoned agroforests			
Chraïbi, E., de Boissieu, F., Barbier, N., Luque, S., & Féret, J. B. (2022). Stability in time and consistency between atmospheric corrections: Assessing the reliability of Sentinel-2 products for biodiversity monitoring in tropical forests. <i>International Journal of Applied Earth Observation and Geoinformation</i> , 112, 102884.	Tropical forest (Cameroon)	Satellite, Sentinel-2	Perform a comparative examination of atmospheric correction methods applied to Sentinel-2 images in the context of monitoring tropical forests. Evaluate the consistency of spectral diversity metrics computed through different correction techniques	Spectral diversity metrics, which are related to biodiversity assessment, were consistent through time for all tested atmospheric correction methods	Shannon's H (alpha). Bray-Curtis (beta)	NA	NA
Conti, L., Malavasi, M., Galland, T., Komárek, J., Lagner, O., Carmona, C. P., ... & Šímová, P. (2021). The relationship between species and spectral diversity in grassland communities is mediated by their vertical complexity. <i>Applied Vegetation Science</i> , 24(3).	Grassland ecosystem, mesic meadow (South Bohemia, Czech Republic)	UAV, multispectral data	Assess the relationship between spectral and vegetation species diversity estimating the influence of vegetation structure complexity	Significant but negative correlation between spectral heterogeneity and taxonomic diversity. Vegetation vertical complexity in grassland ecosystems influences the above-mentioned relationship	Mean Euclidean distance	Shannon's H	m
Da Re, D., De Clercq, E. M., Tordoni, E., Madder, M., Rousseau, R., & Vanwambeke, S. O. (2019). Looking for ticks from space: Using remotely sensed spectral diversity to assess <i>Amblyomma</i> and <i>Hyalomma</i> tick abundance. <i>Remote Sensing</i> , 11(7), 770.	Different habitats (Benin, West Africa)	Satellite, MODIS	Assess environmental and species tick diversity	Positive relationships between spectral diversity indices and abundance of some tick species	Variance, entropy, contrast, Rao's Q	Abundance	l
Dahlin, K. M. (2016). Spectral diversity area relationships for assessing biodiversity in a wildland-agriculture matrix. <i>Ecological applications</i> , 26(8), 2758-2768.	Different habitats (mixture of agricultural lands, forests, and lakes) in southwestern Michigan, USA	Airborne, hyperspectral data (AVIRIS)	Assess the applicability of community assembly theory concepts to imaging spectroscopy, to explore spectral diversity-area relationships and the Functional Attribute Representation approach in differentiating between forest patches and agricultural fields.	The study applies community assembly theory to imaging spectroscopy, distinguishing between strongly filtered agricultural fields and near-random mesic forests in a wildland-agriculture matrix. The spectral diversity-area relationships provide insights into landscape-level diversity	Sum of the variance in the first three PCs, convex hull volume	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
				patterns, demonstrating the method's potential in diverse ecosystems.			
Fassnacht, F. E., Müllerová, J., Conti, L., Malavasi, M., & Schmidtlein, S. (2022). About the link between biodiversity and spectral variation. <i>Applied Vegetation Science</i> , 25(1), e12643.	NA	NA	Review of several empirical studies where the SVH has been tested, highlighting the uncertainties and limiting factors of the SVH.	NA	NA	NA	NA
Féret, J. B., & Asner, G. P. (2014). Mapping tropical forest canopy diversity using high fidelity imaging spectroscopy. <i>Ecological Applications</i> , 24(6), 1289-1296.	Tropical forest (Peruvian Amazon)	Airborne, hyperspectral data	Description of the spectral species concept for the estimation of plant alpha and beta diversity	Alpha and beta diversity of spectral species positively correlated with field data in humid tropical forests	Shannon's H (alpha). Bray-Curtis (beta)	Shannon's H (alpha). Bray-Curtis (beta)	h
Féret, J. B., & de Boissieu, F. (2020). biodivMapR: An R package for alpha and beta diversity mapping using remotely sensed images. <i>Methods in Ecology and Evolution</i> , 11(1), 64-70.	Theoretical description and a case study in tropical forest (Cameroon)	Satellite, Sentinel-2	Introduction of the new R biodivMapR package for the assessment of alpha and beta diversity through remote sensing data	NA	NA	NA	NA
Frye, H. A., Aiello-Lammens, M. E., Euston-Brown, D., Jones, C. S., Kilroy Mollmann, H., Merow, C., ... & Silander Jr, J. A. (2021). Plant spectral diversity as a surrogate for species, functional and phylogenetic diversity across a hyper-diverse biogeographic region. <i>Global Ecology and Biogeography</i> , 30(7), 1403-1417.	Different habitats (Greater Cape Floristic Region - Africa)	Field, hyperspectral data	Assess the relationship between vegetation diversity and spectra, phylogenetic and functional diversity over different biomes	The relationship between spectral and species diversity hold true for some distance-based spectral diversity indices. Furthermore it changes between different geographic subregions and biomes	Coefficient of variation, average spectral angle, average spectral information divergence, convex hull area, non-abundance-weighted form of convex hull volume, spectral richness, spectral distance	Shannon's H, species richness	h
Gastauer, M., Nascimento Jr, W. R., Caldeira, C. F., Ramos, S. J., Souza-Filho, P. W. M., & Féret, J. B. (2022). Spectral diversity allows remote detection of the rehabilitation status in an Amazonian iron mining complex. <i>International Journal of Applied Earth Observation and Geoinformation</i> , 106, 102653.	Forest (Mining waste piles - Carajás National Forest, Eastern Amazon, Pará, Brazil)	Satellite, Sentinel-2	Assess the environmental quality of mining waste piles based on spectral diversity from Sentinel-2 data.	The spectral variation of Sentinel-2 can be used to identify environmental gains and losses in forest mining lands under rehabilitation	Species richness, Shannon's H, Simpson's D, functional divergence	LAI, Shannon's H, tree density, basal area, phylogenetic diversity, percentage of native trees, soil organic matter, functional richness, aboveground tree biomass	h
Gholizadeh, H., Dixon, A. P., Pan, K. H., McMillan, N. A., Hamilton, R. G., Fuhlendorf, S. D., ... & Gamon, J. A.	Grassland ecosystem (Joseph H. Williams Tallgrass Prairie Preserve, Oklahoma, USA)	Airborne and satellite (DESI) hyperspectral data	Assess grassland alpha diversity. Understand how the management practices (based on prescribed fire) influence the	The relationship between spectral diversity and species diversity is affected by the species diversity index, by time	Coefficient of variation, convex hull volume, spectral angle mapper.	Shannon's H, Simpson's D, species richness	m for satellite and h for airborne

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
(2022). Using airborne and DESIS imaging spectroscopy to map plant diversity across the largest contiguous tract of tallgrass prairie on earth. Remote Sensing of Environment, 281, 113254.			relationship between spectral diversity and species diversity at different spatial resolution (due to different vectors)	since fire occur and by spatial scale			
Gholizadeh, H., Gamon, J. A., Helzer, C. J., & Cavender-Bares, J. (2020). Multi-temporal assessment of grassland alpha and beta diversity using hyperspectral imaging. Ecological Applications, 30(7), e02145.	Grassland ecosystem (Restored areas, central Platte River ecosystem, south of Wood River in Central Nebraska, USA)	Airborne, hyperspectral data	Assess alpha and beta diversity	High variability in the accuracy of detecting alpha and beta biodiversity over time for all the tested metrics. The use of a series (multi-temporal) of remote sensing observations is recommended to more fully address disturbance, climate variables, and phenology	Coefficient of variation, spectral angle mapper, convex hull volume (alpha). Spectral species concept with Jaccard dissimilarity (beta)	Species richness (alpha). Difference between plant communities (beta)	h
Gholizadeh, H., Gamon, J. A., Townsend, P. A., Zygielbaum, A. I., Helzer, C. J., Hmimina, G. Y., ... & Cavender-Bares, J. (2019). Detecting prairie biodiversity with airborne remote sensing. Remote Sensing of Environment, 221, 38-49.	Grassland ecosystem (Restored areas, central Platte River ecosystem, south of Wood River in Central Nebraska, USA)	Airborne, hyperspectral data	Estimate species diversity of vascular plants in different plots (young and old). Assess the effect of spatial resolution and of flight direction in the relationship spectral heterogeneity and species diversity.	Strong spectral heterogeneity species diversity relationship in the young plots while non-significant one in the old plots. The use of abundance based species diversity indices improve the above mentioned relationship. The higher the spatial resolution, the higher the accuracy of the relationship	Coefficient of variation	Species richness, Shannon's H	h
Gholizadeh, H., Gamon, J. A., Zygielbaum, A. I., Wang, R., Schweiger, A. K., & Cavender-Bares, J. (2018). Remote sensing of biodiversity: Soil correction and data dimension reduction methods improve assessment of alpha diversity (species richness) in prairie ecosystems. Remote sensing of environment, 206, 240-253.	Grassland ecosystem (Prairie grassland, Cedar Creek Ecosystem Science Reserve, Minnesota, USA)	Field and airborne hyperspectral data	Investigate the impact of soil exposure on spectral diversity. Test various heterogeneity indices. Assessed the impact of spatial resolution on spectral diversity metrics.	Removing the soil-induced effects on spectral diversity metrics increases the relationship between spectral heterogeneity and species diversity. The tested heterogeneity metrics behave differently depending on the spatial resolution and on the degree of soil exposure	Coefficient of variation, convex hull volume, spectral angle mapper, spectral information divergence, convex hull area	Species richness	h for field and airborne
Gillespie, T. W. (2005). Predicting woody-plant species richness in tropical dry forests: a case study from south Florida, USA. Ecological Applications, 15(1), 27-37.	Forest (Tropical dry forest, Florida , USA)	Satellite, Landsat ETM+	Estimate tree species diversity	At the stand level, there was a significant positive relationship between mean NDVI and species richness and a significant negative relationship between species richness and standard deviation of NDVI. Patch area, mean NDVI, and standard deviation in NDVI at the stand level were the best predictors of patch species richness	Mean, standard deviation	Species richness	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Gould, W. (2000). Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. Ecological applications, 10 (6), 1861-1870.	Arctic ecosystem (Hood River Region, Canada)	Satellite, Landsat TM	Estimate vegetation species diversity	The standard deviation of NDVI is positively correlated with species richness and a weighted abundance of mapped vegetation types	Standard deviation, abundance of mapped vegetation types weighted by relative potential species richness	Species richness	h
Hall, K., Johansson, L. J., Sykes, M. T., Reitalu, T., Larsson, K., & Prentice, H. C. (2010). Inventorying management status and plant species richness in semi-natural grasslands using high spatial resolution imagery. Applied Vegetation Science, 13(2), 221-233.	Grassland ecosystem (Semi natural areas, Sweden)	Satellite, Quickbird	Estimate vascular plant species richness and grazing intensity	Significant positive relationships between total within-site species richness and different measures of spectral heterogeneity	Standard deviation, range, spectral richness	Species richness	h
Hall, K., Reitalu, T., Sykes, M. T., & Prentice, H. C. (2012). Spectral heterogeneity of QuickBird satellite data is related to fine-scale plant species spatial turnover in semi-natural grasslands. Applied Vegetation Science, 15(1), 145-157.	Grassland ecosystem (Semi natural areas, Sweden)	Satellite, Quickbird	Estimate fine-scale vegetation species diversity	NDVI showed significant associations with total richness. While the spectral heterogeneity of the NIR band was found positively correlated with species spatial turnover	Mean distance from centroid	Species richness, mean within-site species richness, species spatial turnover	m
Hauser, L. T., Timmermans, J., van der Windt, N., Sil, A. F., de Sá, N. C., Soudzilovskaia, N. A., & van Bodegom, P. M. (2021). Explaining discrepancies between spectral and in-situ plant diversity in multispectral satellite earth observation. Remote Sensing of Environment, 265, 112684.	Different habitats (shrublands, forested areas, and chestnut plantations, Montesinho Natural Park ,Portugal)	Satellite, Sentinel-2	Assess the relationship between spectral (from Sentinel-2 and from simulated spectral through the use of different radiative transfer models), taxonomic, and in-situ trait diversity and confounding factors	Spectral diversity of Sentinel-2 is dominated by variation in vegetation cover (vegetation traits ad soil) that, under specific conditions (e.g. heterogeneity index used) can predict taxonomic diversity	Convex hull volume, Rao's Q	Shannon's H	m
Herkül, K., Kotta, J., Kutser, T., & Vahtmäe, E. (2013). Relating remotely sensed optical variability to marine benthic biodiversity. PLoS One, 8(2), e55624.	Marine environment (Saaremaa Island, eastern Baltic Sea, Estonia)	Airborne, hyperspectral data	Assess diversity of benthic macrophytes and invertebrates	Some coverage-based diversity measures and some biomass-based diversity measures of benthic macrophytes and invertebrates showed low but statistically significant positive correlations with spectral heterogeneity	Mean distance from centroid	Abundances, biomasses	l
Hernández-Stefanoni, J. L., Gallardo-Cruz, J. A., Meave, J. A., Rocchini, D., Bello-Pineda, J., & López-Martínez, J. O. (2012). Modeling alpha-and beta-diversity in a tropical forest from remotely sensed and spatial data. International	Forest (Tropical forest , Yucatan Peninsula, Mexico)	Satellite, Landsat 7	Estimating and mapping of tree alpha and beta diversity	Alpha and beta diversity are related to the reflectance of the red and near infrared bands, the NDVI, and several texture attributes	Three first-order, seven second-order texture measurements (alpha). Bray-Curtis (beta).	Species richness (alpha). Detrended correspondence analysis (beta)	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
journal of applied earth observation and geoinformation, 19, 359-368.							
Heumann, B. W., Hackett, R. A., & Monfils, A. K. (2015). Testing the spectral diversity hypothesis using spectroscopy data in a simulated wetland community. Ecological Informatics, 25, 29-34.	Virtual plots (simulated wetland ecosystem)	Field, hyperspectral data	Estimate vegetation species diversity	Significant relationship between spectral diversity and alpha diversity. The predictive models showed the best results when diversity was calculated through Shannon's index. Including flower spectra in the models led to inconsistent results, as both RMSE and correlation increased	Interquartile range divided by the median for each wavelength	Species richness, Shannon's H, Simpson's D	m
Hoffmann, S., Schmitt, T. M., Chiarucci, A., Irl, S. D., Rocchini, D., Vetaas, O. R., ... & Beierkuhnlein, C. (2019). Remote sensing of β -diversity: Evidence from plant communities in a semi-natural system. Applied Vegetation Science, 22(1), 13-26.	Different habitats (elevational gradient from 45m to 2400 m asl, island of La Palma, Canary Islands, Spain)	Satellite, Sentinel-2	Estimate vegetation beta diversity	The variability of remote sensing data (optical Sentinel-2 data <i>in primis</i> and LiDAR in a lower extent) can be used to assess beta diversity in elevation between different communities	Euclidean distance between plots in a NMDS space	Relative abundance	h
Imran, H. A., Gianelle, D., Scotton, M., Rocchini, D., Dalponte, M., Macolino, S., ... & Vescovo, L. (2021). Potential and limitations of grasslands α -diversity prediction using fine-scale hyperspectral imagery. Remote Sensing, 13(14), 2649.	Grassland ecosystem (Experimental Farm, University of Padova and Monte Bondone site, Italy)	Field, hyperspectral data	Estimate vegetation alpha diversity. Understand how the spatial resolution of the optical information influence the SVH.	The relationship between spectral heterogeneity and species diversity was stronger in the study area characterized by low number of species (best spatial resolution was 1mm) while it was lower in the areas with many species (1 cm was the best spatial resolution)	Coefficient of variation, standard deviation	Species richness, Shannon's H, Simpson's D, evenness	m
Jackson, J., Lawson, C. S., Adelmant, C., Huhtala, E., Fernandes, P., Hodgson, R., ... & Salguero-Gómez, R. (2022). Short-range multispectral imaging is an inexpensive, fast, and accurate approach to estimate biodiversity in a temperate calcareous grassland. Ecology and Evolution, 12(12), e9623.	Grassland ecosystem (calcareous grassland in the Upper Seeds field site in Wytham woods, Oxfordshire, UK)	UAV, multispectral data	Evaluate the utility of coarse multispectral imaging from UAVs in estimating plant biodiversity at a fine spatial resolution in a temperate calcareous grassland	Multispectral imaging from commercially available UAVs, provides a cost-effective and high-resolution method for estimating plant biodiversity in a temperate calcareous grassland, showcasing positive associations with biodiversity indices and consistent repeatability across sampling days and heights.	Coefficient of variation, standard deviation, skewness, kurtosis	Species richness, Shannon's H, Simpson's D	NA
Jung, M. (2022). Predictability and transferability of local biodiversity environment relationships. PeerJ, 10, e13872.	Different ecosystem from the Global Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) database	Satellite, MODIS	Assess the global predictability and transferability of model-based predictions for local biodiversity-environment relationships, expecting stronger predictability than transferability and examining variations across biodiversity	In the relationship between spectral heterogeneity and biodiversity, considerable transferability errors emphasize the need for caution in interpreting and applying such relationships, with taxonomic differences and	Mean Euclidean distance to PCA centroid	Total Species richness, total log-transformed abundance, the arcsine square root transformed probability of interspecific encounter as measure of assemblage evenness, logit transformed pairwise	l

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
			measures and taxonomic groups, utilizing data from diverse surveys and advanced modelling techniques.	sampling completeness influencing prediction accuracy.		Sørensen similarity index as measure of difference in assemblage composition	
Kacic, P., & Kuenzer, C. (2022). Forest Biodiversity Monitoring Based on Remotely Sensed Spectral Diversity—A Review. Remote Sensing, 14(21), 5363.	NA	NA	Review of spectral diversity for assessment of biodiversity in forest ecosystems	NA	NA	NA	NA
Khare, S., Latifi, H., & Ghosh, S. K. (2018). Multi-scale assessment of invasive plant species diversity using Pléiades 1A, RapidEye and Landsat 8 data. Geocarto international, 33(7), 681-698.	Forest (Moist deciduous forests, Doon valley, Himalaya, Uttarakhand, India)	Satellite, Pléiades 1A, RapidEye and Landsat 8 OLI	Assess vegetation species diversity in areas affected by invasive species (L. camara) using spectral heterogeneity information extracted from optical data.	Spectral heterogeneity is a proxy for assessing species diversity in areas invaded by invasive species (L. camara) using Landsat-8 OLI, RapidEye, and Pléiades1A data. Results show that higher spatial resolution improves invasive species diversity approximation	Coefficient of variation, Simpson's D, Shannon's H, Renyi	NA	NA
Khare, S., Latifi, H., & Rossi, S. (2019). Forest beta-diversity analysis by remote sensing: How scale and sensors affect the Rao's Q index. Ecological Indicators, 106, 105520.	Forest (Moist deciduous forests, Doon valley, Himalaya, Uttarakhand, India)	Satellite, Pléiades 1A, RapidEye and Landsat 8 OLI	Assess vegetation beta diversity using different heterogeneity indices and optical remote sensing data at different spatial resolution	Vegetation diversity was better approximated by Rao's Q index than Shannon's index in heterogeneous forest environments. Rao's Q index showed a strong scale and spatial resolution dependence on the spectral information	Rao's Q, Shannon's H	NA	NA
Khare, S., Latifi, H., & Rossi, S. (2021). A 15-year spatio-temporal analysis of plant beta-diversity using Landsat time series derived Rao's Q index. Ecological Indicators, 121, 107105.	Forest (Moist deciduous forests, Doon valley, Himalaya, Uttarakhand, India)	Satellite, Landsat 8	Assess vegetation beta diversity using the Rao's Q index with two vegetation indices (MSAVI and NDVI)	Spatiotemporal beta-diversity was assessed using multi-temporal Rao's Q derived from two vegetation indices (MSAVI and NDVI) and environmental factors (temperature and precipitation)	Rao's Q	NA	NA
Laliberté, E., Schweiger, A. K., & Legendre, P. (2020). Partitioning plant spectral diversity into alpha and beta components. Ecology Letters, 23(2), 370-380.	Virtual simulated area and Forest (Bartlett Experimental Forest , USA)	Airborne, hyperspectral data	Measure alpha, beta and gamma diversity in virtual areas and in forest ecosystem	introduction a novel method to partition plant spectral gamma-diversity (region-wide spectral diversity) into alpha-diversity (within community) and beta-diversity (among community) components. This approach, enables the identification of prominent spectral features. Additionally, it allows the assessment of individual plant communities' contributions to spectral diversity	Spectral Variance (alpha, beta and gamma)	NA	NA
Levin, N., Shmida, A., Levanoni, O., Tamari, H., & Kark, S. (2007). Predicting mountain plant richness and rarity from	Forest (open mediterranean forest, Mount Hermon, Israel, Lebanon, Syria)	Satellite, Landsat 7, Aster, and QuickBird	Estimate diversity, richness and rarity of vascular vegetation	Positive significant correlation between plant species richness and spectral heterogeneity of NDVI. The relative range size	Mean, standard deviation, coefficient of variation	Species richness, relative range size, rarity	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
space using satellite-derived vegetation indices. Diversity and Distributions, 13(6), 692-703.				rarity was negatively correlated with NDVI			
Liccari, F., Sigura, M., & Bacaro, G. (2022). Use of Remote Sensing Techniques to Estimate Plant Diversity within Ecological Networks: A Worked Example. Remote Sensing, 14(19), 4933.	Different habitats (intensively and extensively cultivated areas, settlements, semi-natural, and natural habitats, biotopes, wetland areas, Friuli Venezia Giulia region, Italy)	Satellite, Sentinel-2	Assess vegetation alpha and beta diversity	Effectiveness of assessing alpha and beta diversity and environmental heterogeneity using the SVH in particular in areas highly biodiverse	Species richness, Shannon's H, Rao's Q (alpha), Bray-Curtis (beta)	Ratio of alien to native species richness, Shannon's H by land use category (alpha). Transformation-based Redundancy Analysis based on Hellinger distance (beta)	h
Lopes, M., Fauvel, M., Ouin, A., & Girard, S. (2017). Spectro-temporal heterogeneity measures from dense high spatial resolution satellite image time series: Application to grassland species diversity estimation. Remote Sensing, 9 (10), 993.	Grassland ecosystem (South West France)	Satellite, Spot 5	Assess vegetation species diversity	Proposal of a new spectral heterogeneity measure based on Spectral clustering. Low correlation between Spectral Heterogeneity indices and Shannon's H maybe due to spectral and spatial resolution of the used images	Spectral clustering algorithm, mean distance from centroid, entropy	Shannon's H	l
Louail, A., Messner, F., Djellouli, Y., & Gharzouli, R. (2022). Remote Sensing and Phytoecological Methods for Mapping and Assessing Potential Ecosystem Services of the Ouled Hannèche Forest in the Hodna Mountains, Algeria. Forests, 13(8), 1159.	Forest (Ouled Hannèche, Algeria)	Satellite, Landsat 8	Characterization and mapping of ecosystem services through the spectral variation and morphological variation	The spectral variation of optical images is considered a proxy for topo-morphological heterogeneity, an input variables of a quantitative map of the potential ecosystem services provided by the forest	Rao's Q , Shannon's H	NA	NA
Madonsela, S., Cho, M. A., Ramoelo, A., & Mutanga, O. (2017). Remote sensing of species diversity using Landsat 8 spectral variables. ISPRS Journal of Photogrammetry and Remote Sensing, 133, 116-127.	Savannah (Mpumalanga and Limpopo provinces of South Africa)	Satellite, Landsat 8	Assess tree species diversity	Significant positive relationship between vegetation indices and measures of tree species diversity	Mean, standard deviation, range, coefficient of variation, entropy, variance, dissimilarity	Species richness, Shannon's H and Simpson's D	m
Malavasi, M., Bazzichetto, M., Komárek, J., Moudrý, V., Rocchini, D., Bagella, S., ... & Carranza, M. L. (2021). Unmanned aerial systems-based monitoring of the eco-geomorphology of coastal dunes through spectral Rao's Q. Applied Vegetation Science, 24(1), e12567.	Coastal habitat (Coastal dune landscape, Tyrrhenian coast, Lazio region, Central Italy)	UAV, multispectral data	Monitor the eco-geomorphological integrity of coastal dune ecosystems	Spectral heterogeneity assessed with Rao's Q index can quantify the differences in the eco/geomorphological heterogeneity among different coastal areas that have different level of anthropogenic pressure	Rao's Q	Low and high human pressure coastal beaches	NA
Mapfumo, R. B., Murwira, A., Masocha, M., & Andriani, R. (2016). The relationship	Savanna (dry, wet and coastal savanna woodlands, Zimbabwe,	Satellite, Landsat 8 and Worldview 2	Assess the relationship between spectral diversity and tree species diversity.	The relationships between diversity and spectral variation of NDVI holds true in different	Coefficient of variation	Shannon's H and Simpson's D	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
between satellite-derived indices and species diversity across African savanna ecosystems. International journal of applied earth observation and geoinformation, 52, 306-317. Marzialetti, F., Cascone, S., Frate, L., Di Febbraro, M., Acosta, A. T. R., & Carranza, M. L. (2021). Measuring Alpha and Beta Diversity by Field and Remote-Sensing Data: A Challenge for Coastal Dunes Biodiversity Monitoring. Remote Sensing, 13(10), 1928.	Zambia and Mozambique)			ecosystems following a linear and/or hump-shaped relationship			
Marzialetti, F., Di Febbraro, M., Malavasi, M., Giulio, S., Acosta, A. T. R., & Carranza, M. L. (2020). Mapping coastal dune landscape through spectral Rao's Q temporal diversity. Remote Sensing, 12 (14), 2315.	Coastal habitat (Coastal dune landscape, Tyrrhenian coast, Lazio region, Central Italy)	Satellite, PlanetScope	Assess vegetation alpha and beta diversity	Positive relationship between alpha diversity (in particular with species richness) and spectral heterogeneity. Negative significant relationship between beta diversity and spectral heterogeneity (higher decay rates obtained with Bray-Curtis floristic dissimilarity)	Mean Distance from centroid (alpha). Pairwise multivariate Euclidean distance (beta)	Species richness, Shannon's H, Simpson's D (alpha). Jaccard similarity and Bray-Curtis (beta)	m
Michele, T., Duccio, R., Marc, Z., Ruth, S., & Giustino, T. (2018, July). Testing the spectral variation hypothesis by using the RAO-Q index to estimate forest biodiversity: Effect of spatial resolution. In IGARSS 2018-2018 IEEE International Geoscience and Remote Sensing Symposium (pp. 1183-1186). IEEE.	Coastal habitat (Coastal dune landscape, Adriatic coast of Molise region, Central Italy)	Satellite, Sentinel-2	Land cover classification based on the within-year temporal spectral diversity	The proposed methodology showed effective results in the land cover map of heterogeneous landscape as coastal dunes	Rao's Q	NA	h
Möckel, T., Dalmayne, J., Schmid, B. C., Prentice, H. C., & Hall, K. (2016). Airborne hyperspectral data predict fine-scale plant species diversity in grazed dry grasslands. Remote Sensing, 8 (2), 133.	Forest (Alpine coniferous forest, Province of Bolzano/Bozen, Italy)	Satellite, Sentinel-2 and Landsat 8	Estimate the relationship between spectral diversity and tree species diversity. Test the effect of spatial resolution	Spatial resolution affects the correlation between spectral heterogeneity and species diversity in an alpine coniferous forest (10m of Sentinel-2 perform better than 30m of Landsat 8)	Rao's Q	Shannon's H	h
Mohapatra, J., Singh, C. P., Hamid, M., Khuroo, A. A., Malik, A. H., & Pandya, H. A. (2019). Assessment of the alpine plant species biodiversity in the western Himalaya using Resourcesat-2 imagery and field survey.	Grassland ecosystem (Baltic island of Öland, Sweden)	Airborne, hyperspectral data	Estimate vegetation species diversity in dry, grazed grassland ecosystems. Assess the effect of environmental conditions in the relationships	Species diversity was estimated successfully by the spectral response approach but not with through SVH.	Mean distance from centroid	Species richness, Simpson's D	l
	Grassland ecosystem (alpine zone of the Gulmarg target region, state of Jammu and Kashmir in India)	Satellite, Resourcesat-2	Assess vegetation species diversity at local and landscape level	Spectral variation hypothesis does not hold in the alpine ecosystem of the Himalaya. Species diversity in relation to habitat heterogeneity exhibited an elevation-dependent pattern, with the southern aspect of the sub-alpine zone	Simpon's D, Shannon's H, Pielou's J, Rényi's H	Simpon's D, Shannon's H, Pielou's J, Rényi's H	m

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Journal of Earth System Science, 128, 1-16.				having the highest biodiversity. The paper emphasized the importance of higher spatial resolution satellite data for accurate field-level biodiversity assessments.			
Monteiro, A. T., Alves, P., Carvalho-Santos, C., Lucas, R., Cunha, M., Marques da Costa, E., & Fava, F. (2021). Monitoring Plant Diversity to Support Agri-Environmental Schemes: Evaluating Statistical Models Informed by Satellite and Local Factors in Southern European Mountain Pastoral Systems. Diversity, 14(1), 8.	Grassland ecosystem (Peneda-Gerês mountain range, Portugal)	Satellite, Sentinel-2	Assess vegetation species diversity in mountain grasslands using different approaches including the SVH	The study did not find a relationship between spectral heterogeneity and species richness	Standard deviation	Species richness	l
Mpakairi, K. S., Dube, T., Dondofema, F., & Dalu, T. (2022). Spatial Characterisation of Vegetation Diversity in Groundwater-Dependent Ecosystems Using In-Situ and Sentinel-2 MSI Satellite Data. Remote Sensing, 14(13), 2995.	Different habitat (Khakea-Bray Transboundary Aquifer, Botswana and South Africa)	Satellite, Sentinel-2	Estimate vegetation species diversity. Estimate how plant diversity changes in relation to the availability natural water pans	Spectral heterogeneity measured with the Rao's Q index (calculated using the coefficient of variation of the Sentinel-2 band) is related to species diversity. Higher vegetation diversity was found along roads, fence lines, and rivers, increasing with a decreasing distance from natural water pans	Rao's Q	Shannon's H	h
Mutowo, G., & Murwira, A. (2012). Relationship between remotely sensed variables and tree species diversity in savanna woodlands of Southern Africa. International journal of remote sensing, 33 (20), 6378-6402.	Savannah (Zimbabwe)	Satellite, ASTER	Assess tree species diversity	Significant relationship between the standard deviation of ASTER NIR and tree species diversity (Shannon's H and in particular with Simpson's D)	Standard deviation	Shannon's H, Simpson's D	h
Nagendra, H., Rocchini, D., Ghate, R., Sharma, B., & Pareeth, S. (2010). Assessing plant diversity in a dry tropical forest: Comparing the utility of Landsat and IKONOS satellite images. Remote Sensing, 2(2), 478-496.	Forest (Dry tropical forest, central India)	Satellite, IKONOS and Landsat ETM+	Analyse the relationship between spectral and vegetation species diversity. Assess the effect of spatial resolution	Landsat ETM+ images performs better than IKONOS images for assessing plant abundance and biodiversity	Mean, standard deviation, NDVI, greenness, brightness, wetness, IRI, MIRI	Species richness, Shannon's H, abundance	l
Oindo, B. O., & Skidmore, A. K. (2002). Interannual variability of NDVI and species richness in Kenya. International journal of remote sensing, 23(2), 285-298.	Different habitats (Kenya)	Satellite, AVHRR	Assess species richness of various vascular plants and mammals	Spectral heterogeneity of AVHRR NDVI (measured by standard deviation and coefficient of variation) is correlated positively with species richness	Standard deviation, coefficient of variation	Species richness	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Oldeland, J., Wesuls, D., Rocchini, D., Schmidt, M., & Jürgens, N. (2010). Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity?. Ecological Indicators, 10(2), 390-396.	Savannah (Central Namibia)	Airborne, hyperspectral data	Analyse the relationship between vegetation alpha diversity and spectral diversity	The results showed that on the relationship between ecological and spectral variability, tested at different spatial scale, abundance-based diversity measures (such as Shannon's H index) performed better than indices that accounts only to the number of species (e.g. species richness).	Mean distance from centroid	Species richness, Shannon's H	h
Onyia, N. N., Baltzer, H., & Berrio, J. C. (2019). Spectral diversity metrics for detecting oil pollution effects on biodiversity in the Niger Delta. Remote Sensing, 11 (22), 2662.	Coastal ecosystem (plain and freshwater ecological zone, Delta Niger, Rivers State, Nigeria)	Satellite, Sentinel-2	Evaluate the validity of the SVH against the backdrop of oil pollution impact on biodiversity using vascular plant species as surrogates	Spectral diversity metrics correlated negatively with species data on polluted transects and positively on control transects proved to be sensitive to changes in vegetation characteristics following oil pollution Functional diversity can be determined using both reflectance and optical traits, but not all tested metrics were suitable. Rao's Q index, functional dispersion, and functional richness were the most effective metrics. Spatial resolution was found to be the most critical limitation. Sentinel-2 imagery, outperformed DESIS in estimating plant diversity, aligning with simulation results.	Mean, standard deviation, Shannon's , Simpson's , mean distance from centroid, interquartile range divided by the median for each wavelength	Species richness, Shannon's H, Simpson's D, Menhinick, Chao-1	h
Pacheco-Labrador, J., Migliavacca, M., Ma, X., Mahecha, M., Carvalhais, N., Weber, U., ... & Wirth, C. (2022). Challenging the link between functional and spectral diversity with radiative transfer modeling and data. Remote Sensing of Environment, 280, 113170.	Forests (Mediterranean oak and pine woodland, Spain and mountainous mixed conifer and beech, Romania) and virtual communities	Satellite, Sentinel-2 satellite and DESIS and Simulated data,	Evaluate at different scales, the potential of different functional diversity metrics within the SVH using both synthetic and observational datasets. Testing of different remote sensing information.	Functional richness, evenness, diversity, dispersion, Rao's Q		Species richness, Shannon's H	l for hyperspectral satellite and m for multispectral satellite
Pacheco-Labrador, J., de Bello, F., Migliavacca, M., Ma, X., Carvalhais, N., & Wirth, C. (2023). A generalizable normalization for assessing plant functional diversity metrics across scales from remote sensing. Methods in Ecology and Evolution.	Virtual plots (simulated communities of species)	Virtual hyperspectral and resampled to DESIS and to multispectral Sentinel-2, QuickBird-2	To improve the accuracy of estimating Plant Functional Diversity (PFD) from Remote Sensing (RS) data by proposing a generalizable normalization approach and evaluating its effectiveness in enhancing PFD estimation and comparability across different RS missions.	Proposal and validation of a generalizable normalization approach for Remote Sensing data aiming to improve the comparability of Plant Functional Diversity estimates between remote sensing data and field measurements, addressing issues related to differences in spectral configurations and trait correlations across datasets. The study underscores the effectiveness of integrating Spectral Heterogeneity (SH) measures, especially spectral β -diversity, and multitemporal frameworks for accurate habitat mapping, offering	Spectral Variance, Rao's Q and Functional richness	NA	NA
Pafumi, E., Petruzzellis, F., Castello, M., Altobelli, A., Maccherini, S., Rocchini, D., & Bacaro, G. (2023). Using spectral diversity and heterogeneity measures to map habitat mosaics: An	Different habitats (fine mosaic of natural and semi-natural habitats, with grasslands, downy oak woodland and black pine plantations) in the Classical Karst, a	Satellite, Sentinel-2	Assess an integrated approach for mapping a diverse mosaic of natural and semi-natural habitats using remote sensing, with specific objectives to quantify the significance of spectral heterogeneity measures		Rao's Q index and alpha and beta diversity (spectral species) measured with biodivMapR	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
example from the Classical Karst. Applied Vegetation Science, 26(4), e12762.	limestone plateau in the provinces of Trieste and Gorizia- Italy.		for habitat classification and establish a robust framework for incorporating multitemporal remotely sensed data into habitat classification.	valuable insights into vegetation types in complex landscapes using remote sensing.			
Palmer, M. W., Earls, P. G., Hoagland, B. W., White, P. S., & Wohlgemuth, T. (2002). Quantitative tools for perfecting species lists. Environmetrics: The official journal of the International Environmetrics Society, 13 (2), 121-137.	Grassland ecosystem (Tallgrass Prairie Preserve, Oklahoma, USA)	Airborne, Panchromatic images	Assess biodiversity of vascular plants	Positive and significant relationship between the spectral heterogeneity measured through certain heterogeneity indices at certain spatial scale and vegetation diversity (through three different diversity indices)	Mean distance to the nearest neighbour, mean distance from spectral centroid, leverage	Species richness, number of infrequent species, rarity	m
Pangtey, D., Padalia, H., Bodh, R., Rai, I. D., & Nandy, S. (2023). Application of remote sensing-based spectral variability hypothesis to improve tree diversity estimation of seasonal tropical forest considering phenological variations. Geocarto International, 38(1), 2178525.	Forest ecosystem (Himalayan region of Uttarakhand, India)	Satellite, Sentinel-2	Assess the performance of Spectral Variation Hypothesis (SVH) using Sentinel-2 NDVI data in estimating tree diversity in a seasonal tropical forest, considering the asynchronous phenology of different forest types and exploring the potential of multi-temporal spectral variability for improved tree diversity estimation.	Rao's Q index, based on multi-temporal NDVI data from Sentinel-2, shows a significant correlation with in-situ tree species diversity in tropical seasonal forests, especially during the summer season, demonstrating the potential of this approach for landscape-level tree diversity estimation and monitoring biodiversity changes. The study also emphasizes the importance of considering the phenological variability and different forest types when applying Rao's Q index for diversity assessment.	Rao's Q index	Shannon's H	h
Paz-Kagan, T., Chang, J. G., Shoshany, M., Sternberg, M., & Karnieli, A. (2021). Assessment of plant species distribution and diversity along a climatic gradient from Mediterranean woodlands to semi-arid shrublands. GIScience & Remote Sensing, 58(6), 929-953.	Different ecosystems along a climatic gradient in southeastern Israel, encompassing a Mediterranean climate	Airborne, hyperspectral data	Develop a comprehensive approach based on spectral diversity for mapping species diversity (SD) and richness, investigate their relationships with environmental and human-derived factors, and assess improvements in species identification using different spectral band combinations and canopy texture parameterizations	The study demonstrates the effectiveness of spectral diversity derived from hyperspectral remote sensing data in mapping and analysing local tree and shrub species richness, revealing its potential for assessing biodiversity patterns along a climatic gradient.	Mean, variance, homogeneity, contrast, dissimilarity, entropy, second moment, and correlation	Shannon's H	h
Peng, Y., Feng, J., Sang, W., & Axmacher, J. C. (2022). Geographical divergence of species richness and local homogenization of plant assemblages due to climate change in grasslands. Biodiversity and Conservation, 1-14.	Grassland ecosystem (from the World Database on Protected Areas)	Satellite, Landsat TM	Use spectral plant diversity indices from Landsat images to assess global vascular plant diversity in protected grassland areas, testing hypotheses on the impact of future climate change by investigating trends in plant diversity and beta (β)-diversity.	The study predicts a decline in plant richness in most grasslands, excluding arid steppes, and anticipates a significant decrease in plant spectral β-diversity, indicating a trend toward biotic homogenization under future climate change. Different	Coefficient of variation, MSAVI	Species richness	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Perrone, M., Di Febbraro, M., Conti, L., Divíšek, J., Chytrý, M., Keil, P., ... & Malavasi, M. (2023). The relationship between spectral and plant diversity: Disentangling the influence of metrics and habitat types at the landscape scale. Remote Sensing of Environment, 293, 113591.	Different habitats (Czech Republic)	Landsat 8 OLI	Investigate the applicability of spectral diversity for monitoring plant diversity at the landscape scale by comparing the performance of three types of spectral diversity metrics, taking into account habitat type.	climate variables influence plant diversity across diverse grassland types, emphasizing the importance of considering climatic factors in predicting spectral plant diversity. Both species richness and functional diversity showed positive and significant relationships with each spectral diversity metric tested. However, spectral diversity alone accounted for a small fraction of the deviance explained by the models. Furthermore, the strength of the relationship depended significantly on habitat type and was highest in natural areas with transitional bushy and herbaceous vegetation.	Standard deviation of NDVI, Rao's Q index, Spectral Species richness	Species richness, functional diversity (mean pairwise distance)	h
Polley, H. W., Yang, C., Wilsey, B. J., & Fay, P. A. (2019). Spectral heterogeneity predicts local-scale gamma and beta diversity of mesic grasslands. Remote Sensing, 11(4), 458.	Grassland ecosystem (Mesic grasslands, Temple, central Texas, USA)	UAV, Hyperspectral data	Estimate vegetation beta and gamma diversity in mesic grasslands (having different management) at different spatial scales (plot and patch scales)	Spatial heterogeneity in canopy optical information could explain beta and gamma diversity.	Coefficient of variation	Exponential Shannon's H	h
Rahmanian, S., Nasiri, V., Amindin, A., Karami, S., Maleki, S., Pouyan, S., & Borz, S. A. (2023). Prediction of Plant Diversity Using Multi-Seasonal Remotely Sensed and Geodiversity Data in a Mountainous Area. Remote Sensing, 15(2), 387.	Grassland ecosystem (Dakal-kooch mountainous rangeland-Iran)	Satellite, Landsat 8, Sentinel-2	Assess the impact of temporal dynamics on remote sensing of plant diversity in grasslands, using multi-temporal remotely sensed data, geodiversity features, and in situ measurements.	Significant positive relationship between the CV of vegetation indices, diversity indices (especially Shannon's and Simpson's), and vegetation cover across all three seasons. Mid-spring exhibited the highest correlation between species diversity and the CV of vegetation indices	Coefficient of Variation	Species richness, Shannon's H, Simpson's D, abundance	h
Robertson, K. M., Simonson, E., Ramirez-Bullon, N., Poulter, B., & Carter, R. (2023). Effects of Spatial Resolution, Mapping Window Size, and Spectral Species Clustering on Remote Sensing of Plant Beta Diversity Using bioDivMapR and Hyperspectral Imagery. Journal of Geophysical Research: Biogeosciences, 128 (7), e2022JG007350.	Forest ecosystem (longleaf pine savannah ecosystems, southeastern USA)	Airborne, hyperspectral data	To investigate how the capacity to map beta diversity using bioDivMapR is influenced by spatial resolution, mapping window dimensions, and the number of spectral species,	Optimal spatial resolution, mapping window size, and spectral species clustering significantly affect the capacity to map plant beta diversity, emphasizing the importance of fine spatial resolution for reliable biodiversity mapping	Spectral species	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Rocchini, D. (2007). Effects of spatial and spectral resolution in estimating ecosystem alpha-diversity by satellite imagery. Remote sensing of Environment, 111(4), 423-434.	Wetland ecosystem (Montepulciano Lake, Central Italy)	Satellite, Quickbird, Aster and Landsat ETM+	Effect of spatial resolution in assessment of species diversity of vascular plants	Spectral variability of high spatial resolution information (from Quickbird) was efficient to assess species richness at local scale. Coarse resolution images (from Aster and Landsat ETM+) showed contrasting results. Spectral resolution seemed to play a crucial role in compensating for lacks in spatial resolution.	Mean distance from centroid	Species richness	h
Rocchini, D. (2009). Algorithmic foundation of spectral rarefaction for measuring satellite imagery heterogeneity at multiple spatial scales. Sensors, 9(1), 303-310.	Theoretical description	NA	Explain a new method based on ecological theory for assessing spectral heterogeneity at multiple scales simultaneously	NA	NA	NA	NA
Rocchini, D., & Neteler, M. (2012). Spectral rank–abundance for measuring landscape diversity. International Journal of Remote Sensing, 33 (14), 4458-4470.	Theoretical description and empirical example over 3 Mediterranean areas (Italy)	Satellite, Landsat ETM+	Introduce the rank–abundance diagrams as heterogeneity measure (theoretical introduction and empirical example) for landscape diversity	The proposed metric shows to be a powerful tools for the assessment of landscape diversity	Rank–abundance diagram	NA	NA
Rocchini, D., & Vannini, A. (2010). What is up? Testing spectral heterogeneity versus NDVI relationship using quantile regression. International Journal of Remote Sensing, 31(10), 2745-2756.	Different habitats (Tuscany region, Italy)	Satellite, Landsat ETM+	Assess the relationship between local spectral heterogeneity and NDVI	When the Maximum potential spectral variability is considered, a possible correlation between spectral heterogeneity and NDVI is possible	Standard deviation	NA	NA
Rocchini, D., Balkenhol, N., Carter, G. A., Foody, G. M., Gillespie, T. W., He, K. S., ... & Neteler, M. (2010). Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. Ecological Informatics, 5(5), 318-329.	NA	NA	First review of the SVH	NA	NA	NA	NA
Rocchini, D., Chiarucci, A., & Loiselle, S. A. (2004). Testing the spectral variation hypothesis by using satellite multispectral images. Acta Oecologica, 26(2), 117-120.	Wetland ecosystem, (Montepulciano Lake, central Italy)	Satellite, Quickbird	Estimation of vegetation species diversity	Positive and significant correlation between the spectral heterogeneity and the vegetation species diversity. The correlation was influenced by spatial extent of the studied area	Mean distance from centroid	Species richness	h
Rocchini, D., Dadalt, L., Delucchi, L., Neteler, M., & Palmer, M. W. (2014).	Different habitat (the whole North America)	Satellite, MODIS	Assess vegetation alpha diversity (species richness) and	Positive and significant correlation between spectral diversity and species richness,	Natural logarithm of the spectral richness	Species richness	m

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Disentangling the role of remotely sensed spectral heterogeneity as a proxy for North American plant species richness. Community Ecology, 15(1), 37-43.			the impact of the spatial extent of the study area	however, the highest amount of variance was explained by the spatial extent of the sampling units			
Rocchini, D., Luque, S., Pettorelli, N., Bastin, L., Doktor, D., Faedi, N., ... & Nagendra, H. (2018). Measuring beta diversity by remote sensing: A challenge for biodiversity monitoring. Methods in Ecology and Evolution, 9(8), 1787-1798.	Theoretical description and agroforestry systems (southern Portugal)	Satellite, Sentinel-2	Introduction to different methods for the assessment of beta diversity using remote sensing data	The paper propose different techniques to measure beta diversity from remote sensing optical data: a multivariate statistical analysis, the spectral species concept, a self-organizing feature maps, a multidimensional distance matrices and through the concept behind the SVH using the Rao's Q diversity index. The paper introduces the theory and the application of the Rao's Q index. The spectral heterogeneity calculated with the new index using MODIS images over the whole European regions is showed. The free available R code is presented	Rao's Q	NA	NA
Rocchini, D., Marcantonio, M., & Ricotta, C. (2017). Measuring Rao's Q diversity index from remote sensing: An open source solution. Ecological indicators, 72, 234-238.	Theoretical description and different habitats (case study over the whole Europe)	Satellite, MODIS	Explanation of the Rao's Q heterogeneity index		Rao's Q , Shannon's H	NA	NA
Rocchini, D., Marcantonio, M., Da Re, D., Bacaro, G., Feoli, E., Foody, G. M., ... & Ricotta, C. (2021). From zero to infinity: Minimum to Maximum diversity of the planet by spatio-parametric Rao's quadratic entropy. Global Ecology and Biogeography, 30 (5), 1153-1162.	Theoretical description and different habitats (case study over different habitats in California, USA)	Satellite, Sentinel-2	Parameterization of the Rao's Q heterogeneity index	The paper shows the continuum of potential diversity of the Rao's Q index, in one single formula with a visual example of its properties	Rao's Q	Species richness	NA
Rocchini, D., Marcantonio, M., Da Re, D., Chirici, G., Galluzzi, M., Lenoir, J., ... & Ziv, G. (2019). Time-lapsing biodiversity: An open source method for measuring diversity changes by remote sensing. Remote Sensing of Environment, 231, 111192.	Theoretical description and different habitats (case study over different habitats in Italy)	Satellite, MODIS	Assessment of beta diversity through the use of the Rao's Q index	The paper introduces an innovative approach to calculate spatio-temporal beta diversity by using the temporal variation of the Rao's Q index	Rao's Q	NA	NA
Rocchini, D., McGlinn, D., Ricotta, C., Neteler, M., & Wohlgemuth, T. (2011). Landscape complexity and spatial scale influence the relationship between remotely sensed spectral	Different habitats (biogeographic regions over the whole Switzerland)	Satellite, Landsat ETM+	Assess the correlation between spectral and species accumulation at different spatial scales. Effect of landscape complexity.	The correlation between spectral and species accumulation was positive and significant in complex landscapes while not in simple landscapes	Spectral rarefaction	Species richness	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
diversity and survey-based plant species richness. Journal of Vegetation Science, 22(4), 688-698.							
Rocchini, D., Ricotta, C., & Chiarucci, A. (2007). Using satellite imagery to assess plant species richness: The role of multispectral systems. Applied Vegetation Science, 10(3), 325-331.	Wetland (Montepulciano Lake Natural Reserve, Tuscany- Italy)	Satellite, Quickbird	Testing the hypothesis that, within the SVH, a limited number of bands from a multispectral data set, specifically those known to be good indicators of vegetation biomass and growth, can be potentially useful for accurately estimating local species richness through remote sensing	The main outcome of the study suggests a "near infrared way" to assess plant species richness directly from remotely sensed data, with the Quickbird satellite demonstrating potential for estimating species richness, particularly due to the near-infrared band.	Mean Euclidean distance from the centroid	Species richness	h
Rocchini, D., Salvatori, N., Beierkuhnlein, C., Chiarucci, A., de Boissieu, F., Förster, M., ... & Féret, J. B. (2021). From local spectral species to global spectral communities: A benchmark for ecosystem diversity estimate by remote sensing. Ecological informatics, 61, 101195.	Theoretical description and different habitats (case study over the whole Europe)	Satellite, MODIS	Application of the spectral species concept to global spectral communities for the assessment of alpha and beta diversity	The paper proposes an innovative method to derive alpha and beta diversity maps over wide geographical areas using the spectral species concept	Shannon's H (alpha). Bray-Curtis (beta)	NA	NA
Rocchini, D., Santos, M. J., Ustin, S. L., Féret, J. B., Asner, G. P., Beierkuhnlein, C., ... & Lenoir, J. (2022). The spectral species concept in living color. Journal of Geophysical Research: Biogeosciences, 127(9), e2022JG007026.	NA	NA	Review of the spectral species concept used within the SVH	NA	NA	NA	NA
Rocchini, D., Thouverai, E., Marcantonio, M., Iannacito, M., Da Re, D., Torresani, M., ... & Wegmann, M. (2021). rasterdiv—An Information Theory tailored R package for measuring ecosystem heterogeneity from space: To the origin and back. Methods in ecology and evolution, 12(6), 1093.	Theoretical description and different habitats (case study over the mountain regions of the Province of Bolzano/ Bozen, Italy)	Satellite, Sentinel-2	Introduction of the new rasterdiv R package with various heterogeneity indices and their application for assessment of spectral diversity and habitat heterogeneity	Introduction of the new rasterdiv R package with various heterogeneity indices and their application for assessment of spectral diversity and habitat heterogeneity	Berger Parker, copNDVI, CRE, Hill, paRao, Pielou, Rao, RaoAUC, Renyi, Shannon's H	NA	NA
Rocchini, D., Torresani, M., Beierkuhnlein, C., Feoli, E., Foody, G. M., Lenoir, J., ... & Ricotta, C. (2022). Double down on remote sensing for biodiversity estimation: a biological mindset. Community Ecology, 1-10.	Theoretical description and case studies in forest ecosystem (forest area of Monticolo - Italy)	Theoretical description. In the case study Airborne, multispectral data	Review of the spectral species concept within the SVH, test for the assessment of vegetation species diversity (alpha and beta)	NA	Shannon's H (alpha), Bray-Curtis (beta)	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Rocchini, D., Wohlgemuth, T., Ghisleni, S., & Chiarucci, A. (2008). Spectral rarefaction: linking ecological variability and plant species diversity. <i>Community Ecology</i> , 9(2), 169-176.	Different habitats (biogeographic regions over the whole Switzerland)	Satellite, Landsat ETM+	Assess species rarefaction by using spectral heterogeneity	Spectral rarefaction shows to be good proxies for species rarefaction curves	Spectral rarefaction	Species rarefaction	NA
Rocchini, D., Wohlgemuth, T., Ricotta, C., Ghisleni, S., Stefanini, A., & Chiarucci, A. (2009). Rarefaction theory applied to satellite imagery for relating spectral and species diversity. <i>Riv. Ital. di Telerilevamento</i> , 41, 109-123.	Different ecosystems (Switzerland)	Landsat ETM+	To introduce a method that concurrently assesses spectral heterogeneity at various scales, drawing from ecological theory, and to demonstrate the close association between measures of spectral heterogeneity and diversity derived from species data. Casy study in Switzerland	Spectral rarefaction serves as a potent tool for identifying variations in biodiversity across different regions.	Spectral rarefaction	Species richness	NA
Rossi, C., & Gholizadeh, H. (2023). Uncovering the hidden: Leveraging sub-pixel spectral diversity to estimate plant diversity from space. <i>Remote Sensing of Environment</i> , 296, 113734.	Grassland ecosystem (Nature Conservancy's TGPP, Oklahoma, USA)	Airborne and spaceborne, hyperspectral (DESI)	Propose a novel approach for remote estimation of plant diversity through quantifying spectral diversity at the sub-pixel level and taking into account the within-pixel variability.	The proposed method applied to DESIS data outperformed a conventional spectral diversity metric based on the coefficient of variation. Spaceborne imaging spectroscopy captures taxonomic and phylogenetic diversity, but the choice of diversity metric and plot size affects the spectral-plant diversity relationship.	Spectral species, Coefficient of variation	Species Richness, Shannon's H, Phylogenetic diversity	h
Rossi, C., Kneubühler, M., Schütz, M., Schaepman, M. E., Haller, R. M., & Risch, A. C. (2021). Remote sensing of spectral diversity: A new methodological approach to account for spatio-temporal dissimilarities between plant communities. <i>Ecological Indicators</i> , 130, 108106.	Grassland ecosystem (subalpine and alpine grassland, Switzerland)	Satellite, Sentinel-2	Measure multi-temporal vegetation alpha, beta and gamma diversity	Introduction to a new methodological approach to account for spatio-temporal dissimilarities between plant communities in the calculation of spectral diversity	Spectral variance (alpha, beta and gamma)	Bray-Curtis dissimilarity	m
Rossi, C., Kneubühler, M., Schütz, M., Schaepman, M. E., Haller, R. M., & Risch, A. C. (2021). Spatial resolution, spectral metrics and biomass are key aspects in estimating plant species richness from spectral diversity in species-rich grasslands. <i>Remote Sensing in Ecology and Conservation</i> .	Grassland ecosystem (alpine grassland, Switzerland)	UAV, multispectral and airborne, AVIRIS-NG data. Fusion to get hyperspectral data	Estimation of plot-level vegetation species diversity. Investigation of confounding factors of the spectral diversity-biodiversity relationship	Success of SVH depends on spatial resolution, spectral metrics, and awareness of confounding factors (e.g. plant biomass), which may be ecosystem specific	Coefficient of variation, convex hull volume, spectral richness	Species richness	m for UAV and l for airborne
Rugani, B., & Rocchini, D. (2017). Boosting the use of spectral heterogeneity in the	Agricultural ecosystem (vineyards in the Province of Trento, Italy)	Satellite, Landsat ETM+ and Landsat 8	Assess the land use impact assessment on biodiversity in agricultural areas	The SVH can be used to assess the life cycle impact assessment on biodiversity and to estimate	Interspersion	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
impact assessment of agricultural land use on biodiversity. Journal of Cleaner Production, 140, 516-524.				local or regional biodiversity change			
Sagang Takougoum, L. B., Ploton, P., Viennois, G., Féret, J. B., Sonké, B., Couteron, P., & Barbier, N. (2022). Monitoring vegetation dynamics with open earth observation tools: the case of fire-modulated savanna to forest transitions in Central Africa.	Forest ecosystem (forest savanna in the Mpem & Djim National Park - Cameroon)	Landsat	Enhance understanding of forest-savanna transitions, evaluating the impact of fire regimes on woody encroachment, species composition, and above-ground carbon storage,	Utilizing the biodivMapR package with Sentinel 2 imagery is possible to characterizes vegetation dynamics, fire regimes, and species assemblages, providing valuable insights into the impact of woody encroachment and forest progression on biodiversity, carbon sequestration, and the need for active management strategies in the region. Sentinel-2 spectral and spatial resolutions are suitable for detecting relationships between optical diversity and productivity in grassland ecosystems. Good linear correlation between optical proxies of ecosystem productivity and optical diversity. There is a scale-dependency in these relationships at increasing pixel sizes.	Spectral dissimilarity on spectral species	NA	NA
Sakowska, K., MacArthur, A., Gianelle, D., Dalponte, M., Alberti, G., Gioli, B., ... & Vescovo, L. (2019). Assessing across-scale optical diversity and productivity relationships in grasslands of the Italian Alps. Remote Sensing, 11(6), 614.	Grassland ecosystem (Viote del Monte Bondone, Trentino province - Italy)	Airborne (hyperspectral) and spaceborne (Sentinel-2)	Exploring optical diversity and productivity patterns across different scales	SVH does not hold across landscapes using MODIS images. The correlation is influenced by the location and extent of the study area, by the heterogeneity indices and by the seasonality	Coefficient of Variation	NA	NA
Schmidtlein, S., & Fassnacht, F. E. (2017). The spectral variability hypothesis does not hold across landscapes. Remote Sensing of Environment, 192, 114-125.	Different habitats (biogeographic regions in Southern Germany)	Satellite, MODIS	Assess vegetation species richness	The spatial heterogeneity assessed at the spatial resolution of 30m (same as some upcoming satellite missions) catch changes in plant species composition (beta-diversity). The relationship between spectral heterogeneity and alpha diversity is influenced by different environmental characteristics such as pixel-to-plant size ratio and LAI	Mean distance from centroid, number of classes of an unsupervised k-means classification in each mapping unit	Species richness	l
Schweiger, A. K., & Laliberté, E. (2022). Plant beta-diversity across biomes captured by imaging spectroscopy. Nature Communications, 13(1), 1-7.	Different Habitats (biogeographic regions across the USA)	Airborne, hyperspectral data	Assess the relationship between spectral heterogeneity and vegetation alpha and beta diversity at landscape level		Spectral alpha-diversity (sum of the squared deviations of every pixel and spectral feature per community from the mean spectral feature of that community standardized by the number of pixels in the community) (alpha). Hellinger distances (beta)	Species richness, Shannon's H, phylogenetic distance (alpha). Hellinger distances (beta)	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Schweiger, A. K., Cavender-Bares, J., Townsend, P. A., Hobbie, S. E., Madritch, M. D., Wang, R., ... & Gamon, J. A. (2018). Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. <i>Nature Ecology & Evolution</i> , 2(6), 976-982.	Grassland ecosystem (prairie grassland, Cedar Creek Ecosystem Science Reserve, Minnesota, USA)	Field, hyperspectral data	Predict ecosystem functional, phylogenetic and taxonomic diversity	Spectral diversity was as predictive of ecosystem function as functional, phylogenetic or taxonomic diversity	Dispersion based on three components: the number of units per community (image pixels) the regularity (evenness) and dispersion (distance from centroid)	Functional and phylogenetic distances	h
Shahtahmassebi, A. R., Lin, Y., Lin, L., Atkinson, P. M., Moore, N., Wang, K., ... & Zhao, M. (2017). Reconstructing historical land cover type and complexity by synergistic use of landsat multispectral scanner and corona. <i>Remote Sensing</i> , 9(7), 682.	Different ecosystem (forest, rural urban cover, mining and agriculture, southern portion of Fu Yang County, Zhejiang Province, China)	Satellite, Landsat MSS	Reconstruct historical land cover types and complexity under the SVH	Texture based indices on specific bands and vegetation indices were related to land cover. Hence, spectral diversity could be used to assess land cover type and complexity	Image texture	NA	NA
Somers, B., Asner, G. P., Martin, R. E., Anderson, C. B., Knapp, D. E., Wright, S. J., & Van De Kerchove, R. (2015). Mesoscale assessment of changes in tropical tree species richness across a bioclimatic gradient in Panama using airborne imaging spectroscopy. <i>Remote Sensing of Environment</i> , 167, 111-120.	Forest (tropical forest, isthmus of Panama)	Airborne, hyperspectral data	Assess tree alpha and beta diversity	Spectral heterogeneity measured with CV showed a significant and positive correlation with tree species richness. The spectral similarity between plots shows to be a good proxy of beta diversity. The spectral heterogeneity was in general higher for the moist forest site compared to wet and dry forests. Visible and shortwave-infrared bands were the driver of the spectral variation.	Coefficient of variation (alpha). Spectral similarity (beta)	Species richness (alpha). Spectral distance-decay (beta)	h
Sun, H., Hu, J., Wang, J., Zhou, J., Lv, L., & Nie, J. (2021). RSPD: A Novel Remote Sensing Index of Plant Biodiversity Combining Spectral Variation Hypothesis and Productivity Hypothesis. <i>Remote Sensing</i> , 13(15), 3007.	Forest (urban forests, cities of Beijing and Huai'an, China)	Satellite, Pléiades-1 and Sentinel-2	Estimate vegetation species diversity combining the SVH with the productivity hypothesis through the new RSPD index	The new proposed RSPD index performed better than the CV as heterogeneity index for the assessment of species diversity using Sentinel-2 and Pléiades-1 data	Coefficient of variation, a new index called RSPD	Shannon's H, Simpson's D	h
Taddeo, S., Dronova, I., & Harris, K. (2019). The potential of satellite greenness to predict plant diversity among wetland types, ecoregions, and disturbance levels. <i>Ecological Applications</i> , 29(7), e01961.	Wetland ecosystems (USA)	Satellite, Landsat 5 TM and Landsat 7 ETM+	Assess the relationships between satellite-derived vegetation indices/spectral heterogeneity (spectral greenness and heterogeneity) and plant species richness/diversity	Positive correlations between plant species richness/diversity and spectral greenness and heterogeneity, especially in models that combines both the information	Standard deviation	Species richness, native species richness, family richness, alien species richness, Shannon's H, species cover	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Taddeo, S., Dronova, I., & Harris, K. (2021). Greenness, texture, and spatial relationships predict floristic diversity across wetlands of the conterminous United States. <i>ISPRS Journal of Photogrammetry and Remote Sensing</i> , 175, 236-246.	Wetland ecosystems (USA)	Satellite, Landsat 5 TM, Landsat 7 ETM+ and airborne multispectral images	Assess the relationships between spectral heterogeneity and plant species richness/diversity through a univariate and multivariate predictive model	Singular texture metrics could predict around 35% of richness and diversity. The combination with annual greenness improved the prediction. Best results were achieved when in the models the spatial relations among site were included	Dissimilarity, entropy, sum average, sum variance, correlation, site greenness	Species richness, native species richness, alien species richness, Shannon's H, species cover	h for airborne and satellite
Tagliabue, G., Panigada, C., Celesti, M., Cogliati, S., Colombo, R., Migliavacca, M., ... & Rossini, M. (2020). Sun-induced fluorescence heterogeneity as a measure of functional diversity. <i>Remote Sensing of Environment</i> , 247, 111934.							
Tan, X., Shan, Y., Wang, L., Yao, Y., & Jing, Z. (2023). Density vs. Cover: Which is the better choice as the proxy for plant community species diversity estimated by spectral indexes?. <i>International Journal of Applied Earth Observation and Geoinformation</i> , 121, 103370.	Forest (temperate forest, Alsace province, France)	Airborne, hyperspectral data	To map the functional diversity of terrestrial ecosystems through assessment of heterogeneity of vegetation indices and induced chlorophyll fluorescence	Good correlation between functional diversity and the Rao's Q spectral heterogeneity index based on far-red sun-induced chlorophyll fluorescence	Rao's Q , coefficient of variation	Species richness, Shannon's H	h
Tan, X., Shan, Y., Wang, X., Liu, R., & Yao, Y. (2022). Comparison of the predictive ability of spectral indices for commonly used species diversity indices and Hill numbers in wetlands. <i>Ecological Indicators</i> , 142, 109233.	Wetland (Sanjiang Nature Reserve - China)	UAV, multispectral data	To investigate the relationship between plant species cover and spectral-species diversity by comparing the ability of spectral indexes to predict various species diversity indexes computed based on species density and cover across the entire species diversity continuum.	Spectral indexes were more strongly correlated with species diversity computed by species cover than by species density, improving the robustness of predicting plant species diversity based on spectral information, and suggested Hill numbers as a more suitable choice for spectral-species diversity studies across varied community types	Standard deviation, Coefficient variation	Hill numbers, Species richness, Shannon's H, Simpson's D	h
Tan, X., Shan, Y., Wang, X., Liu, R., & Yao, Y. (2022). Comparison of the predictive ability of spectral indices for commonly used species diversity indices and Hill numbers in wetlands. <i>Ecological Indicators</i> , 142, 109233.	Wetland (Sanjiang Nature Reserve - China)	UAV, multispectral data	Assess the improved predictive ability of species diversity by combining the mean NDVI and standard deviation of NDVI, compared to using mean of NDVI alone, and to evaluate the suitability of Hill numbers in spectral-species diversity relationship research, addressing questions about the limitations of mean of NDVI and exploring predictive abilities across the entire diversity continuum	The study highlights limitations in using mean of NDVI alone for predicting species diversity in wetlands, demonstrating a substantial improvement when combined with the standard deviation of NDVI. NDVI-related indices, particularly Hill numbers, show superior predictive ability compared to commonly used species diversity indices	Standard deviation, Coefficient variation	Species richness, Shannon's H, Shannon entropy, Gini index, Simpson's Reciprocal Index, Hill numbers	h
Tassi, A., & Gil, A. (2020). A Low-cost Sentinel-2 Data and Rao's Q Diversity Index-based Application for Detecting, Assessing and Monitoring Coastal Land-cover/Land-use Changes at High Spatial	Coastal habitat(Coastal zones landscape, Terceira Island, Azores, Portugal)	Satellite, Sentinel-2	Detecting and monitoring coastal land-cover/land-use changes	The proposed remote sensing approach efficiently detects coastal change detection in land cover, improving cost-effective on-site assessments, monitoring, and interventions	Rao's Q	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Resolution. Journal of Coastal Research, 95(SI), 1315-1319. Tassi, A., Massetti, A., & Gil, A. (2022). The spectralrao-monitoring Python package: A RAO's Q diversity index-based application for land-cover/land-use change detection in multifunctional agricultural areas. Computers and Electronics in Agriculture, 196, 106861.	Agricultural ecosystem ("Charneca do Infantado", Ribatejo region, Portugal)	Satellite, Landsat 8	Introduction to the open-source Python code of Rao s' Q index and use of the index for detection and mapping of Land Cover changes	The results showed the strength of the Rao's Q index (used with a single layer - NDVI- or with multiple Landsat 8 bands) to detect and map land use changes	Rao's Q	NA	h
Thornley, R., Gerard, F. F., White, K., & Verhoef, A. (2022). Intra-annual taxonomic and phenological drivers of spectral variance in grasslands. Remote Sensing of Environment, 271(January), 112908.	Grasslands ecosystem (Dawcombe nature reserve, Betchworth, Surrey, UK)	Field, hyperspectral data	Testing the SVH over different phenological stages in two grassland sites	SVH only held at the high diversity site and only for certain metrics and at particular time points	Coefficient of variation	Species richness, Simpson's D, Simpson evenness	h
Thouverai, E., Marcantonio, M., Bacaro, G., Re, D. D., Iannacito, M., Marchetto, E., ... & Rocchini, D. (2021). Measuring diversity from space: a global view of the free and open source rasterdiv R package under a coding perspective. Community Ecology, 22(1), 1-11.	Theoretical description and a case study over the whole world	Satellite, PROBA-V	Explanation of different heterogeneity indices included in the R rasterdiv package for assessment of habitat heterogeneity	NA	Shannon's H, Pielou's , Berger Parker, Rao's Q , CRE, Renyi, Hill.	NA	NA
Torresani, M., Feilhauer, H., Rocchini, D., Féret, J. B., Zebisch, M., & Tonon, G. (2021). Which optical traits enable an estimation of tree species diversity based on the Spectral Variation Hypothesis?. Applied Vegetation Science, 24(2), e12586.	Forest (alpine coniferous forest, Province of Bolzano/Bozen, Italy)	Satellite, Sentinel-2	Understand which optical traits drives the SVH for the assessment of tree species diversity	Different optical traits (in particular "brown pigments", "carotenoids" and "chlorophyll content" derived from radiative transfer models) are the main drivers of the correlation between spectral heterogeneity and species diversity in alpine coniferous forest	Rao's Q	Shannon's H	h
Torresani, M., Masiello, G., Vendrame, N., Gerosa, G., Falocchi, M., Tomelleri, E., ... & Zardi, D. (2022). Correlation Analysis of Evapotranspiration, Emissivity Contrast and Water Deficit Indices: A Case Study in Four Eddy Covariance Sites in Italy with Different Environmental Habitats. Land, 11(11), 1903.	Forest (Renon, Lavarone, Bosco della Fontana, Italy) and grassland ecosystems (Monte Bondone, Italy)	Satellite, MODIS	Side-goal of the study was to assess the environmental heterogeneity (over different study areas where eddy covariance tower were located) through the SVH	The spectral variation of NDVI MODIS images were used to assess the environmental heterogeneity. In the area with high spectral heterogeneity the correlation between eddy covariance data and emissivity contrast indices were lower.	Rao's Q	NA	NA

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Torresani, M., Rocchini, D., Sonnenschein, R., Zebisch, M., Marcantonio, M., Ricotta, C., & Tonon, G. (2019). Estimating tree species diversity from space in an alpine conifer forest: The Rao's Q diversity index meets the spectral variation hypothesis. <i>Ecological Informatics</i> , 52, 26-34.	Forest (alpine coniferous forest, Province of Bolzano/Bozen, Italy)	Satellite, Sentinel-2 and Landsat 8	Estimate tree species diversity testing the Rao's Q index using a multitemporal approach (effect of phenology on the spectral heterogeneity)	The relationship between spectral heterogeneity and species diversity is affected by the acquisition time (time of the year) of the images (both Sentinel-2 and Landsat 8). Spatial resolution of the images affect the results (Sentinel-2 performed better than Landsat 8)	Rao's Q, Coefficient of variation	Shannon's H	h
Ustin, S. L., & Gamon, J. A. (2010). Remote sensing of plant functional types. <i>New Phytologist</i> , 186(4), 795-816.	NA	NA	NA	The paper proposes "optical types," a novel concept merging plant functional types with advanced remote sensing, to address scale-dependence issues in vegetation classification, aiming for a direct correlation between ecological traits and remote sensing data beyond traditional discrete categorizations. The feasibility of utilizing spectral diversity as an indicator for taxonomic diversity in grasslands depends on specific conditions and should not be assumed solely based on the SVH. A comprehensive understanding of the biological characteristics of a community is essential before considering spectral diversity as a tool for monitoring taxonomic diversity.	NA	NA	NA
Van Cleemput, E., Adler, P., & Suding, K. N. (2023). Making remote sense of biodiversity: What grassland characteristics make spectral diversity a good proxy for taxonomic diversity?. <i>Global Ecology and Biogeography</i> , 32(12), 2177-2188.	Grassland ecosystem (included in the National Ecological Observatory Network - NEON- USA)	Airborne, hyperspectral data	To investigate the influence of three potential moderators, namely vegetation density, spatial distribution of species, and invasion of non-native species, on the relationship between taxonomic and spectral diversity in herbaceous ecosystems	low-resolution spectral indicators derived from a narrow extent exhibit the highest correlations with forest α -diversities and compositional variances. The best spectral indicators are obtained from the scores of the first axis of principal component analysis and the near-infrared band.	Coefficient of Variation, spectral angle mapper, convex hull volume	Species richness, Shannon's H, inverse Simpson's D	h
Végh, L., & Tsuyuzaki, S. (2021). Remote sensing of forest diversities: the effect of image resolution and spectral plot extent. <i>International Journal of Remote Sensing</i> , 42 (15), 5985-6002.	Forest ecosystem (Mount Usu - Japan)	Satellite, IKONOS	Validate the impact of image resolution and varying spectral plot extents on the SVH. Additionally, the study seeks to determine if incorporating herb layer diversity improves the precision of diversity estimation.		Mean, standard deviation, coefficient of variation, mean distance from centroid, species richness calculated with RS data, Shannon's H, Simpson's D, Shannon's J, true diversity of order 1, and true diversity of order 2	species richness, Shannon's H, Simpson's D, Shannon's J, true diversity of order 1, and true diversity of order 2	m

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Villoslada, M., Bergamo, T. F., Ward, R. D., Burnside, N. G., Joyce, C. B., Bunce, R. G. H., & Sepp, K. (2020). Fine scale plant community assessment in coastal meadows using UAV based multispectral data. <i>Ecological Indicators</i> , 111, 105979.	Coastal habitat (Baltic coastal meadows, Silma Nature Reserve, West Estonia)	UAV, multispectral data	Assess the relationship between spectral heterogeneity of UAV multispectral images and species diversity	The relationship between species diversity and spectral diversity is positive until a certain point and then it turns negative. This it might be due to the sensitivity of spectral diversity to biomass or due to artefacts produced by the high resolution of the UAV images. Spectral diversity is associated with tree species diversity, no direct or indirect effects on carbon content were observed.	Standard deviation	Shannon's H	l
Wallis, C. I., Crofts, A. L., Inamdar, D., Arroyo-Mora, J. P., Kalacska, M., Laliberté, É., & Vellend, M. (2023). Remotely sensed carbon content: The role of tree composition and tree diversity. <i>Remote Sensing of Environment</i> , 284, 113333.	Forest ecosystem (forest sites of the Parc national du Mont Mégantic and Parc national du Mont-Saint-Bruno in southern Quebec - Canada)	Airborne, hyperspectral	Explore how spectral composition and spectral diversity predict carbon content, and disentangling the influence of tree composition, tree diversity, and unmeasured canopy aspects using structural equation modelling.	The findings emphasize the significance of tree composition (rather than diversity) in mediating the relationship between hyperspectral data and forest carbon content	Convex hull volume	Shannon's H	h
Wang, D., Qiu, P., Wan, B., Cao, Z., & Zhang, Q. (2022). Mapping α -and β -diversity of mangrove forests with multispectral and hyperspectral images. <i>Remote Sensing of Environment</i> , 275, 113021.	Forest ecosystem (heterogeneous mangrove forest located in Hainan, Qinglangang Provincial Nature Reserve -China)	Satellite, WorldView-2, Sentinel-2, and hyperspectral Zhuhai-1	Assess and map mangrove species diversity using the SVH, with specific objectives to evaluate a novel holistic diversity method with various satellite images, compare its performance with benchmark diversity methods in terms of α -diversity, and analyse the contributions of individual spectral features to both α - and β -diversities.	The study successfully applied a novel approach using satellite data to map plant diversity in mangrove ecosystems, providing insights into α - and β -diversities, with operational satellites (WorldView-2, Sentinel-2, and Zhuhai-1), contributing to potential rapid biodiversity monitoring on a broader scale.	Coefficient of variation, Rao's Q index	Shannon's H	m
Wang, R., & Gamon, J. A. (2019). Remote sensing of terrestrial plant biodiversity. <i>Remote Sensing of Environment</i> , 231, 111218.	NA	NA	NA	Review on remote sensing of biodiversity, outlining major and emerging applications related to biodiversity assessment using remote sensing, with a particular emphasis on recent advancements in the detection of plant diversity through spectral diversity.	NA	NA	NA
Wang, R., Gamon, J. A., & Cavender-Bares, J. (2022). Seasonal patterns of spectral diversity at leaf and canopy scales in the Cedar Creek	Grassland ecosystem (Prairie grassland, Cedar Creek Ecosystem Science Reserve, Minnesota, USA)	Field, hyperspectral data	Estimate the changes of spectral heterogeneity at leaf and canopy scales in grassland ecosystem. Understand how the seasonal changes of leaf pigments	Strong scale dependence on the seasonal relationship between spectral heterogeneity and species diversity. Phenological effects (seasonal patterns),	Coefficient of variation	Shannon's H	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
prairie biodiversity experiment. Remote Sensing of Environment, 280, 113169.			influence the relationship between spectral diversity and species diversity.	biological, statistical and ecological (effect of soil) influence the spectral heterogeneity at leaf and canopy level in grassland ecosystems.			
Wang, R., Gamon, J. A., Cavender-Bares, J., Townsend, P. A., & Zygielbaum, A. I. (2018). The spatial sensitivity of the spectral diversity–biodiversity relationship: an experimental test in a prairie grassland. Ecological Applications, 28 (2), 541-556.	Grassland ecosystem (Prairie grassland, Cedar Creek Ecosystem Science Reserve, Minnesota, USA)	Field and airborne, hyperspectral data	Assess species diversity of vascular plants testing the effect of spatial resolution.	High-resolution imaging spectrometer data, most sensitive to diversity, showed reduced detectability of biodiversity with decreasing spatial resolution. The optimal pixel size for distinguishing diversity in prairie plots was 1 mm to 10 cm, similar to an herbaceous plant's size. Results reveal a scale dependence in spectral diversity-biodiversity relationships, emphasizing spectral diversity's efficacy in detecting species richness and evenness, but weaker detection of phylogenetic diversity	Coefficient of variation	Species Richness, Shannon's H, Simpson's D, phylogenetic species variation, phylogenetic species evenness	h for field and l for airborne
Wang, R., Gamon, J. A., Emmerton, C. A., Li, H., Nestola, E., Pastorello, G. Z., & Menzer, O. (2016). Integrated analysis of productivity and biodiversity in a southern Alberta prairie. Remote Sensing, 8(3), 214.	Grassland ecosystem (Prairie grassland, Mattheis Research Ranch, Calgary, Alberta, Canada)	Airborne, hyperspectral data	Assess the spatial pattern of production and biodiversity in grassland ecosystems and the relationship between spectral heterogeneity and species richness/diversity and productivity	Good correlation between spectral heterogeneity and species diversity (Shannon's H performed better than species richness) as well as with productivity (NDVI)	Coefficient of variation	Species richness, Shannon's H	h
Wang, R., Gamon, J. A., Schweiger, A. K., Cavender-Bares, J., Townsend, P. A., Zygielbaum, A. I., & Kothari, S. (2018). Influence of species richness, evenness, and composition on optical diversity: A simulation study. Remote sensing of environment, 211, 218-228.	Grassland ecosystem (Prairie grassland, Cedar Creek Ecosystem Science Reserve, Minnesota, USA)	Field, hyperspectral data	Assess the effect of species richness, evenness and composition on optical diversity. Estimate the influence of different heterogeneity metrics. Measure the effect of sampling methods and soil background on optical diversity.	Good correlation between spectral heterogeneity and species diversity. The correlation is influenced by the species diversity indices (metrics that combined richness and evenness are more correlated with spectral heterogeneity), by the sampling method, by the vegetation traits (collected at leaf or plot level) and by soil background.	Coefficient of variation, partial least squares discriminant analysis	Species richness, Shannon's H, Simpson's D, Evenness' s J	h
Warren, S. D., Alt, M., Olson, K. D., Irl, S. D., Steinbauer, M. J., & Jentsch, A. (2014). The	Different habitats (forests, grasslands, plantations, Grafenwöhr	Satellite, IKONOS	Assess the relationship between spectral heterogeneity, habitat	Good correlation between spectral heterogeneity and plant species richness as well as	168 indices	Species richness	h

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Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity index	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
relationship between the spectral diversity of satellite imagery, habitat heterogeneity, and plant species richness. Ecological Informatics, 24, 160-168.	Training Area, Bavaria, Germany)		diversity and plant species richness.	with habitat heterogeneity (the latter was less strong)			
White, J. C., Gómez, C., Wulder, M. A., & Coops, N. C. (2010). Characterizing temperate forest structural and spectral diversity with Hyperion EO-1 data. Remote Sensing of Environment, 114(7), 1576-1589.	Forest (Coastal temperate forest, Vancouver Island, British Columbia, Canada)	Satellite, Hyperion EO-1	Assess the relationship between forest canopy structural diversity and spectral heterogeneity	Spectral heterogeneity is more directly correlated to structural diversity than to species diversity.	26 variables representing spectral diversity in each stand, which included mean and standard deviation values for each band.	Normalized root mean square difference based on number of unique species and their relative abundance	l
Xu, C., Zeng, Y., Zheng, Z., Zhao, D., Liu, W., Ma, Z., & Wu, B. (2022). Assessing the Impact of Soil on Species Diversity Estimation Based on UAV Imaging Spectroscopy in a Natural Alpine Steppe. Remote Sensing, 14(3), 671.	Grassland ecosystem (Natural alpine grassland, Sanjiangyuan National Nature Reserve, Qinghai Province, China)	UAV, hyperspectral data	Investigate the relationship between spectral heterogeneity and species diversity in natural alpine grassland. Assess the impact of soil background.	Good correlation between spectral heterogeneity and species diversity. The correlation is influenced by the spectral heterogeneity index used (Coefficient of variation showed the best results) and by the species diversity index (Shannon's H performed better than species richness). The correlation was significantly improved after removing the soil information.	Coefficient of variation, convex hull volume, convex hull area	Species richness, Shannon's H	h
Zhang, Y., Tang, J., Wu, Q., Huang, S., Yao, X., & Dong, J. (2023). Assessment of the Capability of Landsat and BiodivMapR to Track the Change of Alpha Diversity in Dryland Disturbed by Mining. Remote Sensing, 15(6), 1554.	Different habitats in dryland disturbed by mining in northern China	Satellite, Landsat 5 and 8	Evaluate Landsat imagery and the biodivMapR package for monitoring alpha diversity changes in drylands affected by mining disturbance, focusing on parameter optimization, relationship with field-surveyed data, impact of vegetation community types, and detection of variations.	The study demonstrates the effectiveness of using Landsat imagery and the biodivMapR package for accurate estimation and monitoring of alpha diversity in drylands, with considerations for optimal parameters, vegetation community types, and identification of regions with diversity changes	Spectral species measured with biodivMapR	Shannon's H	h
Zhao, Y., Sun, Y., Chen, W., Zhao, Y., Liu, X., & Bai, Y. (2021). The potential of mapping grassland plant diversity with the links among spectral diversity, functional trait diversity, and species diversity. Remote Sensing, 13 (15), 3034.	Grassland ecosystem (Semi-arid grassland monoculture experimental site,Xilin River Basin, Inner Mongolia Autonomous Region, China).	UAV, hyperspectral data	Assess the correlation between species diversity, functional trait diversity, and spectral diversity in a semi-arid grassland ecosystem	Species richness was positively correlated with functional traits and spectral heterogeneity in a nonlinear way, tending to saturate.	Coefficient of variation	Species richness	h

Funding information

M.T. and D.R. were partially supported by the H2020 Project SHOWCASE (Grant agreement No 862480). D.R. was also partially supported by the H2020 COST Action CA17134 'Optical synergies for spatiotemporal sensing of scalable ecophysiological traits (SENSECO)'. J.-B. Féret acknowledges financial support from Agence Nationale de la Recherche (BioCop project—ANR – 17 – CE32– 0001) and TOSCA program grant of the French Space Agency (CNES) (HyperTropik/HyperBIO projects). C.R. and L.T.H. acknowledge contributions from the 'Biodiv-Watch' project, supported by the ESA Initial Support for Innovation (EISI) [Grant Number 4000138090]. P.K. acknowledges funding from the DFG (Deutsche Forschungsgemeinschaft) within the framework of the Research Unit BETA-FOR (Enhancing the structural diversity between patches for improving multidiversity and multifunctionality in production forests) (grant no. FOR 5375/1, project number 459717468). M.P. was supported by (Internal Grant Agency) grant from the Faculty of Environmental Sciences at the Czech University of Life Sciences Prague (project n. 2022B0003). This study was funded within the Horizon Europe project EarthBridge (ID: 101079310). Funded by the European Union. Views and opinions expressed are, however, those of the author(s) only and do not necessarily reflect those of the European Union. Neither the European Union nor the granting authority can be held responsible for them.

AI statement

During the preparation of this work, the author(s) utilized ChatGPT to enhance the phrasing, spelling, and grammar of the manuscript. After employing this tool, the author(s) reviewed and edited the content as necessary and assume(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

Michele Torresani: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christian Rossi:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Michela Perrone:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Leon T. Hauser:** Writing – review & editing, Validation, Investigation, Conceptualization. **Jean-Baptiste Féret:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Vítězslav Moudrý:** Writing – review & editing, Visualization, Investigation, Conceptualization. **Petra Simova:** Writing – review & editing. **Carlo Ricotta:** Writing – review & editing, Writing – original draft, Validation, Investigation, Conceptualization. **Giles M. Foody:** Writing – review & editing, Validation, Investigation, Conceptualization. **Patrick Kacic:** Writing – review & editing, Investigation, Conceptualization. **Hannes Feilhauer:** Writing – review & editing, Investigation, Conceptualization. **Marco Malavasi:** Writing – review & editing, Investigation, Conceptualization. **Roberto Tognetti:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Duccio Rocchini:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

None.

Data availability

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

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