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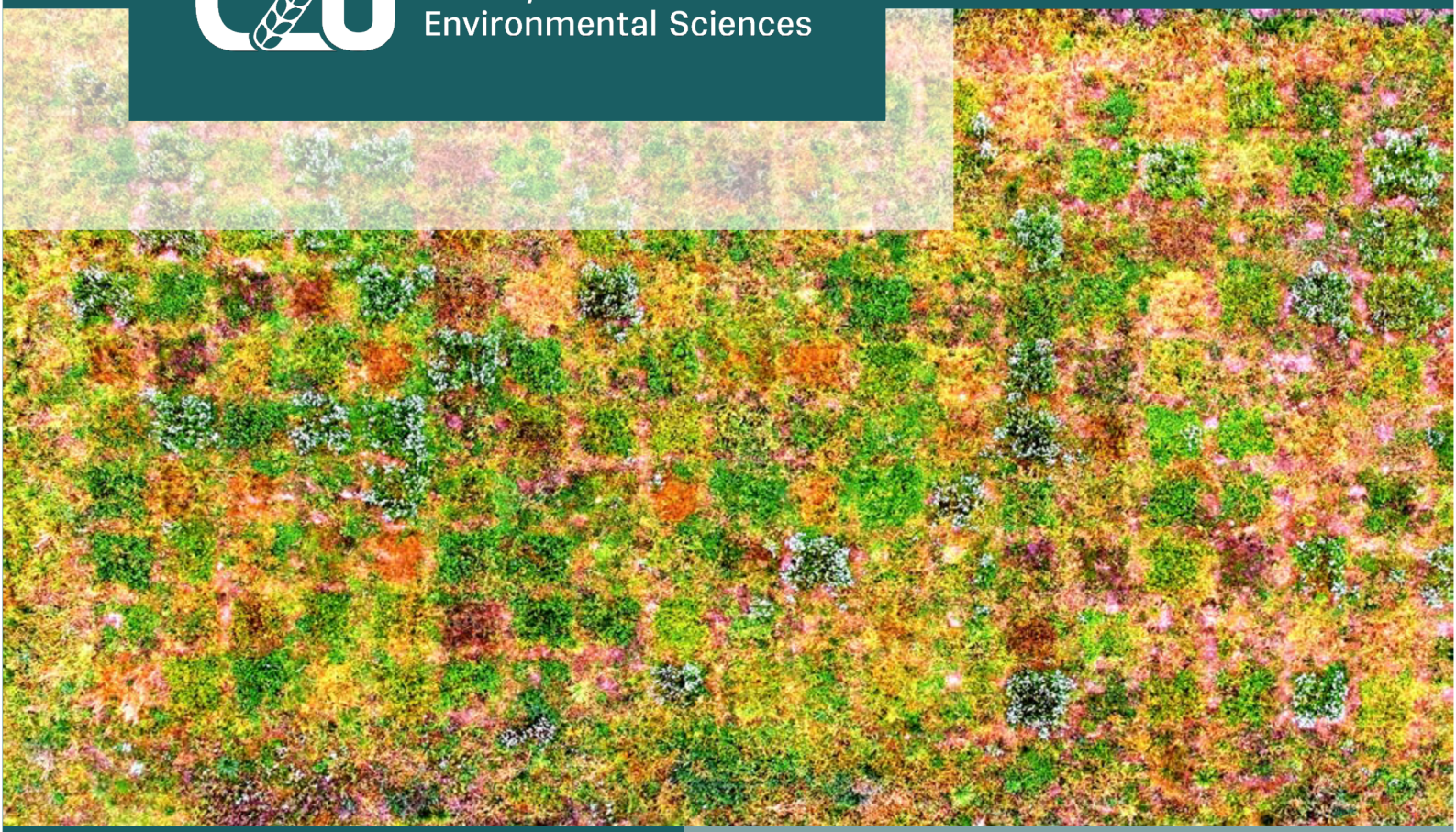

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Assessing plant biodiversity by remote sensing at different ecological scales

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PhD thesis

Czech University of Life Sciences Prague

Faculty of Environmental Sciences

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This thesis is submitted for the degree of *Doctor of Philosophy* at the Department of Spatial Sciences.

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PhD Thesis

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I hereby declare that the thesis entitled *Assessing plant biodiversity by remote sensing at different ecological scales* submitted for the Degree of Philosophy of Environmental Sciences is my original work guided by my supervisors. All sources of information, text, illustrations, tables and images have been specifically cited.

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Michela Perrone

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Abstract

Biodiversity monitoring is essential for ecosystem conservation, yet traditional field methods are often limited by high costs and labour intensity. The Spectral Variation Hypothesis (SVH) assumes a positive correlation between spectral diversity from optical remote sensing and species richness, based on the premise that areas with high spectral heterogeneity contain more ecological niches. Over the past two decades, the SVH has been rigorously tested across various ecosystems using diverse remote sensing data, revealing both its potential and limitations.

Through a systematic review and two empirical studies, this thesis aims to provide further insights into the relationship between spectral diversity and biodiversity, highlighting the factors and conditions that influence such a relationship, and propose guidelines for researchers to navigate the complexities of using spectral diversity for biodiversity monitoring across different ecosystems and spatial scales. Specifically, in this thesis I 1) review and discuss recent methodological developments and uncertainties in applying the SVH for biodiversity estimation, 2) investigate the applicability of spectral diversity for monitoring plant diversity at the landscape scale by comparing different spectral diversity metrics, and 3) assess the impact of flowering and spatial resolution on the effectiveness of various spectral diversity metrics for plant diversity monitoring in grasslands.

The findings of the studies presented in this thesis confirm the potential of spectral diversity when used to estimate biodiversity, but also highlight the limitations and weaknesses of the SVH. Notably, its variable success depends on data characteristics and contexts. Moreover, the results of the empirical studies showed that the relationship between spectral and plant diversity is context-dependent and influenced by habitat type, phenology, and the metrics used to quantify spectral diversity. These findings underscore the need for careful consideration of specific factors and conditions when envisaging the use of spectral diversity for biodiversity monitoring.

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Part I

Introduction and Theory

1

Thesis preface

1.1 Foreword

The interplay between biodiversity and remote sensing has been an evolving frontier in ecological research over the past two decades. In this context, the Spectral Variation Hypothesis (SVH) emerged as a pivotal concept, proposing a direct correlation between spectral diversity derived from remote sensing data and biodiversity. This thesis embarks on an in-depth exploration of SVH, its theoretical foundations, practical applications, and inherent challenges, particularly focusing on its efficacy in biodiversity monitoring across various ecosystems.

This thesis is not just a scientific endeavour but also a demonstration of the collaborative spirit of the research community. Precious contributions from colleagues and mentors and insights gained from participating in international conferences and working groups have all played a crucial role in shaping this work. The experiences gained through internships and collaborative projects have further enriched my perspective and skills. Thus, I am deeply grateful to all who have supported and inspired me throughout this journey.

As our planet faces unprecedented ecological challenges, the need for robust, efficient, and scalable methods to monitor biodiversity has never been more critical. It is my hope that this thesis will contribute to the ongoing dialogue in the field, offering new perspectives and practical approaches for leveraging remote sensing technologies in the service of biodiversity conservation.

1.2 Scientific motivation

Traditional methods of biodiversity assessment, while invaluable, are often constrained by logistical challenges, including high costs, extensive labour requirements, and limited spatial and temporal coverage, making them insufficient for the comprehensive monitoring required to inform effective conservation strategies. As a result, there is a critical demand for innovative approaches that can provide comprehensive, accurate, and scalable biodiversity data. Remote sensing, with its ability to capture large-scale environmental information frequently and in near-real-time, offers a promising solution to these limitations. Particularly, the SVH provides a conceptual framework for utilizing remote sensing in biodiversity studies.

Despite its potential, so far the application of SVH has yielded mixed results, with varying success across different ecosystems and scales. This variability underscores the necessity of a comprehensive investigation into the conditions under which spectral diversity reliably indicates biodiversity. Given that this field of research has been very productive in the past decade, I recognised the need to provide an updated overview of the advances and uncertainties related to the application of spectral diversity as a proxy of biodiversity and enhance our understanding of the spectral diversity-biodiversity relationship by critically addressing several crucial gaps and challenges in the current literature.

My dissertation is thus motivated by the desire to leverage advanced remote sensing technologies to address critical challenges in biodiversity monitoring. By refining the application of the SVH and enhancing our understanding of the spectral diversity-biodiversity relationship, this

research aims to contribute to the development of more effective conservation tools and strategies, thereby supporting global efforts to mitigate biodiversity loss and ensure the sustainability of natural ecosystems. Therefore, the chapters that follow delve into the nuances of the SVH, with the aim of systematically reviewing its application and examining its efficacy in different contexts for biodiversity monitoring.

1.3 Thesis structure

The thesis is structured into two parts and seven chapters. **Part I** provides a general introduction to the use of remote sensing and, more specifically, of spectral diversity for plant diversity monitoring and sets the framework for the main research questions. **Part II** represents the core of this thesis and consists of three published studies, which originate from three research questions addressing fundamental challenges of plant diversity monitoring using remote sensing. Finally, a closing chapter reviews and summarises the main findings of this thesis contextualising them in future research perspectives.

Study 1 Peer-reviewed article published in *Ecological Informatics* (Torresani et al., 2024) providing a comprehensive review and discussing recent methodological developments in the use of spectral diversity for plant diversity monitoring.

Study 2 Peer-reviewed article published in *Remote Sensing of Environment* (Perrone et al., 2023) that addresses the relationship between spectral and plant diversity at the landscape scale accounting for the influence exerted by metrics and habitat type.

Study 3 Peer-reviewed article published in *Ecological Informatics* (Perrone et al., 2024) that evaluates the effect of phenology (flowering) on the relationship between spectral and plant diversity at the community scale.

2

Thesis objectives

The overall aim of this thesis is to provide a systematic insight into the applicability of spectral diversity for plant biodiversity monitoring by exploring how acknowledged key factors affect the spectral-plant diversity relationship. Specifically, the present thesis sets out to the following research objectives (RO):

RO 1 – Defining and discussing the spectral diversity concept

This objective is addressed by providing a systematic review of more than 130 publications which gives an overview of the different remote sensing data characteristics (i.e., spatial, spectral and temporal resolution), metrics, tools, ecosystems, and applications for which the SVH was tested and the strength of the association between spectral and plant diversity metrics reported by each study.

RO 2 – Investigating the link between spectral and plant diversity at the landscape scale

The second objective is addressed by assessing the performance of three types of spectral diversity metrics in estimating plant species richness and functional diversity, taking into account the effects of habitat types. An extensive, spatially continuous, field-collected dataset covering the Czech

Republic and a multi-temporal Landsat-8 OLI composite were used to test the relationship.

RO 3 – Investigating the link between spectral and plant diversity at the community scale

The third objective is addressed by testing six spectral diversity metrics while considering flowering as a factor potentially affecting the relationship using ground observations and multispectral UAV data from mesic grassland communities in South Bohemia (Czech Republic). Additionally, the influence of changing the spatial resolution (from 2 cm to 5 cm) on the observed relationship was investigated.

3

Introduction

3.1 The need for plant diversity data

Plant diversity is fundamental to Earth's primary productivity and sustains essential ecosystem services vital for human health and activities, including food production and clean air and fresh water supply (Cavender-Bares et al., 2020). About 20% of the more than 390.000 vascular plant species known to science are currently threatened with extinction, according to IUCN Red List criteria (Kew Royal Botanic Gardens, 2016). A multitude of global change factors, such as drought stress, exotic invasive species, pathogens, chemical use, overexploitation, fragmentation, and, particularly, land use change, pose significant risks to numerous plant species, increasing their vulnerability to extinction (Cavender-Bares et al., 2020). The current biodiversity loss experienced worldwide, given that its magnitude is in proportion to past extinction events, is referred to as the "sixth mass extinction" (Leakey 1996; Kolbert 2014; Wilting et al., 2017) and makes species conservation one of the most pressing priorities of our times. Thus, improving the detection and monitoring of plant biodiversity at various

scales, from genetic variation within and among species to the entire plant tree of life, is crucial at a time when human-induced biodiversity decline is accelerating at an unprecedented rate (Jetz et al., 2016; Turner, 2014).

Global initiatives aimed at conserving biodiversity and establishing assessment procedures, such as those led by the United Nations and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES; Díaz et al., 2015), emphasise the urgent need for biodiversity monitoring worldwide and across multiple spatial scales (Cavender-Bares et al., 2020). However, biodiversity evaluation and monitoring are still limited and lack standardized methods for reproducible data gathering (Palmer et al., 2002; Skidmore et al., 2015; Wang and Gamon, 2019). To address this issue, recent proposals advocate for a global biodiversity monitoring system in which remote sensing is deemed to play a pivotal role (Jetz et al., 2016; Proença et al., 2017).

3.2 Remote sensing

The field of ecology is increasingly relying on remotely sensed data as they provide valuable and often exclusive information on the Earth's surface for the study of vegetation systems and their functions (Gergel and Turner, 2017; Jones and Vaughan, 2010). While *in situ* collection of biodiversity data by traditional methods is expensive and labour-intensive, as well as spatially and temporally limited (Cavender-Bares et al., 2020), remote sensing measurements offer efficient and cost-effective ways to assess plant and ecosystem diversity across extensive regions (Nagendra, 2001), playing a crucial role in long-term global biodiversity assessments (Turner, 2014). Indeed, remote sensing can potentially address biodiversity data gaps at both fine and large scales, especially in remote and inaccessible areas. Additionally, it allows the detection of temporal variations across various spatial scales thanks to the multiple available platforms and sensors (Cavender-Bares et al., 2020). Remote sensing, thus, has great potential for meeting the current requirements for biodiversity conservation-relevant data collection from local to global scales (Chave, 2013; Feilhauer et al., 2012; Rocchini et al., 2010; Wang and Gamon, 2019).

3.2.1 Fundamentals of optical remote sensing

Optical remote sensing is the science of collecting spatial data at a distance from the target using sensors mounted on different types of platforms. These sensors record the solar electromagnetic radiation reflected by objects on the Earth's surface (Clark et al., 1999; Chuvieco, 2020). The sensors used for optical (passive) remote sensing detect the solar electromagnetic radiation reflected at wavelengths between 400 and 2500 nm, which encompass the visible (400-750 nm), near-infrared (700-1400 nm; NIR), and shortwave infrared (1400-2500 nm; SWIR) regions of the spectrum. Electromagnetic radiation interacts with surfaces differently based on wavelength and material (Jones & Vaughan, 2010). When passing through the atmosphere, part of this incoming radiation is filtrated during its journey to the surface and, upon reflection, back to the sensor due to the absorption and scattering processes caused by atmospheric particles. This atmosphere-generated noise calls for removal for accurate surface target observation, a process called atmospheric correction (Jones & Vaughan, 2010; Ollinger, 2010). The electromagnetic radiation that reaches the Earth's surface, if not absorbed by the target and/or the atmosphere, is reflected to and detected by the sensor. In the case of vegetation, the interaction with electromagnetic radiation is dependent upon the wavelength and its incidence but also on the structure and biochemical properties of plant leaves, such as leaf type, morphology, and water and pigment content. Vegetation has low reflectance in the visible region due to the strong absorption by leaf pigments (i.e., chlorophyll a, chlorophyll b, carotenoids, and xanthophylls) and strong reflectance in the NIR (Gates et al., 1965). Such reflectance is known as the NIR reflectance plateau and is due to leaf structural characteristics and the energy level of the NIR radiation, which would be too low for photosynthesis and cause overheating to the plant. The reflectance in the SWIR region depends on the leaf water content, which strongly absorbs light in this domain and determines distinct absorption features at 1450 and 1950 nm (Chuvieco, 2020). The reflectance spectrum resulting from these unique spectral properties of vegetation (Fig.

1.1) is very sensitive to differences among plant species traits and leaf age, nutrient stress, and health (Jones & Vaughan, 2010). The patterns in the vegetation reflectance spectrum thus reveal important information on leaf and canopy properties, which can be assessed at multiple spatial scales with technologies ranging from field spectrometers to satellite systems.

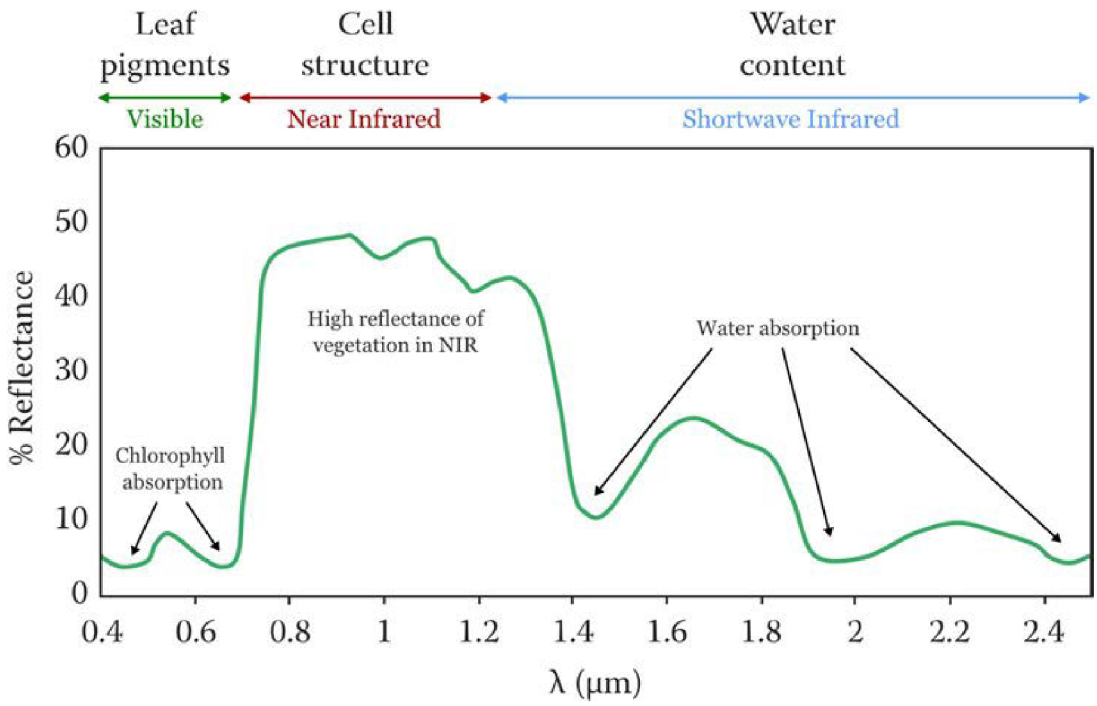

Fig. 1.1. Typical spectral reflectance of vegetation displaying the key absorption features related to plant physiological and biochemical properties.

3.2.2 Platforms and Sensors

The first application of remote sensing for environmental research dates back to the 1910s when it was used to better understand forest extent and condition. Following the introduction of aerial cameras in the 1920s, many countries started to acquire imagery for agricultural land surveying and mapping of land cover and its changes. Satellite-based remote sensing began in the late 1950s and early 1960s for military purposes. The launch of the first of the Landsat series satellites (ERTS Landsat-1) in 1972 gave way to the civilian application of spaceborne remote sensing systems and represented a revolution in the field of earth observation, given its multispectral scanning technology and 80-m spatial resolution (Jones and

Vaughan, 2010). Since then, more than 100 satellite-based sensors have been deployed in national and international remote sensing programs, and the science and use of optical remote sensing for monitoring plant properties and functions have increased substantially (Gergel & Turner, 2017; Cavender-Bares et al., 2020). From then on, earth observation missions have increased exponentially (Chuvieco, 2020).

In terms of spaceborne sensors, there is currently a growing number of satellite missions in orbit that provide optical imagery with plenty for diverse applications, including vegetation monitoring. Recent Earth observation missions (e.g., NASA/USGS Landsat and ESA Copernicus Sentinel) feature open access to data and, in addition to the raw and calibrated data, enhanced products such as corrected reflectances and final products (e.g., temperature; Normalized Difference Vegetation Index, i.e., NDVI), making remotely sensed data more accessible to non-experts. As of the time of writing this thesis, notable resources for obtaining (and processing) non-commercial satellite optical imagery are the Copernicus Data Space Ecosystem (for the ESA missions' catalogues) and the Google Earth Engine database (which includes, among many others, a full Landsat historical archive).

Nowadays, a multitude of platforms are available for remote sensing applications in spatial ecology, from the already mentioned spaceborne ones to close-range and airborne platforms, each with its own advantages and challenges. In particular, uncrewed aerial vehicles (UAVs) have recently become a relevant technology for vegetation data collection thanks to their high flexibility and low operation costs. Their increased availability and (relative) simplicity of use have opened up new opportunities for monitoring and managing natural ecosystems, providing appropriate spatial and temporal resolutions to describe ecological processes taking place at local scales and advancing our understanding of the links between optical diversity and various dimensions of biodiversity (Anderson & Koh, 2018).

Solar reflectance can be recorded using various combinations of sensors and platforms, which differ in spatial resolution (i.e., spatial extent and pixel size), temporal resolution (i.e., acquisition frequency), and spectral

resolution (i.e., number of bands and their bandwidths) of the collected data. According to their spectral resolution, optical sensors can be categorized as multispectral (generally 3 to 15 bands) or hyperspectral (hundreds to thousands of very narrow bands) sensors. Depending on the platform on which these sensors are mounted, the spatial resolution of the acquired data differs: from close-range sensors (e.g., UAVs) with very high spatial resolutions (i.e., small pixel size, small extent) to spaceborne sensors with moderate to coarse resolutions (i.e., coarse pixel size, broad extent). Thus, the type of platform and the sampling scale must be selected to best match the scale of the ecological process under consideration. While UAV platforms can be efficiently used for plant observation at the individual and community scales, spaceborne sensors provide spectral datasets relevant to landscape-scale studies.

In this thesis, multispectral data provided by spaceborne (Chapter 5) and UAV-borne (Chapter 6) sensors were used to investigate the link between spectral diversity and plant diversity.

3.2.3 Remote sensing for plant diversity monitoring

Remote sensing has been acknowledged as a valuable tool for providing an efficient and cost-effective method to assess plant and ecosystem diversity (Nagendra, 2001; Turner et al., 2003; Turner, 2014), given its ability to offer consistent, repeatable, and non-destructive measurements over large areas. Initially, vegetation studies involving remote sensing received a significant boost with the development of vegetation indices and were primarily focused on habitat mapping and evaluation (Nagendra, 2001; Turner et al., 2003; Wang & Gamon, 2019). More recently, modern remote sensing techniques are frequently used to retrieve remotely measurable parameters such as biomass, productivity, and canopy structure (e.g., height, leaf area index), which serve as proxies for estimating species richness or distribution patterns (Turner et al., 2003).

Within the Essential biodiversity variables framework (EBVs; Pereira et al., 2013), remote sensing has also been recognized with the potential to

play an important role in predicting the responses of a set of remote sensing-enabled EBVs to environmental drivers at multiple scales (Pettorelli et al., 2016; Skidmore et al., 2015). Such variables are considered indirectly related to ecosystem function or community composition variables through habitat type characterisation, dominant vegetation, or vegetation functional traits estimation (Cavender-Bares et al., 2020; Wang & Gamon, 2019). However, the exact role remote sensing can play in a forthcoming global biodiversity monitoring system is still unclear, as the mismatch between remote sensing metrics and field sampling criteria poses challenges, though spectral diversity methods may offer new ways to explore the relationships between remote sensing and traditional metrics of biodiversity (Wang & Gamon, 2019).

As reported by Wang and Gamon (2019), biodiversity can be explored using RS by mapping habitats and distributions of individuals, estimating functional diversity, and from patterns of spectral variation. The studies estimating biodiversity through habitat mapping rely on the premise that habitat diversity is crucial for species richness and is expected to correlate positively with biodiversity (Stein et al., 2014). In this type of studies, habitat heterogeneity is indirectly related to biodiversity using remotely sensed indices that evaluate environmental factors associated with "geodiversity" (e.g., climate, habitat structure, geology, and topography) (Beier et al., 2015; Turner et al., 2003). Conversely, mapping distributions of species or functional types is based on spectral and structural differences, which require very fine spatial and spectral resolutions and, thus, are mainly restricted to airborne hyperspectral and Light Detection and Ranging (LIDAR) data (Liu et al., 2017). Functional diversity can be assessed through remote sensing by detecting variations in plant optical properties (i.e., light absorption and scattering), which depend on plant functional traits (Asner et al., 2016; Ustin & Gamon, 2010). Finally, spectral diversity, i.e., the spatial variation in reflectance values across a set of wavelengths, has emerged as a potential proxy of plant diversity, by integrating differences within and across species for multiple facets of biodiversity, including taxonomical, functional, and phylogenetic diversity (Schweiger et al., 2018; Ustin & Gamon, 2010; Wang & Gamon, 2019). The following

section will be dedicated to delving more into the spectral diversity concept, its challenges and knowledge gaps.

3.3 Spectral diversity: a proxy for plant diversity

The spectral diversity concept was originally framed within the Spectral Variation Hypothesis (SVH, Palmer et al., 2000, 2002), which assumes a link between the spatial variability of spectral patterns and environmental diversity, the latter acting as an indicator of species richness. The SVH builds upon environmental surrogacy (Hauser et al., 2021b; Magurran, 2004), suggesting that the link between spectral and plant diversity is mediated by landscape heterogeneity, which reflects the amount of ecological niches available in a region measured through its reflectance variability (Wang & Gamon, 2019). Such an indirect link can be captured by medium/coarse spatial resolution spectral data, with pixel size exceeding the size of individual plants. In contrast, multispectral data obtained from UAVs offer a finer spatial resolution, typically in the centimetre range, allowing for capturing the direct link between plant diversity at the leaf and canopy levels and spectral attributes, which are associated with plant functional and structural properties (Ustin & Gamon, 2010). However, at pixel scales corresponding to individual plant sizes or even smaller, intra-specific variability in plant optical traits may influence the relationship between spectral diversity and biodiversity, especially in challenging ecosystems such as grasslands (Conti et al., 2021).

Even though spectral diversity holds promise for biodiversity monitoring, its alleged link with plant diversity still needs to be fully addressed (Fassnacht et al., 2022; Pacheco-Labrador et al., 2022). Despite empirical support for the use of spectral diversity in estimating plant diversity (Levin et al., 2007; Rocchini, 2007; Rocchini et al., 2014), criticism persists regarding its reliability and consistency (Conti et al., 2021; Schmidtlein & Fassnacht, 2017). This inconsistency may stem from insufficient consideration of key factors affecting the spectral-plant diversity

relationship. Recently, Fassnacht et al. (2022) identified four critical factors affecting this relationship: spatial scale (i.e., spatial grain and extent), reflectance changes over time (i.e., seasonality), identity and number of habitat or vegetation types considered, and metrics chosen to quantify spectral diversity (Cavender-Bares et al., 2020; Rocchini et al., 2010, 2017; Rossi et al., 2021a; Wang et al., 2022). Specifically, the metrics used to quantify SD can be either continuous (i.e., based on variation in traditional vegetation reflectance indices or on the full spectral information) or categorical (i.e., relying on the categorization of the spectral space), with no consensus on which ones most effectively relate to plant diversity (Féret & Asner, 2014; Wang & Gamon, 2019).

Within this framework, understanding how the aforementioned factors drive the relationship between SD and biodiversity, as well as identifying circumstances under which the relationship is stable, is crucial for determining whether and how SD-based RS approaches could support biodiversity monitoring across scales and ecosystems. In light of this, a thorough and comprehensive review of the state-of-the-art on spectral diversity is presented in this thesis (Chapter 4), followed by two studies on the key factors influencing the link with plant diversity at the landscape (Chapter 5) and the community scale (Chapter 6).

Part II

Research

4

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

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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.

Keywords: biodiversity, environmental heterogeneity, mapping, remote sensing, review, spectral heterogeneity, spectral variation hypothesis.

4.1 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 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 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 & 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; Moudrỳ et al., 2023; Simonson et al., 2012; Torresani et al., 2020) and related biodiversity (Moudrỳ 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 & Kuenzer, 2022; Wang & 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 & 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 & Gamon, 2010), 'spectranomics' (Asner & Martin, 2009), 'spectral species' (Féret & 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 & 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 preprocessing, 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 4.1 provides definitions of alpha, beta, and gamma diversity.

Table 4.1. 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.

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.

4.2 Systematic literature review and overview

4.2.1 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 ("1") 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.

4.2.2 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. 4.1). 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 Praire 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 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.

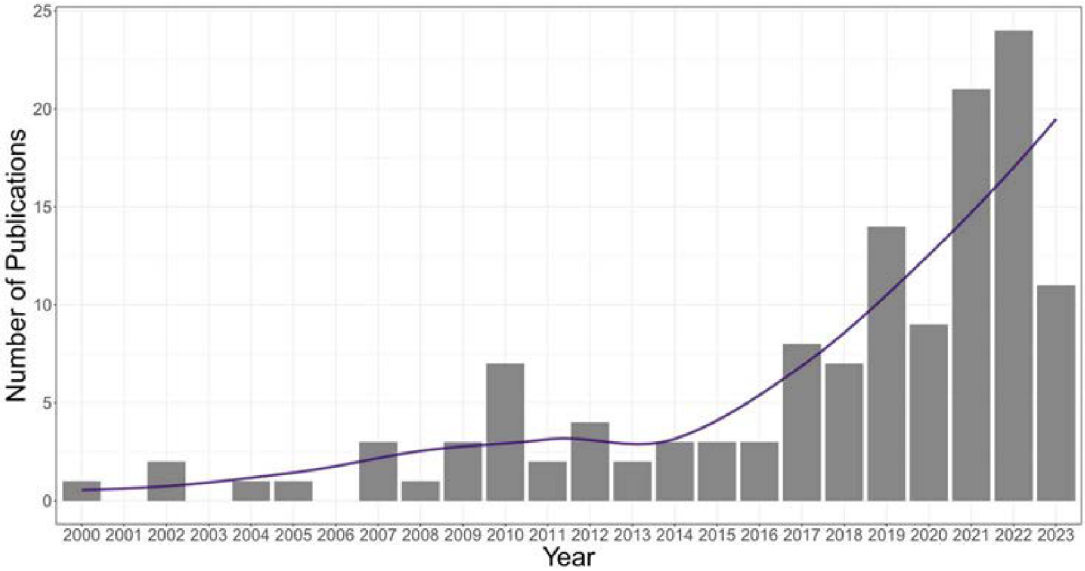

Fig. 4.1. Temporal distribution of publications testing the Spectral Variation Hypothesis between 2000 and 2022. The purple trend line shows the constant increase of SVH-related publications over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

In total, the SVH has been tested in 35 different countries included in this review (Fig. 4.2). 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.

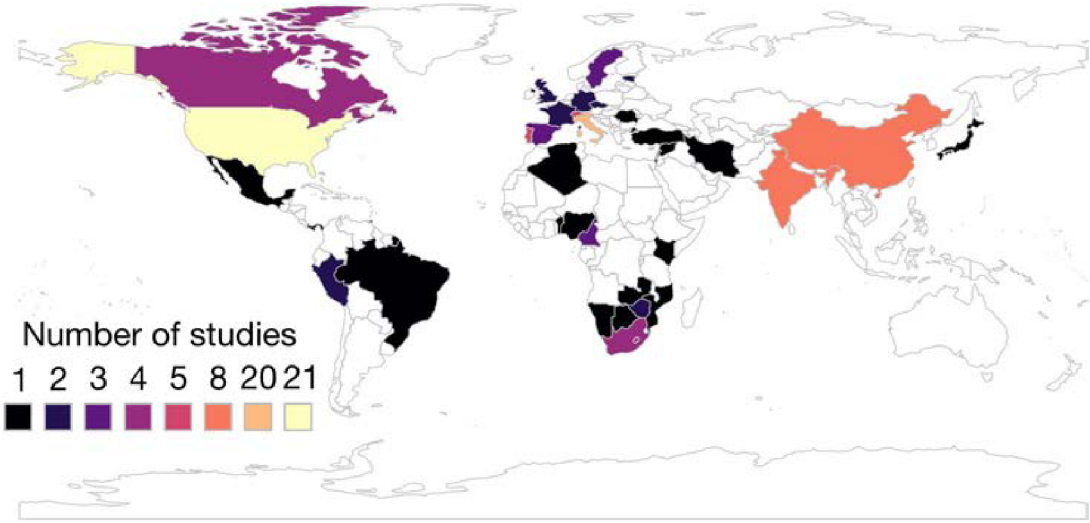

Fig. 4.2 Spatial distribution map showcasing the test locations where the Spectral Variation Hypothesis was tested.

4.3 An ecosystem-oriented review of the application of SVH

The review of the SVH encompasses studies conducted in various ecosystem types (Fig. 4.3). 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; Gillespie, 2005; Féret & 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 & 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; Marzialetti et al., 2021; Marzialetti et al., 2020), as well as in various other ecosystems present within coastal areas (Tassi & 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 & Rocchini, 2017) abundance and diversity of agricultural lands, as well as in abandoned agricultural fields (Aneece 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 & Neteler, 2012b; Rocchini et al., 2010; Rocchini et al., 2022a).

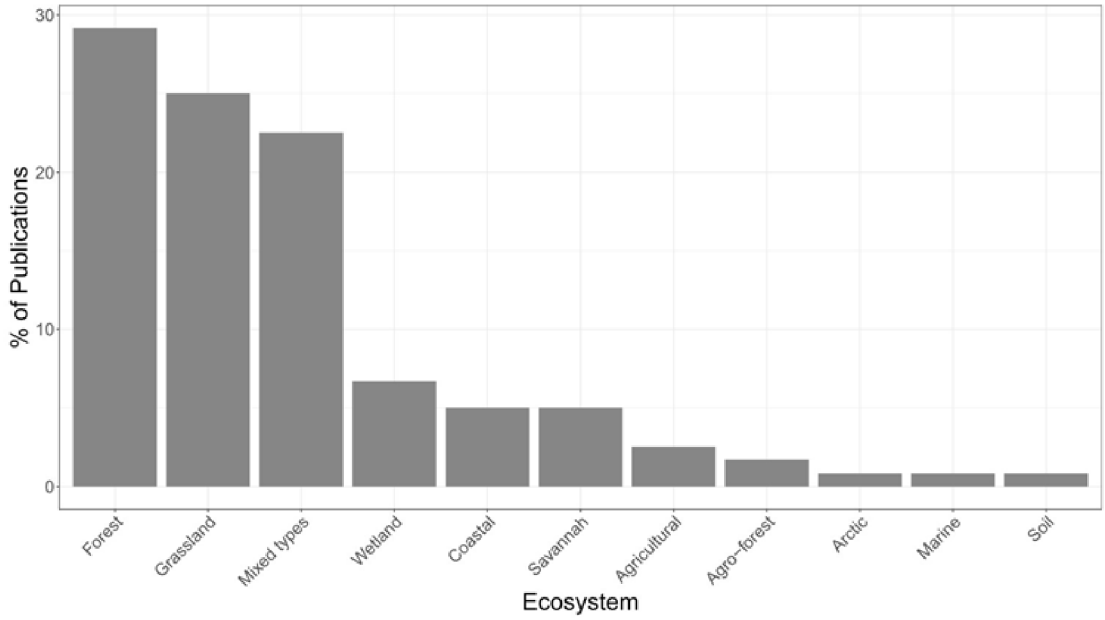

Fig. 4.3 Percentage of studies testing the Spectral Variation Hypothesis across different ecosystems.

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 & 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. 4.4 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 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.

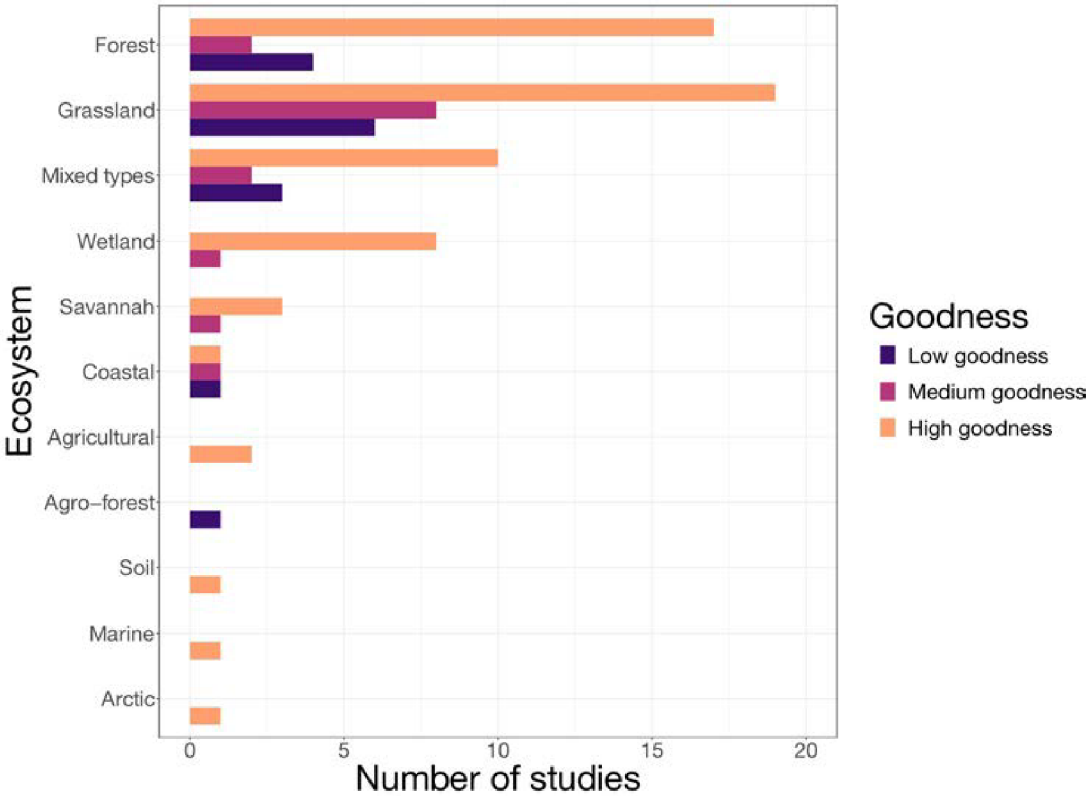

Fig. 4.4 Number of studies testing the Spectral Variation Hypothesis divided by goodness results. This is based on the highest correlation coefficient found in a study (R, Spearman's rho, accuracy, and Kendall's tau values). Ranging from 0 to 0.5 = Low goodness. From 0.51 to 0.65 = Medium goodness. From 0.66 to 1 = High goodness.

4.4 Remote sensing data used to test the SVH

4.4.1 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 4.2 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.

Table 4.2. 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.

Over the past 50 years, numerous Earth observation platforms have been developed and launched to collect images of the Earth's surface, with sensors exhibiting various spatial and spectral properties and the ability to capture repeated acquisitions over time (Crowley & Cardille, 2020; Wulder et al., 2022). According to our analysis (Fig. 4.5), 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 & 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 & 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.

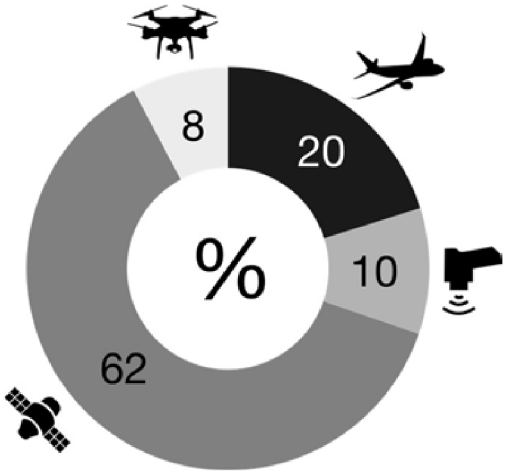

Fig. 4.5 Percentage of publications across remote sensing platforms (satellite, UAV, airplane and field).

Upon in-depth analysis of studies assessing the SVH across diverse platforms and sensors, clear patterns in accuracy emerge (Fig. 4.6). 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; Schmidtlein & 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 & 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.

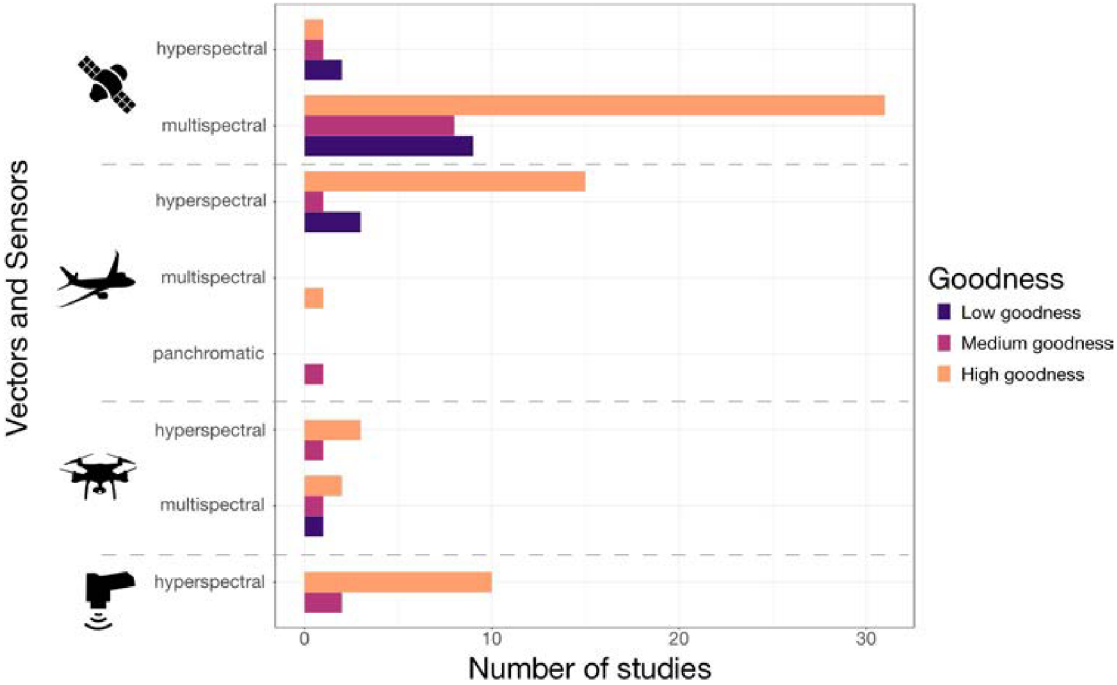

Fig. 4.6 Number of studies testing the Spectral Variation Hypothesis divided by levels of goodness across different platforms (satellite, airplane, unoccupied aerial vehicle, field) and sensors. The goodness is based on the highest correlation coefficient found in a study (R, Spearman's rho, accuracy, 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.

Among all the used sensors, Landsat has the highest representation with 31 studies of the total publications (Taddeo et al., 2021; Rugani & Rocchini, 2017; Perrone et al., 2023; Levin et al., 2007; Madonsela et al., 2017) (Fig. 4.7. The total sum of sensors exceeds the total number of analyzed studies because individual studies often tested different sensors). The series of Landsat satellites represents 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 applications, despite the potential of such data for biodiversity and natural retrospective ecosystems monitoring. It is followed by Sentinel-2 (Liccari 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 & 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 & Murwira, 2012), Pleiades (Khare et al., 2018; Khare et al., 2019), IKONOS (Nagendra et al., 2010; Végh & Tsuyuzaki, 2021), RapidEye (Khare et al., 2018), AVHRR (Oindo & Skidmore, 2002), CORONA (Shahtahmassebi et al., 2017), DESIS (Pacheco-Labrador et al., 2023), PlanetScope (Marzialetti 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.

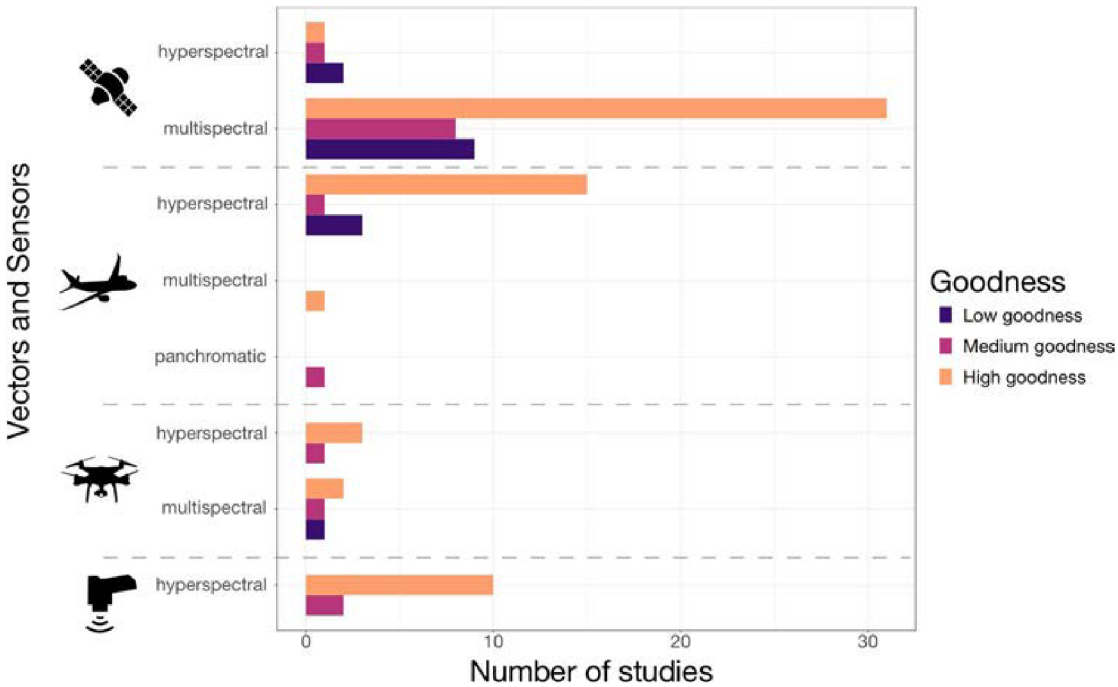

Fig. 4.7 Distribution of publications across remote sensing platforms (satellite, airplane, unoccupied aerial vehicle, field) with their spectral

sampling, spatial resolution and revisit frequency. Satellite sensors are featured within the grey dotted box.

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 & 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 & 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 resolution. 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. 4.6) 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. 4.8, uncovers ecosystem-dependent variations in the effectiveness of the SVH for biodiversity assessments.

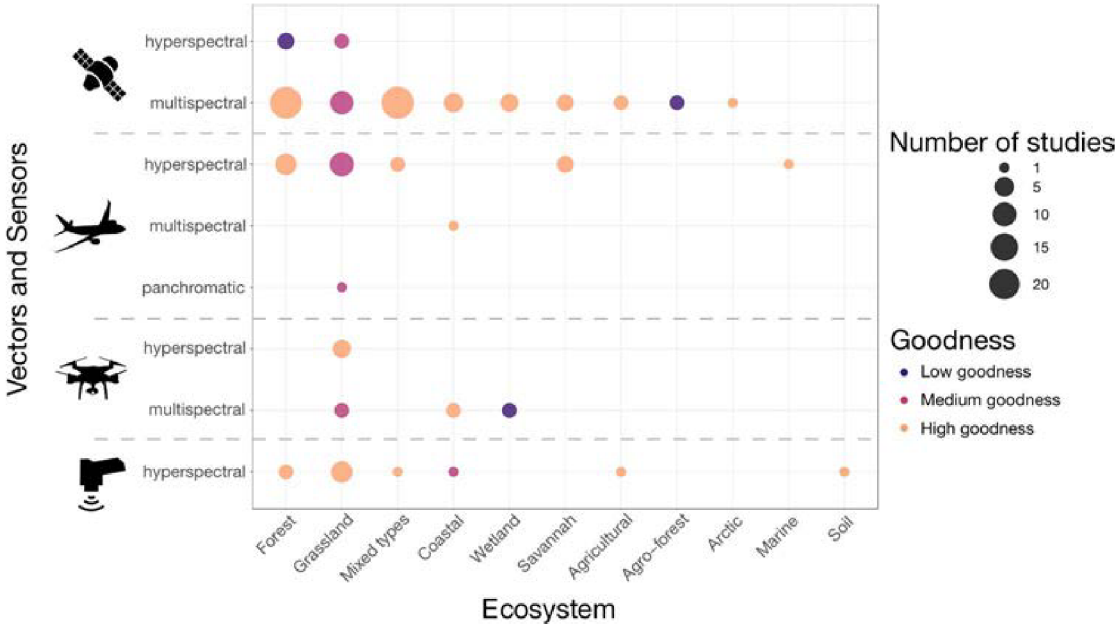

Fig. 4.8 Number of studies testing the Spectral Variation Hypothesis across different ecosystems using different platforms and sensors and levels of goodness (in this case the average value of all the studies per ecosystem). This was based on the highest correlation coefficient found in a study (R, Spearman's 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.

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). 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.

4.4.2 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 (Moudrỳ 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).

4.4.2.1 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. 4.8, 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. 4.8, 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.

4.4.2.2 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).

4.4.3 Spectral resolution

4.4.3.1 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 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 4.6 ('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.

4.4.4 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. 4.9 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; Gholizadeh 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 & Kuenzer, 2022), thus only assessing the SVH at a single temporal snapshot and not investigating aforementioned temporal influences.

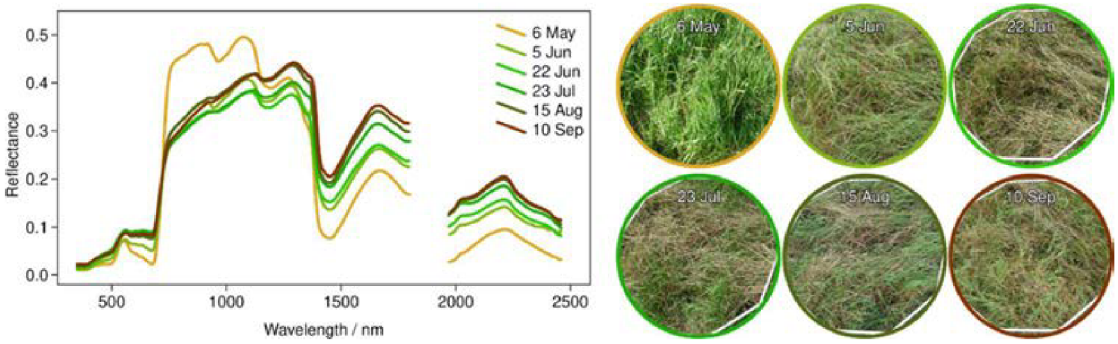

Fig. 4.9 Grassland seasonal development and related spectral signals of the canopy. Data are taken from Feilhauer and Schmidtlein (2011).

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 remote sensing as a tool for biodiversity monitoring.

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

4.5.1 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. 4.10A 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 4.3) are more appropriate when computed from low spectral 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 & 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 4.3 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 & 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.

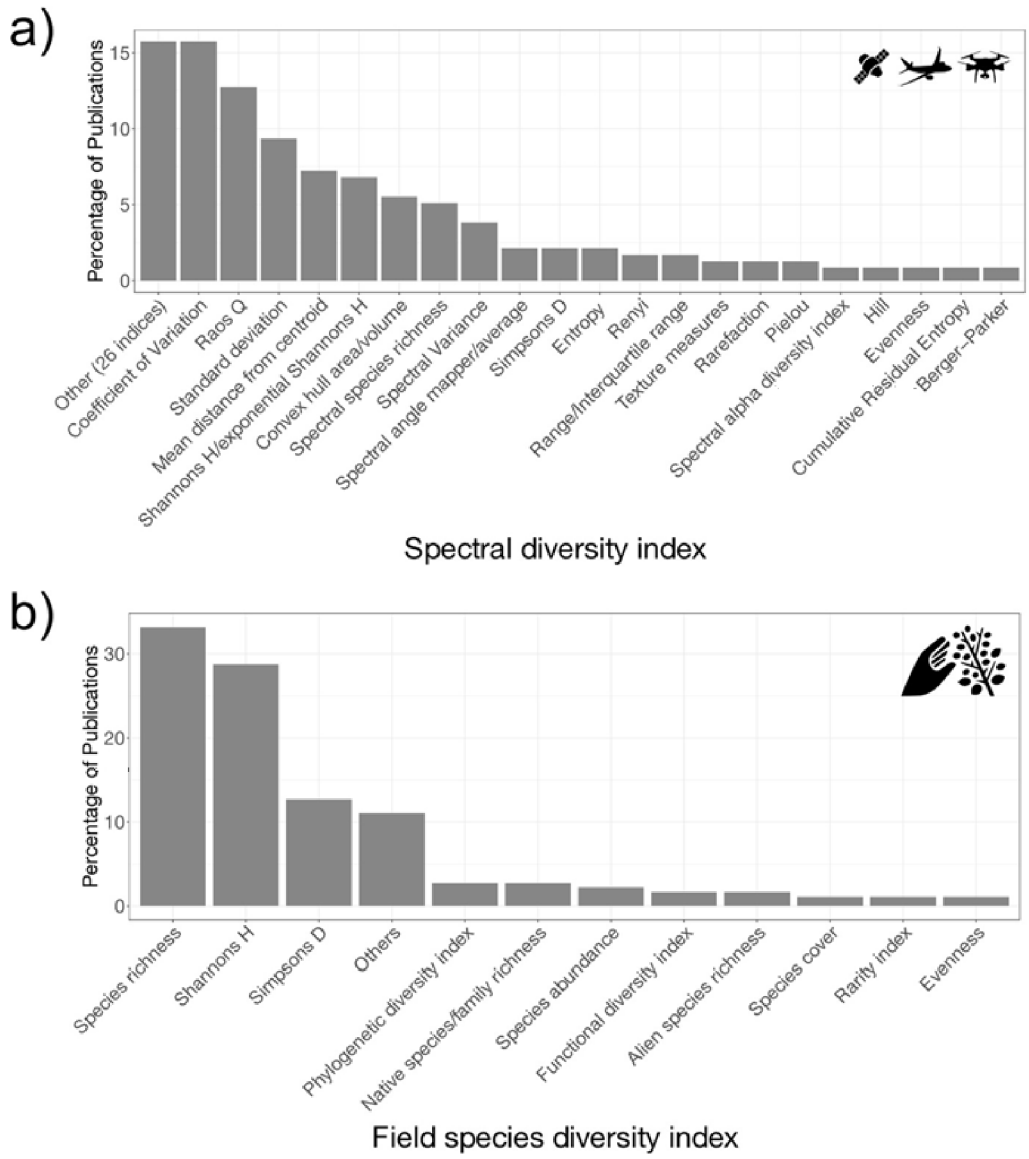

Fig. 4.10 Distribution of Publications across heterogeneity indices used to assess the Spectral Heterogeneity.

Table 4.3. 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

4.5.2 Open-source tools for spectral heterogeneity assessment

Recently, various authors have developed open-source packages facilitating the estimation of diverse heterogeneity indices (Table 4.4). 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*, 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 4.4. Open-source tools for spectral heterogeneity assessment in biodiversity studies.

Package name	Language	Key features	Source	Reference
rasterdiv	R	Computes various heterogeneity indices from raster datasets	CRAN	Rocchini et al., 2021c
spectralraomonitoring	Python	Calculates the Rao's Q diversity index from raster datasets	GitHub	Tassi et al., 2022
biodivMapR	R	Computes alpha and beta diversity from raster datasets	GitHub	Féret & de Boissieu, 2020
stdiversity	R	Calculates spectral diversity over time	GitHub	Rossi et al., 2021

		from optical information		
unmix	R	Assesses spectral diversity at subpixel level from optical information	GitHub	Rossi & Gholizade, 2023

Table 4.5 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.

Table 4.5. Open-source tools for assessing diversity via traits and methods for alpha and beta diversity estimation.

Package name	Language	Key features	Reference
vegan	R	Community ecology package, diversity indices	Oksanen, 2015
FD	R	Functional diversity metrics from traits	Laliberté et al., 2014

picante	R	Phylogenetic and trait diversity	Kembel et al., 2010
gdm	R	Generalized Dissimilarity modeling	Mokany et al., 2022

4.5.3 Field diversity data

A comprehensive review of field species diversity indices reveals a diverse landscape of metrics employed in biodiversity studies (Fig. 4.10B). 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.

4.5.4 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 & 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 & 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 & 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 & 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 (Gholizadeh et al., 2020; Arekhi et al., 2017), and the Hellinger distance (Liccari et al., 2022; Schweiger & 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 4.5.1) 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.

4.6 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, cannot 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; Chraibi 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.

4.6.1 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 (Chraibi 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 & Kuenzer, 2022; Chraibi 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 & Kuenzer, 2022; Chraibi et al., 2022; Ludwig et al., 2024).

4.6.2 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.

4.6.3 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 of considering ecological knowledge of 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 & 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.

4.6.4 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 Fassnacht 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.

4.6.5 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, Schmidtlein and Fassnacht (2017) stated that a moving window approach could fail to estimate plant diversity in a heterogeneous human-dominated landscape 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.

4.6.6 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 & 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.

4.7 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 interconnectivity 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.

4.7.1 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 & Gholizadeh, 2023). Furthermore, finer spatial resolution does not systematically benefit remote sensing applications (section 6.4). 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.

4.7.2 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' (HVH) and states 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; Moudrỳ et al., 2023; Alvites et al., 2021; Kissling & 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;

Fjeldså et al., 2012), emphasizing that complex topographic areas, such as mountain ecosystems, create diverse habitats where animal and vegetation species evolve and diversify.

4.7.3 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 spare, 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.

4.8 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 & 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).

Table

Study reference	Ecosystem/Area of study	Remote sensing data used	Goal of the study	Main Outcome	Heterogeneity	Field diversity index	Goodness standardized (h=high, m=medium, l=low)
Aneece et al., 2017	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 changes 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 et al., 2017	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, 2015	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 & Martin, 2009	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 & Martin, 2011	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 et al., 2022	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 and taxonomic diversity were strongly correlated	Spectral Variance	Species richness, Shannon's H and Simpson's D	h
Baldeck & Asner, 2013	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.	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 et al., 2019	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 correlates better with spectral heterogeneity).	Coefficient of variation, standard deviation	Species richness, Shannon's H, Simpson's D, Pielou	h
Cavender-Bares et al., 2020	NA	NA	NA	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.	NA	NA	NA
Chaurasia et al., 2020	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 et al., 2019	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 et al., 2021	Agro-forest ecosystem (Northern Range of Trinidad and Tobago, West Indies)	Satellite, Sentinel-2	Assess tree alpha and beta diversity.	No direct correlations between diversity 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.	Exponential Shannon's H (alpha). Bray-Curtis (beta)	Exponential Shannon's H (alpha). Bray-Curtis (beta)	l
Chraibi et al., 2022	Tropical forest (Cameroon)	Satellite, Sentinel-2	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 et al., 2021	Grassland ecoststem, mesic meadow (South Bohemia, Czech Republic)	UAV, multispectral data	Assess the relatonship 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 et al., 2019	Different habitats (Benin, West Afrca)	Satellite, MODIS	Assess environmental and species tick diversity.	Positive relationships between spectral diversity indices and the abundance of some tick species.	Variance, entropy, contrast, Rao's Q	Abundance	l
Dahlin et al., 2016	Different habitats (mixture of agricultural lands, forests, and lakes)	Airborne, hyperspectral data (AVIRIS)	Assess the applicability of community assembly theory concepts to imaging spectroscopy, to explore	The study applies community assembly theory to imaging spectroscopy, distinguishing between strongly filtered	Sum of the variance in the first three PCs,	NA	NA

	in southwestern Michigan, USA		spectral diversity–area relationships and the Functional Attribute Representation approach in differentiating between forest patches and agricultural fields.	agricultural fields and near-random mesic forests in a wildland–agriculture matrix. The spectral diversity–area relationships provide insights into landscape-level diversity patterns, demonstrating the method's potential in diverse ecosystems.	convex hull volume		
Fassnacht et al., 2022	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 & Asner, 2014	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 & de Boissieu, 2020	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 et al., 2021	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 holds 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	Shannon's H, species richness	h

					richness, spectral distance		
Gastauer et al., 2022	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 et al., 2022	Grassland ecosystem (Joseph H. Williams Tallgrass Prairie Preserve, Oklahoma, USA)	Airborne and satellite (DESIS) hyperspectral data	Assess grassland alpha diversity. Understand how the management practices (based on prescribed fire) influence the relationship between spectral diversity and species diversity at different spatial resolutions (due to different vectors).	The relationship between spectral diversity and species diversity is affected by the species diversity index, by the time since fire occurred and by the spatial scale.	Coefficient of variation, convex hull volume, spectral angle mapper.	Shannon's H, Simpson's D, species richness	m for satellite and h for airborne
Gholizadeh et al., 2020	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 et al., 2019	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 flight direction in the relationship between 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 improves the relationship. The higher the spatial resolution, the higher the accuracy of the relationship.	Coefficient of variation	Species richness, Shannon's H	h
Gholizadeh et al., 2018	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, 2005	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

Gould, 2000	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 et al., 2010	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 et al., 2012	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 et al., 2021	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 spectra through the use of different radiative transfer models), taxonomic,. in-situ trait diversity and confounding factors.	Spectral diversity of Sentinel-2 is dominated by variation in vegetation cover (vegetation traits and 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 et al., 2013	Marine environment (Saaremaa Island, eastern Baltic Sea, Estonia)	Airborne, hyperspectral data	Assess the 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	Mean distance from centroid	Abundances, biomasses	l

				significant positive correlations with spectral heterogeneity			
Hernández-Stefanoni et al., 2012	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
Heumann et al., 2015	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 et al., 2019	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 in primis and LiDAR to a lower extent) can be used to assess beta diversity in elevation between different communities	Euclidean distance between plots in an NMDS space	Relative abundance	h
Imran et al., 2021	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 influences the SVH.	The relationship between spectral heterogeneity and species diversity was stronger in the study area characterized by a low number of species (the best spatial resolution was 1mm) while it was lower in the areas with many species	Coefficient of variation, standard deviation	Species richness, Shannon's H, Simpson's D, evenness	m

				(1 cm was the best spatial resolution)			
Jackson et al., 2022	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, 2022	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 measures and taxonomic groups, utilizing data from diverse surveys and advanced modelling techniques.	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 sampling completeness influencing prediction accuracy.	Mean Euclidean distance to PCA centroid	Total Species richness, total log-transformed abundance, the arcsine square root transformed probability of interspecific encounter as a measure of assemblage evenness, logit transformed pairwise Sørensen similarity index as a measure of difference in	1

						assemblage composition	
Kacic & Kuenzer, 2022	NA	NA	Review of spectral diversity for assessment of biodiversity in forest ecosystems.	NA	NA	NA	NA
Khare et al., 2018	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 et al., 2019	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 et al., 2021	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 et al., 2020	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 of a novel method to partition plant spectral gamma-diversity (region-wide spectral	Spectral Variance (alpha, beta and gamma)	NA	NA

				diversity) into alpha-diversity (within communities) and beta-diversity (among communities) components. This approach enables the identification of prominent spectral features. It also allows the assessment of individual plant communities' contributions to spectral diversity.			
Levin et al., 2007	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 rarity was negatively correlated with NDVI.	Mean, standard deviation, coefficient of variation	Species richness, relative range size, rarity	h
Liccari et al., 2022	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 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 et al., 2017	Grassland ecosystem (Southwest France)	Satellite, Spot 5	Assess vegetation species diversity.	Proposal of a new spectral heterogeneity measure based	Spectral clustering	Shannon's H	l

				on Spectral clustering. Low correlation between Spectral Heterogeneity indices and Shannon's H, maybe due to the spectral and spatial resolution of the used images.	algorithm, mean distance from centroid, entropy		
Louail et al., 2022	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 variable of a quantitative map of the potential ecosystem services provided by the forest	Rao's Q, Shannon's H	NA	NA
Madonsela et al., 2017	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 et al., 2021	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 levels of anthropogenic pressure.	Rao's Q	Low and high human-pressure coastal beaches	NA
Mapfumo et al., 2016	Savanna (dry, wet and coastal savanna woodlands, Zimbabwe, Zambia and Mozambique)	Satellite, Landsat 8 and Worldview 2	Assess the relationship between spectral diversity and tree species diversity.	The relationship between diversity and spectral variation of NDVI holds true in different ecosystems following a linear and/or hump-shaped relationship	Coefficient of variation	Shannon's H and Simpson's D	h

Marzialetti et al., 2021	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
Marzialetti et al., 2020	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 landscapes as coastal dunes.	Rao's Q	NA	h
Michele et al., 2018	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 performs better than 30m of Landsat 8).	Rao's Q	Shannon's H	h
Möckel et al., 2016	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 on the relationships.	Species diversity was estimated successfully by the spectral response approach but not with through SVH.	Mean distance from the centroid	Species richness, Simpson's D	l
Mohapatra et al., 2019	Grassland ecosystem (alpine zone of the Gulmarg target region, state of Jammu and Kashmir in India)	Satellite, Resourcesat-2	Assess vegetation species diversity at the 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-	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

				alpine zone having the highest biodiversity. The importance of higher spatial resolution satellite data for accurate field-level biodiversity assessments is emphasised.			
Monteiro et al., 2021	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 et al., 2022	Different habitats (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 of natural water pans.	Spectral heterogeneity measured with 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 et al., 2012	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 et al., 2010	Forest (Dry tropical forest, central India)	Satellite, IKONOS and Landsat ETM+	Analyze the link between spectral and vegetation species diversity. Assess the effect of spatial resolution.	Landsat ETM+ images perform 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 & Skidmore, 2002	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
Oldeland et al., 2010	Savannah (Central Namibia)	Airborne, hyperspectral data	Analyze 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 scales, abundance-based diversity measures (such as Shannon's H index) performed better than indices that account only for the number of species (e.g. species richness).	Mean distance from centroid	Species richness, Shannon's H	h
Onyia et al., 2019	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's 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.	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 et al., 2022	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 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	Functional richness, evenness, diversity, dispersion, Rao's Q	Species richness, Shannon's H	L for hyperspectral satellite and m for multispectral satellite

				resolution was found to be the most critical limitation. Sentinel-2 imagery, outperformed DESIS in estimating plant diversity, aligning with simulation results.			
Pacheco-Labrador et al., 2023	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 from Remote Sensing 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.	Spectral Variance, Rao's Q and Functional richness	NA	NA
Pafumi et al., 2023	Different habitats (fine mosaic of natural and semi-natural habitats, with grasslands, downy oak woodland and black pine plantations) in the Classical Karst, a limestone plateau in the provinces of Trieste and Gorizia- Italy.	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 for habitat classification and establish a robust framework for incorporating multitemporal remotely sensed data into habitat classification.	The study underscores the effectiveness of integrating Spectral Heterogeneity (SH) measures, especially spectral β-diversity, and multitemporal frameworks for accurate habitat mapping, offering valuable insights into vegetation types in complex landscapes using remote sensing.	Rao's Q index and alpha and beta diversity (spectral species) measured with biodivMapR	NA	NA
Palmer et al., 2002	Grassland ecosystem (Tallgrass Prairie	Airborne, Panchromatic images	Assess the biodiversity of vascular plants.	Positive and significant relationship between the spectral heterogeneity	Mean distance to the nearest neighbour, mean	Species richness, number of	m

	Preserve, Oklahoma, USA)			measured through heterogeneity indices at certain spatial scales and vegetation diversity (through three diversity indices).	distance from the spectral centroid, leverage	infrequent species, rarity	
Pangtey et al., 2023	Forest ecosystem (Himalayan region of Uttarakhand, India)	Satellite, Sentinel-2	Assess the performance of the 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 et al., 2021	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 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 analyzing 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 et al., 2022	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 climate variables influence plant diversity across diverse grassland types, emphasizing the importance of considering climatic factors in predicting spectral plant diversity.	Coefficient of variation, MSAVI	Species richness	h
Perrone et al., 2023	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.	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 et al., 2019	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 heterogeneity in canopy optical information could explain beta and gamma diversity.	Coefficient of variation	Exponential Shannon's H	h

			spatial scales (plot and patch scales).				
Rahmanian et al., 2023	Grassland ecosystem (Dakal-kooh 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 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 et al., 2023	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
Rocchini, 2007	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 in assessing species richness at the local scale. Coarse-resolution images (from Aster and Landsat ETM+) showed contrasting results. The spectral resolution seemed to play a crucial role in compensating for the lack of spatial resolution.	Mean distance from centroid	Species richness	h
Rocchini, 2009	Theoretical description	NA	Explain a new method based on ecological theory for	NA	NA	NA	NA

			assessing spectral heterogeneity at multiple scales simultaneously.				
Rocchini & Neteler, 2012	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 tool for the assessment of landscape diversity.	Rank–abundance diagram	NA	NA
Rocchini & Vannini, 2010	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 correlation between NDVI and spectral heterogeneity is possible.	Standard deviation	NA	NA
Rocchini et al., 2010	NA	NA	First review of the SVH	NA	NA	NA	NA
Rocchini et al., 2004	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 the spatial extent of the studied area.	Mean distance from centroid	Species richness	h
Rocchini et al., 2014	Different habitat (the whole North America)	Satellite, MODIS	Assess vegetation alpha diversity (species richness) and the impact of the spatial extent of the study area.	Positive and significant correlation between spectral diversity and species richness, however, the highest amount of variance was explained by the spatial extent of the sampling units.	Natural logarithm of the spectral richness	Species richness	m
Rocchini et al., 2018	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 proposes different techniques to measure beta diversity from remote sensing optical data: a multivariate statistical analysis, the	Rao's Q	NA	NA

				spectral species concept, self-organizing feature maps, multidimensional distance matrices and through the concept behind the SVH using the Rao's Q diversity index.			
Rocchini et al., 2017	Theoretical description and different habitats (case study over the whole Europe)	Satellite, MODIS	Explanation of the Rao's Q heterogeneity 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 region is shown. The free available R code is presented.	Rao's Q, Shannon's H	NA	NA
Rocchini et al., 2021	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 et al., 2019	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 calculating spatiotemporal beta diversity by using the temporal variation of the Raos' Q index.	Rao's Q	NA	NA
Rocchini et al., 2011	Different habitats (bio-geographic 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

Rocchini et al., 2007	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 et al., 2021	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 et al., 2022	NA	NA	Review of the spectral species concept used within the SVH.	NA	NA	NA	NA
Rocchini et al., 2021	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 et al., 2022	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 assesment of vegetation species diversity (alpha and beta).	NA	Shannon's H (alpha), Bray-Curtis (beta)	NA	NA

Rocchini et al., 2008	Different habitats (bio-geographic regions over the whole Switzerland)	Satellite, Landsat ETM+	Assess species rarefaction by using spectral heterogeneity.	Spectral rarefaction shows to be a good proxy for species rarefaction curves.	Spectral rarefaction	Species rarefaction	NA
Rocchini et al., 2009	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 et al., 2023	Grassland ecosystem (Nature Conservancy's TGPP, Oklahoma, USA)	Airborne and spaceborne, hyperspectral (DESIS)	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 et al., 2021	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 spatiotemporal dissimilarities between plant communities in the calculation of spectral diversity.	Spectral variance (alpha, beta and gamma)	Bray-Curtis dissimilarity	m
Rossi et al., 2022.	Grassland ecosystem (alpine grassland, Switzerland)	UAV multispectral, airborne data	Estimation of plot-level vegetation species diversity. Investigation of confounding factors of the spectral	Success of SVH depends on spatial resolution, spectral metrics, and awareness of confounding factors (e.g. plant	Coefficient of variation, convex hull volume, spectral richness	Species richness	m for UAV and l for airborne

		AVIRIS-NG. Hyperspectral fused data	diversity–biodiversity relationship.	biomass), which may be ecosystem specific.			
Rugani & Rocchini, 2017	Agricultural ecosystems (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 local or regional biodiversity change.	Interspersion	NA	NA
Takougoum Sagang et al., 2022	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 makes it possible to characterize 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.	Spectral dissimilarity on spectral species	NA	NA
Sakowska et al., 2019	Grassland ecosystem (Viote del Monte Bondone, Trentino province - Italy)	Airborne (hyperspectral) and spaceborne (Sentinel-2)	Exploring optical diversity and productivity patterns across different scales.	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	Coefficient of Variation	NA	NA

				relationships at increasing pixel sizes.			
Schmidtlein & Fassnach, 2017	Different habitats (bio-geographic regions in Southern Germany)	Satellite, MODIS	Assess vegetation species richness.	SVH does not hold across landscapes using MODIS images. The correlations are influenced by the location and extent of the study area, by the heterogeneity indices and by the seasonality.	Mean distance from centroid, number of classes of an unsupervised k-means classification in each mapping unit	Species richness	l
Schweiger & Laliberté, 2022	Different Habitats (bio-geographic regions across the USA)	Airborne, hyperspectral data	Assess the relationship between spectral heterogeneity and vegetation alpha and beta diversity at the landscape level.	The spatial heterogeneity assessed at the spatial resolution of 30m (same as some upcoming satellite missions) catches 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.	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
Schweiger et al., 2018	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	Functional and phylogenetic distances	h

					(evenness) and dispersion (distance from centroid)		
Shahtahmassebi et al., 2017	Different ecosystems (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 et al., 2015	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 drivers of the spectral variation.	Coefficient of variation (alpha). Spectral similarity (beta)	Species richness (alpha). Spectral distance-decay (beta)	h
Sun et al., 2021	Forest (urban forests, cities of Beijing and Huai'an, China)	Satellite, Pléiades-1 and Sentinel-2	Estimate vegetation species diversity by combining the SVH with the productivity hypothesis through the new RSPD index.	The 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 et al., 2019	Wetland ecosystems (USA)	Satellite, Landsat 5 TM and	Assess the relationships between satellite-derived vegetation indices/spectral	Positive correlations between plant species richness/diversity and spectral	Standard deviation	Species richness, native species	h

		Landsat 7 ETM+	heterogeneity (spectral greenness and heterogeneity) and plant species richness/diversity.	greenness and heterogeneity, especially in models that combine both the information.		richness, family richness, alien species richness, Shannon's H, species cover	
Taddeo et al., 2021	Wetland ecosystems (USA)	Satellite, Landsat 5 TM, Landsat 7 ETM+ and airborne multispectral aerial 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 sites 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 et al., 2020	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 et al., 2023	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 et al., 2022	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 the mean of NDVI alone, and to evaluate the suitability of Hill numbers in spectral-species diversity relationship research, addressing questions about the limitations of the mean of NDVI and exploring predictive abilities across the entire diversity continuum.	The study highlights limitations in using the 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 & Gil, 2020	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
Tassi et al., 2022	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 et al., 2022	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 points in time.	Coefficient of variation	Species richness, Simpson's D, Simpson evenness	h
Thouverai et al., 2021	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	NA	Shannon's H, Pielou's, Berger Parker, Rao's Q, CRE, Renyi, Hill.	NA	NA

			assessment of habitat heterogeneity.				
Torresani et al., 2021	Forest (alpine coniferous forest, Province of Bolzano/Bozen, Italy	Satellite, Sentinel-2	Understand which optical traits drive 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 et al., 2022	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 towers were located) through the SVH.	The spectral variation of NDVI images was 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
Torresani et al., 2019	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). The spatial resolution of the images affects the results (Sentinel-2 performed better than Landsat 8)	Rao's Q, Coefficient of variation	Shannon's H	h
Ustin & Gamon, 2010	NA	NA	NA	The paper proposes "optical types," a novel concept merging plant functional types with advanced remote sensing, to address scale-dependence	NA	NA	NA

				issues in vegetation classification, aiming for a direct correlation between ecological traits and remote sensing data beyond traditional discrete categorizations.			
Van Cleemput et al., 2023	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.	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.	Coefficient of Variation, spectral angle mapper, convex hull volume	Species richness, Shannon's H, inverse Simpson's D	h
Végh & Tsuyuzaky, 2021	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.	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.	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	species richness, Shannon's H, Simpson's D, Shannon's J, true diversity of order 1, and true diversity of order 2	m

					diversity of order 2		
Villoslada et al., 2020	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 might be due to the sensitivity of spectral diversity to biomass or due to artefacts produced by the high resolution of the UAV images.	Standard deviation	Shannon's H	l
Wallis et al., 2023	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 disentangle the influence of tree composition, tree diversity, and unmeasured canopy aspects using structural equation modelling.	Spectral diversity is associated with tree species diversity, no direct or indirect effects on carbon content were observed. 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 et al., 2022	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 analyze 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 & Gamon, 2019	NA	NA	NA	Review on remote sensing of biodiversity, outlining major and emerging applications related to biodiversity assessment using remote sensing, with emphasis on recent advancements in the detection of plant diversity through spectral diversity.	NA	NA	NA
Wan et al., 2022	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 ecosystems. Understand how the seasonal changes of leaf pigments influence the relationship between spectral diversity and species diversity.	Strong scale dependence on the seasonal relationship between spectral heterogeneity and species diversity. Phenological effects (seasonal patterns), biological, statistical and ecological (effect of soil) influence the spectral heterogeneity at the leaf and canopy level in grassland ecosystems.	Coefficient of variation	Shannon's H	h
Wang et al., 2018a	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	Coefficient of variation	Species Richness, Shannon's H, Simpson's D, phylogenetic species variation, phylogenetic species evenness	h for field and l for airborne

				detecting species richness and evenness, but weaker detection of phylogenetic diversity.			
Wang et al., 2016	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 et al., 2018b	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 J	h
Warren et al., 2014	Different habitats (forests, grasslands, plantations, Grafenwöhr Training Area, Bavaria, Germany)	Satellite, IKONOS	Assess the relationship between spectral heterogeneity, habitat diversity and plant species richness.	Good correlation between spectral heterogeneity and plant species richness as well as with habitat heterogeneity (the latter was less strong).	168 indices	Species richness	h
White et al., 2010	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	Normalized root mean square difference based on the number of unique species	l

					deviation values for each band.	and their relative abundance	
Xu et al., 2022	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 soil information.	Coefficient of variation, convex hull volume, convex hull area	Species richness, Shannon's H	h
Zhang et al., 2023	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 et al., 2021	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

5

The relationship between spectral and plant diversity: Disentangling the influence of metrics and habitat types at the landscape scale

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Abstract

Biodiversity monitoring is crucial for ecosystem conservation, but ground data collection is limited by cost, time, and scale. Remote sensing is a convenient approach providing frequent, near-real-time information with fine resolution over wide areas. According to the Spectral Variation Hypothesis (SVH), spectral diversity (SD) is an effective proxy of environmental heterogeneity, which ultimately relates to plant diversity. So far, studies testing the relationship between SD and biodiversity have reported contradictory findings, calling for a thorough investigation of the key factors (i.e., metrics applied, habitat type, scale, and temporal effects) and conditions under which such a relationship exists. This study investigates the applicability of the SVH for monitoring plant diversity at the landscape scale by comparing the performance of three types of SD metrics. Species richness and functional diversity were calculated for >2000 grid cells of $5' \times 3'$ covering the Czech Republic. Within each cell, we quantified SD using a Landsat-8 "greenest pixel" composite by applying (i) the standard deviation of NDVI, (ii) Rao's Q entropy index and (iii) the richness of "spectral communities". Habitat type (i.e., land cover) was included in the models of the relationship between SD and ground biodiversity. Both species richness and functional diversity showed positive and significant relationships with each SD metric tested. However, SD 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. Our results underline that despite the stability of the significance of the relationship between SD and plant diversity at this scale, the applicability of SD for biodiversity monitoring is context-dependent and the factors mediating such a relationship must be carefully considered to avoid misleading conclusions.

Keywords: biodiversity monitoring, plant functional traits, remote sensing, species richness, spectral variation hypothesis, vascular plants.

5.1 Introduction

Biodiversity supports multiple ecosystem functions, which ultimately provide the ecosystem services essential to sustain human societies (Cardinale et al., 2012; de Groot et al., 2002). However, human exploitation of Earth's natural resources has led to alterations in plant species' distribution and abundance to the extent that over one-fifth of all vascular plant species are threatened (Díaz and Malhi, 2022; Willis, 2017). There is an urgent need to improve ways to monitor biodiversity effectively across broad spatial scales and assess how plant communities respond to global change. Nonetheless, the ability to measure and monitor biodiversity continues to lag behind (Skidmore et al., 2021). Remote sensing (hereafter RS) offers remarkable opportunities for biodiversity monitoring from local to global scales (Rocchini et al., 2010; Wang & Gamon, 2019). Among the approaches studied, spectral diversity (SD), originally developed in the framework of the Spectral Variation Hypothesis (SVH, Palmer et al., 2000, 2002), has been gaining attention as a basis for relating the remotely sensed spectral signal to ground biodiversity at different spatial scales and resolutions (Fassnacht et al., 2022; Marzialetti et al., 2021; Rocchini et al., 2010, 2021b; Tagliabue et al., 2020; Torresani et al., 2019). At coarser spatial resolution, the underlying assumption is that the spatial variation in reflectance values in a given area (i.e., SD) is likely correlated with the spatial variation in the environment and therefore related to the number of species present. At very fine spatial resolution, the relationship is assumed to be direct, with SD directly related to plant diversity through the diversity of species-specific optical traits associated with plant functional and structural properties (Ustin & Gamon, 2010).

Despite the potential of RS in biodiversity monitoring systems, the hypothesised relationship between spectral diversity and plant ground diversity still needs to be addressed (Fassnacht et al., 2022; Pacheco-Labrador et al., 2022). Although several empirical studies have validated the use of spectral diversity to estimate plant species diversity (Levin et al., 2007; Rocchini, 2007; Rocchini et al., 2014), others have criticised it for being unstable and not reliable in every context (Conti et al., 2021;

Schmidtlein and Fassnacht, 2017). Such inconsistent findings may be due to a need for more systematic consideration of the key factors that influence the relationship between plant biodiversity and SD, which complicates the interpretation of spectral variation in many contexts (Fassnacht et al., 2022). Recently, Fassnacht et al. (2022) discussed four of the most important factors that may affect such a relationship: 1) the scale considered, both in terms of spatial extent (i.e., size of the study area) and spatial grain (i.e., pixel size); 2) reflectance changes over time (e.g., seasonality); 3) effects of the metric chosen for quantifying SD; and 4) the identity and number of habitat or vegetation types considered (Czyż et al., 2023; Gamon et al., 2019; Rocchini et al., 2010, 2018; Rossi et al., 2021; Schmidtlein and Fassnacht, 2017; Wang et al., 2022).

The type of habitats considered may strongly influence the relationship between SD and biodiversity, so all other factors should be adjusted accordingly. For instance, small patches of calcareous grassland embedded in intensively managed arable land may be very rich in species. However, when observed with medium-resolution sensors, they have low SD, while surrounding arable land has high SD but very low species richness (Fassnacht et al., 2022). Similarly, the spatial changes in fractional vegetation cover (which encompasses spatial variability in canopy architecture, fraction of bare soil, and plant litter spectra) can be different across habitats and, thus, strongly affect the spectral signal (Hauser et al., 2021b). Consequently, not considering the variety and types of habitat can be particularly problematic when multiple habitat types are examined simultaneously, as is the case at large to medium observation scales (Fassnacht et al., 2022; Schmidtlein and Fassnacht, 2017). Similarly, the SD metrics are thought to be linked to plant diversity through different pathways, which may lead to different results. Several SD metrics have been proposed so far as proxies for biodiversity, with no consensus on which of them best fulfils this role. Wang and Gamon (2019) have described three main classes of SD metrics:

i. metrics based on variation in traditional vegetation reflectance indices based on the correlation between productivity and plant diversity (Tilman et al., 2001; Zhang et al., 2012);

ii. metrics based on spectral information content, which condense the full-spectral information through statistical metrics of variability or spectral entropy;

iii. metrics based on "spectral species" (or "spectral types") that have similar spectral signatures and are derived from partitioning the spectral space (Féret and Asner, 2014).

To date, most empirical studies investigating the relationship between SD and plant diversity have relied on limited datasets (Fassnacht et al., 2022). In addition, efforts to link plant diversity at the landscape scale to SD have focused mainly on taxonomic diversity (e.g., species richness or evenness). However, species influence ecosystem processes and stability through their functional composition, diversity, and abundance (de Bello et al., 2010; Tilman et al., 1997). Functional diversity represents the variability in plant functional traits in a given area. The spatiotemporal mapping of functional diversity at large scales could thus support assessing how environmental changes affect ecosystem functioning. Nonetheless, the potential of SD to infer functional diversity at the landscape scale remains to be demonstrated (Cavender-Bares et al., 2022; Frye et al., 2021; Hauser et al., 2021b; Schweiger et al., 2018).

Here we investigate whether plant diversity (species richness and functional diversity) at the landscape scale is related to SD. To assess the context-dependence of such a relationship, we will test the performance of three types of SD metrics, taking into account the effects of habitat types. Specifically, we rely on an extensive, spatially continuous, field-collected dataset covering the Czech Republic and a multi-temporal Landsat-8 OLI composite.

5.2 Materials and Methods

5.2.1 Plant diversity data

Data on plant diversity were obtained from the Pladias Database of the Czech Flora and Vegetation (Chytrý et al., 2021). This nationwide database contains >13 million records of species occurrence (many of them critically

reviewed and validated) and traits of almost 5000 taxa (species, subspecies, varieties, and hybrids) of the Czech vascular flora (Chytrý et al., 2021; Wild et al., 2019). We used the latest update of taxonomic concepts and nomenclature (Kaplan et al., 2019). The collection of the species records used for our analysis started in the late 18th century, but >60% of the records were collected in the last 20 years (for a detailed description of the records, see Wild et al., 2019). The data include all native or spontaneously established alien vascular plant taxa, as well as some commonly cultivated crops and woody plants. The study area covers an altitudinal range from 115 to 1603 m a.s.l. with annual precipitation varying from about 400 mm to 1450 mm (Brázdil et al., 2021; Tolasz et al., 2007) and a wide range of environmental conditions, from dry and warm forest-steppe areas to mountainous areas with subalpine vegetation (Chytrý et al., 2017). We counted the number of species, i.e., species richness (SR), and calculated functional diversity (FD) in grid cells of 5′ × 3′ (approx. 6.0 × 5.5 km), forming a grid of >2000 cells covering the entire Czech Republic (Fig. 1) (Wild et al., 2019). The size of the grid cells corresponds to quadrants of the basic fields of the grid template used for Central European floristic mapping (Central European Basic Area; Petřík et al., 2010). All marginal grid cells that were not entirely within the country were excluded from our analysis to avoid potential bias due to undersampling.

To calculate FD, we selected a list of optically and ecologically relevant functional traits. The majority of traits were available in Pladias (see Chytrý et al., 2021 for their description): Mean Height, Growth Form, Life Form, Leaf Shape, Flower Colour, and three traits were taken to Pladias from the BiolFlor database (Klotz et al., 2002): Leaf Life Span, Leaf Anatomy and Reproduction Type. We also added three traits from the LEDA database (Kleyer et al., 2008) that are not included in the Pladias Database: Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), and Seed Mass (Supplementary material 5.A). We relied on database-derived functional trait values as it was not possible to measure them for all species in each grid cell. Since the trait data used in this study come from databases of Central European flora, we assume they accurately represent the trait values present in our study region. For those numerical traits which have

measurements from multiple individuals (i.e., traits from LEDA database), we confirmed that, within our dataset, interspecific variation is higher than intraspecific variation. We did it by comparing, for each trait, the standard deviation calculated from the mean values of each species with the mean value of all species' standard deviations (Supplementary material 5.A). The assumption behind the use of database-derived data is that they are a good approximation of the actual trait diversity of the area. The mean trait values coming from databases result from hundreds of measurements done in different habitats, under different management practices, and variable soil conditions. For this reason, the intraspecific variability that can be estimated from the database approximately corresponds to the in situ intraspecific variability. We compiled trait values for a minimum of 1463 species for LDMC, and for a maximum of 3087 species for Leaf Shape. To account for potential bias due to missing values, only those grid cells that had at least 70% coverage for each of the traits considered were included in the analysis, resulting in a total of 2361 grid cells. For each grid cell, we calculated FD as the mean pairwise distance (MPD) between species in the functional trait space defined by the above-mentioned traits (Fig. 5.1).

Trait distances were measured using Gower distance, where each numerical trait is first standardised by dividing each value by the range of the corresponding trait, after subtracting the minimum value; consequently, the rescaled trait variable has the range [0,1] (Gower, 1971).

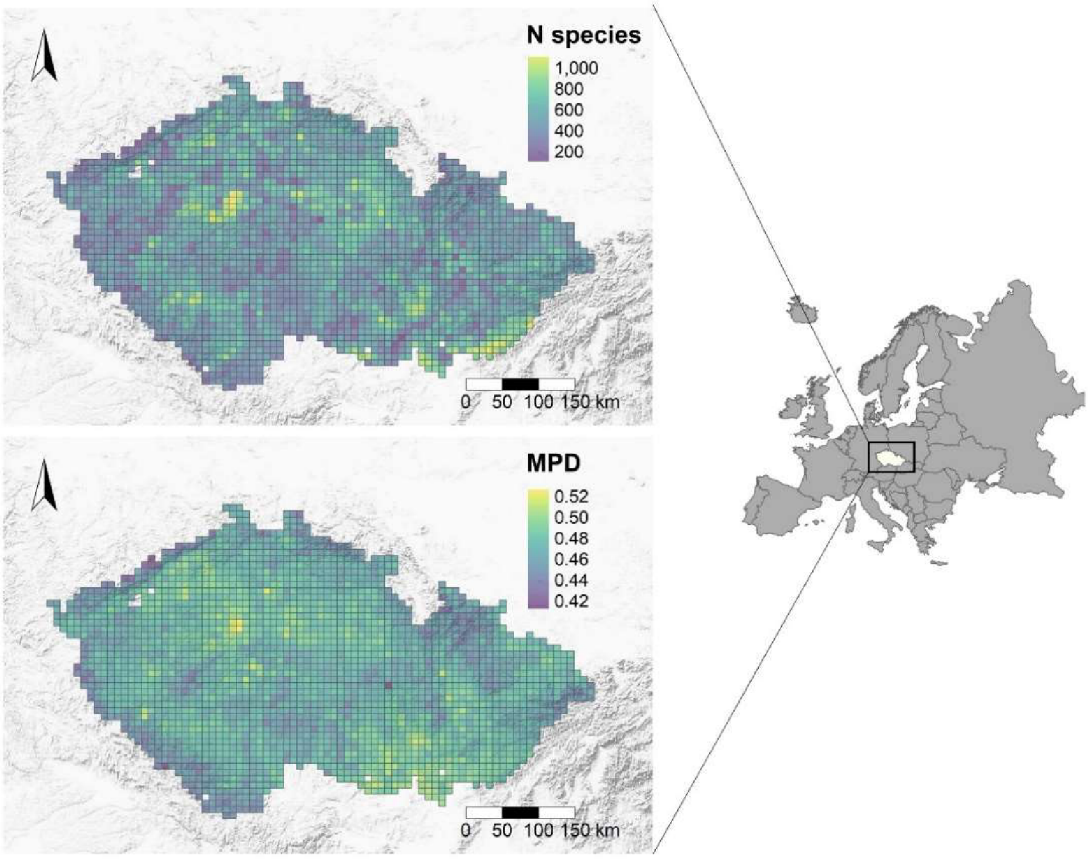

Fig. 5.1. Plant diversity within each grid cell (n = 2361) covering the Czech Republic. Species richness (SR, number of species, top) was obtained from the Pladias Database of the Czech Flora and Vegetation (Chytrý et al., 2021). Functional diversity (FD), expressed as mean pairwise distance (MPD) in plant traits (bottom), was calculated based on a list of functional traits available in the Pladias and LEDA databases (Chytrý et al., 2021; Kleyer et al., 2008).

5.2.2 Spectral data

We used the USGS Landsat 8 atmospherically corrected Surface Reflectance catalogue of data acquired with the Operational Land Imager (OLI) sensor and available in Google Earth Engine (GEE) (Gorelick et al., 2017). Specifically, we used Earth's atmospherically corrected surface reflectance in six bands in the visible (B2, B3, B4), near infrared (B5) and short-wave infrared (B6, B7) range of the electromagnetic spectrum, with a spatial resolution of 30 m and a revisit time of 16 days. To select reflectance

data for the same phenological period in which the ground biodiversity measurements were made (i.e., the growing season), we processed OLI images acquired over the area of interest during the growing seasons (i.e., between May and August each year) from 2013 to 2017. The annual range was chosen to overlap with the period of field records. Despite the shorter period covered by OLI than Landsat-7 Enhanced Thematic Mapper Plus (ETM+), we chose the OLI dataset due to the Scan Line Corrector (SLC) ETM+ failure in 2003, which has affected data acquisition since then. To further address the temporal mismatch between field data collection and available spectral data, we masked out from the images all pixels where land cover changed between 2000 and 2012 based on the CORINE Land Cover (CLC) classification. This was done to exclude from our analyses those areas that may have experienced changes or severe disturbances during the period when most field data were collected (i.e., after 2000). To minimise weather-related noise, cloud-covered pixels were filtered out based on the Pixel quality attributes (pixel_qa) band (Foga et al., 2017). Then, the Normalized Difference Vegetation Index (NDVI) was calculated, and the NDVI layer was added to each image. Finally, we generated a "greenest-pixel" composite image by selecting the pixels with the highest NDVI value of the overlapping images for the studied time period. This was done to best capture the vegetation cover and smooth out inter-annual variability. By selecting the greenest pixel over the entire period rather than using a median composite, we aimed to get the optimal vegetation cover of the area (which matches the time of the year when field data were collected) and to avoid the effects of extreme events, such as floods or fires. For the sake of completeness, the results of the analyses using the median composite are presented in Supplementary material 5.B, showing consistent but weaker results compared to the greenest-pixel composite. Indeed, previous studies have shown that the relationship between reflectance variability in space and plant diversity tends to be higher when vegetation is near its optimum, i.e., when the cover of photosynthetically active vegetation is at its maximum (Feilhauer and Schmidtlein, 2011; Thornley et al., 2022; Torresani et al., 2019).

5.2.3 Spectral diversity metrics

We quantified the SD values within each 5' × 3' grid cell using three different methods, each representing one of the main categories proposed by Wang and Gamon (2019): i) the standard deviation of NDVI (sdNDVI), ii) Rao's Q quadratic entropy index (Rao, 1982; Rocchini et al., 2017), and iii) richness of "spectral communities" (SpecCom) (Rocchini et al., 2021b).

5.2.3.1 sdNDVI

The Normalized Difference Vegetation Index (NDVI) is a traditionally used vegetation reflectance index used to quantify vegetation greenness (Tucker, 1979). sdNDVI has often been used as a continuous measure of the dispersion (variation) of NDVI values in a given area since it explains a reasonable portion of the variability in the in-situ diversity data (Gillespie, 2005; Gillespie et al., 2009; Gould, 2000; Hall et al., 2010; Levin et al., 2007).

5.2.3.2 Rao's Q

Rao's Q index is a continuous metric that quantifies the difference in reflectance values between two pixels drawn randomly with replacement from a defined set of neighbouring pixels, taking into account their abundance and the relative Euclidean distance between them:

$$Q = \Sigma\Sigma d_{ij} \times p_i \times p_j$$

where d_{ij} is the spectral distance between pixels i and j, and p_i and p_j are the relative proportions of pixels i and j, respectively (Rocchini et al., 2017). The advantage of applying Rao's Q index to spectral data, as opposed to other diversity indices (e.g., Shannon's H'), is its ability to explicitly account for the numerical size of pixels rather than just the relative abundance (evenness) of reflectance values. To calculate Rao's Q index within each grid cell, we used the function `RaoQArea` written in the R language (R Core Team, 2021) and stored in the GitHub repository https://github.com/micheletorresani/RaoQarea. `RaoQArea` calculates Rao's Q heterogeneity index for a limited area based on the Euclidean distance between pixels of a single-band raster. In our case, the `RaoQArea`

function was applied to the single-band raster derived by selecting the first component from a principal component analysis (PCA) applied to a large random subset of pixels of the original multi-band image. PCA was performed to simplify spectral information and remove band collinearity.

5.2.3.3 SpecCom

To differentiate spectral communities as a function of the optical traits underlying the reflectance of each pixel, we used the R package `biodivMapR` (Féret and de Boissieu, 2020), which allows spectral diversity mapping based on the partitioning of the spectral space of RS images into subunits called as "spectral species" (following Féret and Asner, 2014). Due to the resolution of the spectral data used, a direct link between the identified spectral subunits and in-situ plant species is not feasible. Therefore, we refer to such partitions in the spectral space as "spectral communities" (sensu Rocchini et al., 2021b, 2022), assuming that they are linked to a higher level of ecological organisation. After a series of pre-processing steps that are part of the package workflow, e.g., spectral normalisation (i.e., continuum removal) and dimensionality reduction (by PCA), the mapping of spectral communities was based on k-means clustering. Clustering was performed on relevant PCA axes (i.e., three out of four) selected by visual inspection, in which we rejected principal components with no relevant information or including artefacts possibly due to sensor properties (Féret and Asner, 2014). The number of k clusters was set to 200 after a trial-and-error procedure as the trade-off between the number of clusters with stable results and computational effort (Féret and de Boissieu, 2020; Rocchini et al., 2021a). Based on the resulting map of "spectral communities", we calculated the categorical metric "spectral communities" richness (SpecCom) within each grid cell.

5.2.4 Accounting for habitat type

We hypothesised that habitat type might play a role in the relationship between SD and plant diversity (Schmidtlein & Fassnacht, 2017). In the present study, habitat type was defined by CLC because of the broad coverage and validation of these data. We assigned each 5' × 3' grid cell to the most represented CLC type (reference year 2012) within the cell. Although classifying each grid cell with the predominant CLC is an approximation, no other options were possible due to the grain mismatch between the available ground and CLC data. Level I CLC nomenclature was used for artificial land cover types. For forests and semi-natural areas, we assigned land cover codes according to the Level III CLC nomenclature. For agricultural land, we used the Level II nomenclature for arable land and level III for pastures. As a result, the following categories were assigned to the grid cells: CLC 1, CLC 21, CLC 231, CLC 311, CLC 312, CLC 313, and CLC 324 (see Supplementary material 5.C for a description of the CLC types used). No specific landscape features were masked from our spectral data, as this would be in contrast with the original formulation of SVH (please note that the reason behind the masking described in section 2.2 is only linked to land cover change).

5.2.5 Statistical analyses

All statistical analyses were performed in R 4.1.2 (R Core Team, 2021). We modelled the relationship between in-situ diversity and SD through generalized additive models (GAMs) using the `mgcv` package *v. 1.8.39* (Wood, 2017), with SR or FD as response variables for a total of six models. For SR, we used a negative binomial (NB) error distribution to account for possible over-dispersed SR count data. For FD, we used the Gaussian error distribution. Each model had the following three sets of predictors terms:

1. An interaction between SD and the dominant CLC type. This represents the effect of CLC type on the relationship between SD and plant diversity. In other words, this models the possibility of having different SD-SR or SD-FD relationships in different CLC types.

2. Sampling effort, represented by the logarithm of the number of plant species records within each grid cell. This corrects for the possible effects of uneven sampling effort, when grid cells have higher species diversity because they have been sampled with a higher intensity. Indeed, not considering uneven sampling effort may be a source of bias in models based on species counts (Chao and Chiu, 2016).

3. Smooth two-dimensional splines on a sphere (Wood, 2017) to model the effect of spatial autocorrelation (i.e., spatial pseudo-replication) in the response variable, which can be caused either by the effect of spatially autocorrelated environment, or by contagious biological processes such as species dispersal (Dormann et al., 2007; Legendre, 1993).

To account for possible non-linear patterns, the response of SR and FD to all continuous predictors was modelled as a second-order polynomial (the full six models' formulas are available in Supplementary material 5.D). To estimate the relative importance of the effects of the three sets of predictors above (i.e., SD, sampling effort, and spatial autocorrelation), we used partitioning of deviance (Aragón et al., 2010; Carrete et al., 2007), an approach related to variance partitioning (Borcard et al., 1992). Specifically, the deviance from a null model with no predictors was partitioned to (i) a fraction explained by spectral diversity and its interaction with CLC, (ii) an effect of sampling effort, and (iii) a fraction explained by spatial autocorrelation. We estimated both the independent effects of these, as well as their overlapping fractions, where the overlap is caused by collinearity between the predictors (for the formulas used, see Anderson and Cribble, 1998, and Lobo et al., 2002). The data and code used in the analyses are available at https://github.com/MichelaPerrone/SVH_CZ.git under CC-BY license.

5.3 Results

5.3.1 Relationship between plant diversity and SD

We found statistically significant relationships between plant diversity (SR and FD) and SD. The models with SR and FD as responses were similar, all showing positive relationships with SD. The explanatory power of the models, expressed as explained deviance, ranged from 71.7% to 75.3% for models explaining species richness and from 57.6% to 65.4% for models explaining functional diversity (Fig. 5.2). For both SR and FD, the models where SD was calculated using SpecCom showed the lowest explained deviance, while the models with continuous metrics (i.e., sdNDVI and Rao's Q) showed the highest explained deviance (Fig. 5.2).

5.3.2 Variation partitioning

Variation partitioning showed that the unique contribution of SD accounts for only a small fraction of the total variability, ranging from 2.4% to 6.0% in SR models (Fig. 5.3a, c, and e), and from 5.4% to 13.2% in FD models (Fig. 5.3b, d, and f), with the unique contribution of SD showing the highest values when calculated using continuous metrics (i.e., sdNDVI and Rao's Q). Moreover, the partitions of deviance show different results between SR and FD models in terms of relative values of the unique contribution of SD, spatial autocorrelation, and sampling effort, as well as of their shared fractions. Indeed, in SR models, sampling effort alone explained almost half of the deviance (between 47.2% and 48.0%), while the unique contribution of spatial autocorrelation accounts for a small fraction (Fig. 5.3a, c, and e). In contrast, in FD models, most of the variability was jointly explained by SD and spatial autocorrelation (between 25.5% and 29.6%) and by spatial autocorrelation alone (between 25.6% and 33.0%), with sampling effort accounting for the smallest independent effect (Fig. 5.3b, d, and f).

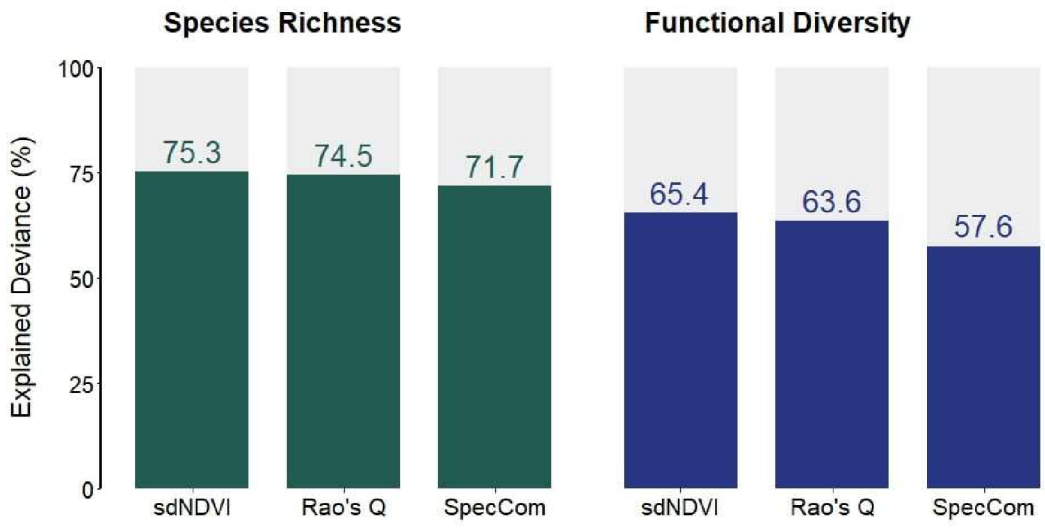

Fig. 5.2. Total explained percentage deviance of models explaining species richness and functional diversity based on three types of spectral diversity (sdNDVI, Rao's Q, SpecCom), sampling effort, and spatial autocorrelation.

5.3.3 Effect of habitat type

For simplicity, we focus primarily on how the direction of the relationship between SD and biodiversity varies with CLC types, therefore we describe only the effects of the interaction between the first power of the SD variables and habitat type, since it is the power that determines the direction of the effect (the full list of coefficient estimates can be found in Supplementary material 5.E). We found that the significance, magnitude, and sign of the effect of SD varied depending on the CLC type dominating the landscape (i.e., grid cell) (Fig. 5.4). Specifically, in the landscapes dominated by arable land (CLC 21), coniferous forests (CLC 312), and transitional woodland-shrubs (CLC 324), the effect of SD was always significant and positive (Fig. 5.4a, b, c, d, e, and f). In addition, the effects of SD in transitional woodland-shrubs (CLC 324) were remarkably higher than the other interactions (Fig. 5.4), suggesting that increases in SD were associated with either a higher increase in plant diversity, fractional tree cover and portion of understory visible, or a combination of the three in transitional woodland-shrubs than in other habitat types. In the case of artificial surfaces (CLC 1), the effect of SD was significant and positive only

when considering sdNDVI and Rao's Q in both SR and FD models (Fig. 5.4a, b, c, and d). The effect in pastures (CLC 231) was significant and positive only in FD models where SD was calculated using sdNDVI and SpecCom (Fig. 4b and f). The effect in broad-leaved forests (CLC 311) was significantly positive in the FD model where SD was calculated using sdNDVI and in both SR and FD models using SpecCom (Fig. 5.4b, e, and f). The effect in mixed forests was significant and positive in all models (Fig. 5.4b, d, e and f) except for SR models where SD was calculated through sdNDVI and Rao's Q. The only case where we observed a significant negative effect of the interaction with the predominant habitat type was when considering artificial surfaces (CLC 1) in the models relating plant diversity to SpecCom (Fig. 5.4e and f). In all other cases, the effects of predominant habitat type on the relationship between SD and plant diversity were not significant.

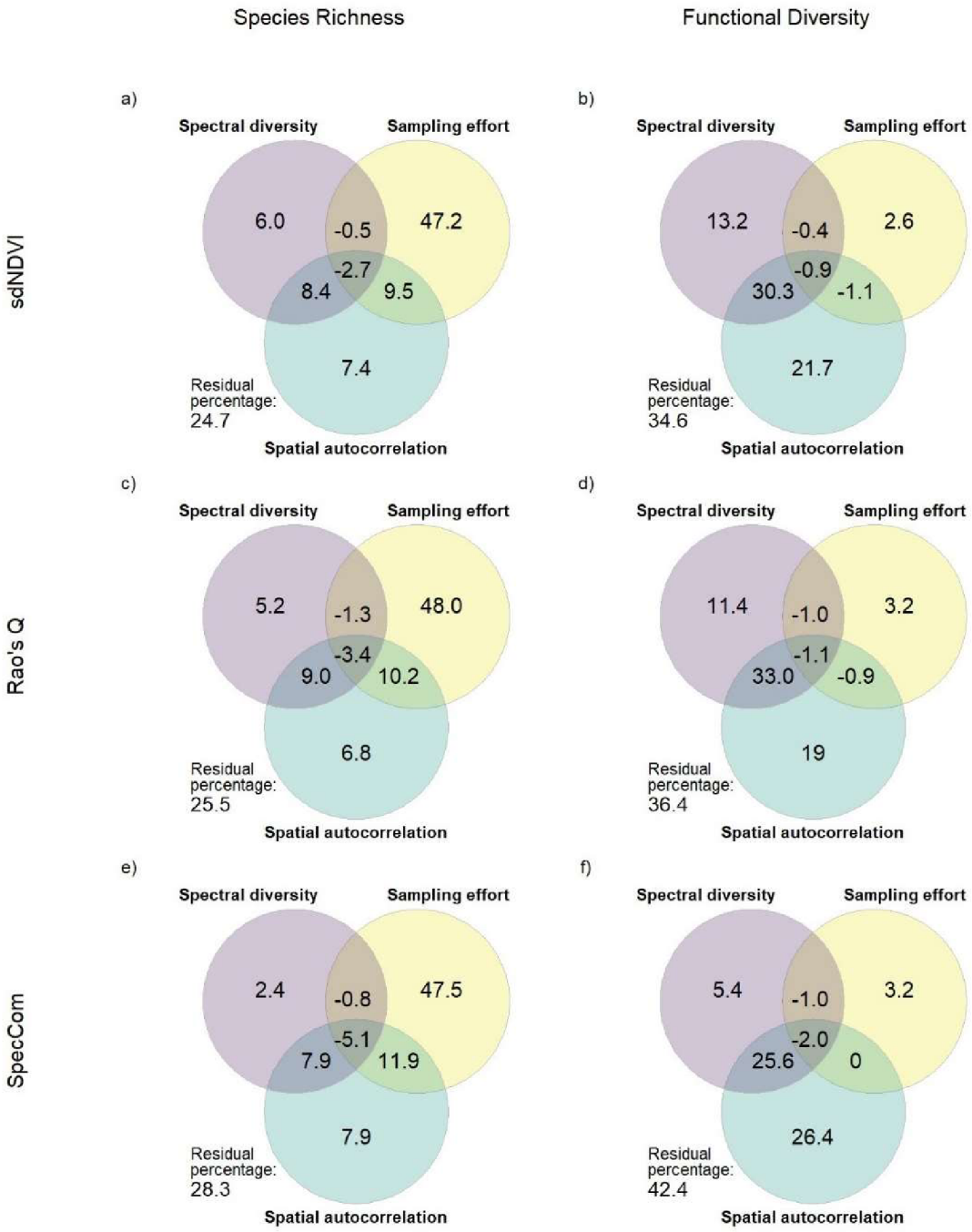

Fig. 5.3. Venn diagrams showing the percentage of explained deviance in plant diversity explained by the three groups of predictors: spectral diversity, sampling effort, and spatial autocorrelation (splines). Overlaps among circles represent fractions of the variation that cannot be unequivocally attributed to one of the overlapping predictors. For example, when spectral diversity is also spatially autocorrelated, some fraction of the explained deviance will be shared between spatial autocorrelation and spectral diversity. Negative numbers can arise due to the spline optimisation

algorithm during model fitting, are usually small, and can be interpreted as zeroes.

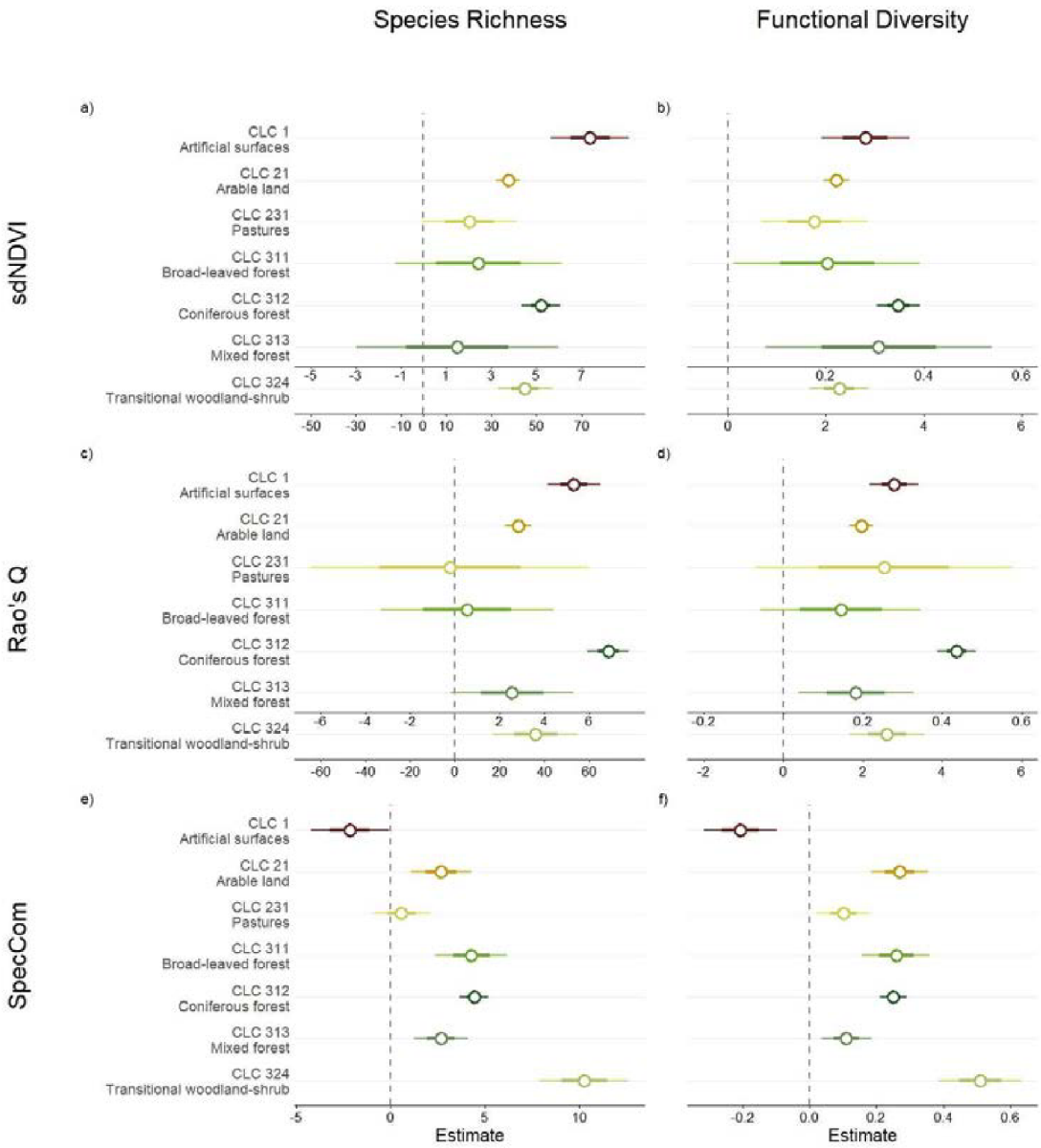

Fig. 5.4. Effect sizes (standardised coefficients) of interactions between SD and land-cover types in the plant diversity ~ SD models. The dots represent coefficient estimates; the outer error bars are 95% confidence intervals, and the inner error bars indicate one standard error on each side. When the 95% coefficient interval includes a value of zero, the interaction between SD and land-cover type is not significant. Due to the different value ranges of CLC 324 estimates, a second x-axis with appropriate scaling is shown.

5.4 Discussion

5.4.1 Spectral diversity and plant diversity

When modelling the ability of different types of SD metrics to explain the variation in plant diversity at the landscape scale, only a small fraction of the variation was explained by SD alone despite the relatively high goodness-of-fit (percentage of explained deviance) observed in our models. However, a relatively large fraction of variation in all models was explained by spatially structured SD, i.e., the joint effect of SD and spatial autocorrelation. Overall, the unique contributions of sampling effort and spatial autocorrelation explained a large portion of the variation in the diversity values. The variation explained by sampling effort was highest in all SR models, while spatial autocorrelation showed a relatively higher explained variation in FD models. The large contribution of sampling effort in SR-based models is not surprising. It is well known that species richness estimates increase with sampling effort (Walther et al., 1995). In contrast, the importance of spatial autocorrelation (modelled using smooth splines) may reflect both the effect of spatially-autocorrelated environment (e.g., topography, climate) and that of dispersal limitation of species (Dormann et al., 2007). Therefore, routinely inferring plant diversity from SD may lead to inaccurate results if sampling effort and spatial autocorrelation are not accounted for in situations similar to this study.

Although SR models had a better goodness-of-fit, SD accounted for a larger fraction of variation in FD models compared to SR models. These results suggest that SD is linked to FD slightly better than to SR. At small scales of observation, a stronger relationship of SD with FD than with SR is assumed when relying on high spatial resolution spectral data, as a direct relationship between pixels' spectra and plant functional and structural properties is expected (Schweiger et al., 2018; Ustin and Gamon, 2010). At the landscape scale, when relying on coarse spatial resolution data, such a correspondence between spectrum and plant properties decreases due to the mismatching size of pixels and individuals. Thus, the link between spectral

and plant diversity can only be of indirect nature and captured through landscape heterogeneity. Our results suggest that SD is more strongly related to FD than SR also when relying on coarser spectral data, differently from what was shown in previous studies (Hauser et al., 2021b). This is in agreement with the original formulation of the SVH (Palmer et al., 2002): the heterogeneity of the landscape estimated through SD reflects the diversity of available niches and, thus, both functional and taxonomic diversity. Indeed, SD does not attempt to directly estimate any specific aspect of plant biodiversity (e.g., taxonomic, phylogenetic, functional) (Laliberté et al., 2020; Schweiger et al., 2018; Wang & Gamon, 2019).

5.4.2 Spectral diversity and effects of habitat type

The differences found in the relationship between SD and ground diversity across the habitat types considered were based mainly on the ability of the different metrics (continuous and categorical) used to capture the relationship and on the strength of the relationship.

In landscapes dominated by artificial surfaces, the ability of continuous metrics of SD to predict biodiversity improved. This is unexpected because, unlike categorical spectral metrics, continuous metrics are sensitive to extreme reflectance values of background material (e.g., bare soil, litter, rocks), which can have a considerable influence on the SD estimation (Fassnacht et al., 2022; Wang et al., 2018b). At finer resolutions, this issue can be tackled by masking out soil pixels and unvegetated areas (e.g., Gholizadeh et al., 2018). At coarser spatial resolutions, as in our case, such masking may lead to the erroneous filtering of mixed pixels corresponding to scarcely vegetated - but biologically relevant – areas, resulting in a consequent loss of information (Schmidtlein and Fassnacht, 2017). Landscape mosaics dominated by urban areas are likely to be very species-rich, as cities and suburban areas often harbour more plant species than the surrounding landscape (Araújo, 2003; Kühn et al., 2004). Moreover, masking landscape features based on their reflectance values would contradict the original formulation of the SVH, which states that it is the

magnitude of variation in spectral characteristics of an area that relates to habitat (or vegetation type) heterogeneity and, thus, to available niche space. An alternative solution to pixel masking is spectral unmixing (Asner and Heidebrecht, 2002), which would allow estimating the per-pixel percentage of vegetation cover. In contrast, in landscapes dominated by urban habitats, the ability of the categorical approach to make inferences about biodiversity was impaired, which suggests that these metrics do not properly capture the heterogeneity of this landscape type.

The categorical approach of the SpecCom metric can still offer relevant benefits (Fassnacht et al., 2022; Schmidtlein and Fassnacht, 2017). Estimating SD through spectral type classification allows summarizing the continuity of spectral space into discrete spatial objects that are likely to correspond to distinct landscape features. With this approach, there is less risk of disproportionate influence of extreme pixel values on the spectral variation metric since they would constitute individual categories among equally meaningful others (Wang & Gamon, 2019). Moreover, spectrally homogeneous spatial units can be identified even when plant optical characteristics change throughout the year according to species phenology, allowing for temporal consistency in spectral type classification. However, this is unlikely to work in larger regions with diverse environmental conditions and, thus, nonsynchronous phenological states across similar ecological entities (e.g., communities). In landscapes dominated by transitional woodland-shrub habitats, both categorical and continuous SD metrics exhibited the strongest (albeit still weak) association with plant diversity. Given the inherent spatial vegetation heterogeneity of such areas, which can likely be detected through RS imagery, these results are unsurprising. Indeed, this land-cover type is characterised by patchy, bushy, and herbaceous vegetation with occasional scattered trees (Bossard et al., 2000), and the resulting spectral heterogeneity can be detected even by current, noncommercial spaceborne sensors.

In landscapes dominated by arable land and coniferous forests, we found the same general positive (although weaker) effect of habitat type on the relationship between SD and diversity, indifferently of which metric was used. The agreement among SD metrics indicates that the relationship

between SD and ground biodiversity is significant and stable. The landscapes dominated by arable land are widespread in Central Europe including the Czech Republic (see Supplementary material 5.C) and are characterized by high spectral heterogeneity, mostly given by the mosaic of heterogeneous and species-poor cultivation patterns. However, these landscapes may harbour small "islands" of natural and semi-natural species-rich habitats (e.g., grasslands and shrublands), which are captured by SD. In the case of landscapes dominated by coniferous forests, the low spectral heterogeneity of the canopy is coupled with low plant diversity, which is mirrored by the positive SD-diversity relationship.

In our study, areas classified as pastures (CLC 231) correspond to managed grasslands and meadows. Therefore, the positive and significant interaction between pastures as the predominant habitat type and SD observed in FD models was less expected than for other habitat types. Indeed, the wide mismatch between pixel resolution and size of individuals and populations of plant species has no negative effect on the SD-diversity relationship, as would be expected based on the smoothed reflectance signal (Wang et al., 2018a; Fassnacht et al., 2022).

5.4.3 Choice of spectral diversity metrics

We found that all of our SD metrics can explain a comparable proportion of the variability in the ground diversity at the scale applied. However, there were differences between categorical (i.e., SpecCom) vs continuous metrics (i.e., Rao's Q and sdNDVI), with the continuous metrics performing slightly better. Their performance depended on the habitat type considered. Moreover, some practical aspects could be crucial in choosing the most appropriate metric.

The application of categorical metrics for the routine production of RS biodiversity products with consistency across large scales is complicated by the need for the user's input. Indeed, it is necessary to conduct preliminary experiments to find the perfect compromise between the number of clusters and the computational effort that would allow reliable results (Féret and de

Boissieu, 2020; Rocchini et al., 2021b). Regarding continuous metrics, those used in this study differ in the spectral information used to compute SD. Indeed, metrics based on variation in vegetation indices (e.g., sdNDVI) rely on the information provided by specific wavebands related to vegetation condition and biomass and allow discrimination between vegetated and non-vegetated areas, and between different vegetation types. However, the use of this specific (limited) set of spectral bands may exclude some important information about other environmental and biochemical properties (e.g., leaf water content, nitrogen content, pigments, and lignin) (Asner and Martin, 2009). In contrast, spectral entropy metrics (e.g., Rao's Q) use all the available spectral information and describe the spectral "dimensionality" of the data (Wang & Gamon, 2019). Still, they can be computationally costly, possibly needing several days to be computed for large areas at a medium-high spatial resolution. As we showed that a simpler vegetation index-based metric (sdNDVI) performs comparably well to a spectral entropy-based Rao's Q, we recommend using the simpler and computationally low-cost sdNDVI, which already proved performing in other studies (Gholizadeh et al., 2019). However, since previous results (Gholizadeh et al., 2018; Wang et al., 2018b) suggest that the most informative spectral regions for biodiversity assessment can vary with spatial resolution, data properties, and scale of observation, further analyses would be needed to assess whether this metric should be used in other analytical contexts.

5.4.4 Limitations and ways forward

We calculated SD based on the "greenest-pixel" composite image obtained from the overlapping images matching the time of the year when field data were collected. We did this to best capture the vegetation cover and smooth out inter-annual variability. This solution performed best within our study framework (see Supplementary material 5.B for comparison with the median-composite approach). However, there still is a knowledge gap about the best way to compute SD on multitemporal imagery, and there are two reasons for this. First, for medium-high resolution multitemporal imagery covering wide areas, it is computationally

demanding to calculate SD over single images and then aggregating them. Second, it is unclear which is the most appropriate criterion for aggregating SD (e.g., median, mode, maximum value), which is likely to depend on the specific study settings (e.g., SD metric applied). Thus, future work should test and compare SD aggregation practices.

According to the SVH, we expected SD to be a proxy for environmental heterogeneity and, thus, related to plant diversity. Our results indicate that this needs to be reconsidered. Rather than the main predictor, SD can be useful as an additional covariate in multivariate models predicting biodiversity (e.g., Kreft and Jetz, 2007; Večeřa et al., 2019), together with well-known predictors of plant diversity such as climate and topography. As we aimed specifically at testing the SVH, building such multivariate models was beyond the scope of this study. Nevertheless, it is a promising topic for future research, which could be addressed through machine learning (Večeřa et al., 2019) and structural equation modelling (SEM) (Fan et al., 2016; Ullman and Bentler, 2012). Alternatively, the "non-spectral" environmental factors could be included in the estimation of landscape heterogeneity through the area-based multidimensional Rao's Q, which is now possible using the `paRao` function available in the `rasterdiv` R package (*v. 0.3.1*; Rocchini et al., 2021b, 2021c).

5.5 Conclusions

We examined the relationship between vascular plant diversity and spectral diversity across >2000 grid cells covering the Czech Republic, taking into account the effects of land cover. We investigated the potential of three SD metrics to infer both species richness and functional diversity. Our results show little to no difference among the metrics tested at this scale, indicating that the association between SD and plant diversity is significant and stable. However, our results confirm that there is no general validity of the SVH. In our setting, only a small percentage of variation could be explained solely by SD and not accounting for sampling effort and spatial autocorrelation in the models could be misleading. We also observed an effect of the habitat type prevalent in the landscape on the relationship

between SD and biodiversity, which is strongest in areas with transitional habitats between forests and shrublands. Still, further analyses testing whether spectral diversity is related to plant diversity after accounting for the vegetation type could help further demonstrate the observed pattern, which could not be done given the present study design.

Supplementary materials

Supplementary materials to this article can be found in the online version at https://doi.org/10.1016/j.rse.2023.113591.

6

"Flower power": How flowering affects spectral diversity metrics and their relationship with plant diversity

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Abstract

Biodiversity monitoring is constrained by cost- and labour-intensive field sampling methods. Increasing evidence suggests that remotely sensed spectral diversity (SD) is linked to plant diversity, holding promise for monitoring applications. However, studies testing such a relationship reported conflicting findings, especially in challenging ecosystems such as grasslands, due to their variety and high temporal dynamism. It follows that a thorough investigation of the key factors influencing these relationships, such as the metrics applied (i.e., continuous, categorical) and phenology (e.g., flowering), is necessary. The present study aims to assess the effect of flowering on the applicability of six different SD metrics for plant diversity monitoring at the local scale and to investigate how spatial resolution affects the results. Taxonomic diversity was calculated based on data collected in 159 plots of 1.5 m × 1.5 m with experimental mesic grassland communities. Spectral information was collected using a UAV-borne sensor measuring reflectance across six bands in the visible and near-infrared range at ~2 cm spatial resolution. Our results showed that, in the presence of flowering, the relationship between SD and plant diversity is significant and positive only when SD is calculated using categorical metrics. Despite the observed significance, the variance explained by the models was very low, with no evident differences when resampling spectral data to coarser pixel sizes. Such findings suggest that new insights into the possible confounding effects on the SD-plant diversity relationship in grassland communities are needed to use SD for monitoring purposes.

Keywords: grasslands, remote sensing, phenology, UAV, spectral variation hypothesis.

6.1 Introduction

The current global biodiversity change rate makes species conservation one of the most pressing priorities of our times (Wilting et al., 2017). While growing attention has been paid to species conservation, biodiversity evaluation and monitoring are still limited and lack standardized methods for quick and scalable data collection (Palmer et al., 2002; Skidmore et al., 2015; Wang & Gamon, 2019). In turn, remote sensing represents a continuous source of data which potentially concerns various aspects of biodiversity, collected across diverse scales in a uniform, borderless, and repeatable way (Turner, 2014). Among the available approaches for the remote monitoring of biodiversity, increasing evidence suggests that remotely sensed spectral diversity (SD), i.e., the variability in the electromagnetic radiation reflected by (vegetated) surfaces measured in the visible, near-infrared and short-wave infrared regions (400–2400nm), is linked to plant diversity (Rocchini et al., 2015; Schweiger et al., 2018). The SD concept was originally framed within the spectral variation hypothesis (SVH; Palmer et al., 2002), which assumes an indirect relationship between spectral and plant diversity through environmental 'surrogacy', i.e., the landscape heterogeneity captured by remote sensing (Hauser et al., 2021b; Torresani et al., 2019). When relying on medium/coarse spatial resolution data, the link between spectral and plant diversity can only be indirect, as pixel size exceeds the size of individual plants. Conversely, multispectral data with fine spatial resolution provided by uncrewed aerial vehicles (UAVs), i.e., in the order of magnitude of centimeters, hold promise for capturing the direct link between the spectral and plant diversity at the leaf and canopy level in herbaceous communities (Rossi et al., 2021a; Thornley et al., 2023). However, when the pixel size corresponds to the size of individual plants (or even the sub-individual level), the intra-specific (or intra-individual) variability in the plant optical traits can play a role in the SD-biodiversity relationship. Studies testing the relationship between SD and plant diversity at fine scales have reported conflicting findings, especially in challenging ecosystems such as grasslands, the biodiversity of which is threatened by their degradation and fragmentation due to

anthropogenic factors (Thornley et al., 2023). Their vast global distribution (Gibson, 2009) and the broad range of ecosystem services they provide make grassland conservation a priority (Hein et al., 2006; Suding, 2011), yet their extensive monitoring is prevented by logistical constraints. Due to its efficiency and cost-effectiveness, SD-based plant diversity monitoring offers an appealing alternative to traditional sampling techniques in grasslands.

Nonetheless, the path towards the routine implementation of SD into grassland monitoring is hampered by the high temporal and spatial variability of such ecosystems, which often exhibit a complex community structure, particularly in natural or semi-natural grasslands (Wilson et al., 2012). Recent studies have highlighted the impact of plant phenology (e.g., flowering, leaf emergence and senescence; Rossi et al., 2021b; Thornley et al., 2022) when addressing the relationship between SD and plant diversity in grasslands. Despite the dynamism of grassland communities, acquiring repeated intra-annual spectral data is time- and resource-consuming. It follows that spectral data are usually acquired to ensure a temporal match with vegetation surveys when the presence of dead biomass and exposed soil is supposed to be the lowest (Asner, 1998). However, this also implies that the species present would potentially be flowering, causing unwanted additional sources of spectral variability. The presence of flowering is likely to have an impact on the SD of a community, as it leads to a high variation in important optical traits and, thus, in the spectral signatures of individual species (Conti et al., 2021; Fassnacht et al., 2022; Gholizadeh et al., 2019; Heumann et al., 2015; Thornley et al., 2022). Being non-photosynthetic organs with distinct spectral features, especially in the visible domain (Schiefer et al., 2021), flowers can affect SD, and the extent of this impact is likely to depend on the characteristics of the SD metrics applied.

The metrics used to quantify SD can be either continuous (i.e., based on variation in traditional vegetation reflectance indices or on the full spectral information) or categorical (i.e., relying on the categorization of the spectral space; Féret & Asner, 2014; Wang & Gamon, 2019). Although continuous SD metrics are the most represented and widely tested, they show weakness in capturing plant diversity by measuring the degree of contrast in the reflectance, which is more related to the specific identity of

the plant species rather than their quantity. Indeed, in cases where a few spectrally distinct species are present in a community, the spectral heterogeneity can be very high even if the plant diversity is low (Fassnacht et al., 2022). Following the same reasoning, continuous SD metrics are likely to be influenced by flowering, soil presence, or the amount of biomass. In contrast, categorical SD metrics are considered less sensitive to extreme reflectance values (e.g., from background material) as extreme values would represent distinct categories alongside other equally significant ones (Rossi et al., 2021a). Even though some studies have tested and compared different SD metrics (Frye et al., 2021; Gholizadeh et al., 2018, 2020; Perrone et al., 2023; Rossi et al., 2021a; Schmidtlein & Fassnacht, 2017; Warren et al., 2014), no consensus has been reached on which metrics would be the best proxy for plant diversity during flowering.

The aim of this study is to assess the applicability of SD for plant species richness monitoring at the local scale. Here, we test six different SD metrics (detailed in Table 1) while considering flowering as a potential factor affecting the spectral-plant diversity relationship using ground observations and multispectral UAV data from mesic grassland communities in South Bohemia (Czech Republic). Additionally, we investigate if changing the spatial resolution (from 2 cm to 5 cm) influences the observed relationship. Building upon Conti et al. (2021) findings, this study also considers the influence of bare soil and shadows on the relationship between spectral and plant diversity.

6.2 Materials and Methods

6.2.1 Field data

Our study is based on vegetation data collected in a permanent grassland experiment run by the University of South Bohemia and located in a mesic meadow in the Vysočina region (South Bohemia, Czech Republic, 49.331 N, 15.003E). As Galland et al. (2019) described, the sowing experiment consisted of 40 mesic grassland communities covering independent gradients of plant functional and phylogenetic diversity. These experimental communities derived from a specific treatment, i.e., either the sowing of a combination of six species drawn from a pool of 19 mesic meadow species naturally present in the area or from monoculture treatments. Each six-species community was sown in two randomly situated 1.5 m $\times$ 1.5 m plots (one fertilized and one unfertilized), while monoculture plots were sown in three replicates each. Thus, the study site encompassed a total of 196 plots, with a buffer zone of 0.5 m between them (Fig. 6.1). Due to the subsequent processing of UAV data (i.e., excluding corrupted areas of the orthomosaic), only 159 out of the 196 plots were considered in this study. Plant species composition within each plot was measured in June 2019. The actual species richness (SR) of the considered experimental communities varied between 12 and 36 species due to the later plot invasion by spontaneously colonizing species.

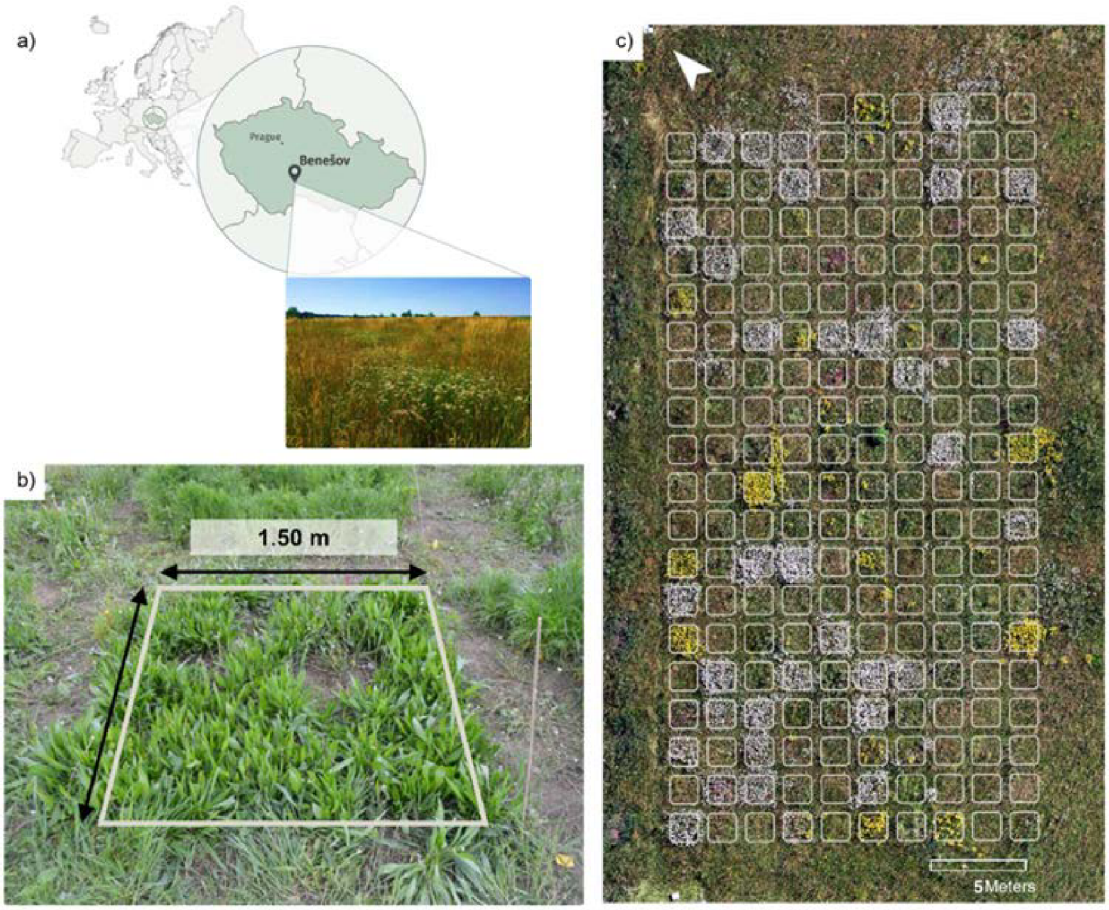

Fig. 6.1. (a) Location of the study area. (b) Example of a 1.5 m × 1.5 m surveyed plot. (c) Natural-colour mosaic of the whole study area.

6.2.2 Spectral data

We used multispectral UAV imagery with ~2 cm spatial resolution (80% frontal and 70% side tile overlapping, 30 m flight altitude) acquired shortly after vegetation sampling (July 2019) using a Kingfisher multicopter (Robodrone Industries, Brno, Czech Republic) equipped with a Micro-MCA6 camera (Tetracam Inc., Chatsworth, CA, United States) measuring reflectance across six bands in the 490–900 nm range of the electromagnetic spectrum with a 10-20 nm-width. The obtained spectral data were processed using a Structure from Motion and Multi- View Stereo algorithms in the Agisoft Metashape image-matching software (Agisoft LLC, St. Petersburg, Russia) to generate an ortho-mosaic. Georeferencing was performed with spatial error of 2 cm using ground control points surveyed through a Leica GPS1200 GNSS receiver (Leica Geosystems AG, Heerbrugg, Switzerland)

in RTK mode. The orthomosaics was radiometrically calibrated using white and grey calibration targets for which the spectral properties were known from manufacturer-provided spectrometer measurements. The ortho-mosaic portions exhibiting processing artefacts were excluded from further analyses, resulting in 37 out of 196 study plots being left out.

Previous studies have reported that the presence of bare soil, due to its spectrum being substantially different from that of the vegetation, proved to significantly deteriorate SD performance in quantifying plant diversity (Gholizadeh et al., 2018; Hauser et al., 2021b). Moreover, the spectral signal has proven to be sensitive to the vertical structure of the plant community, since a complex vertical structure of the community may generate an "occlusion effect" that would lead to the obscuration of shorter species and the presence of shadowed pixels (Conti et al., 2021). Here, we masked shadowed areas and non-vegetated pixels from the multiband ortho-mosaic to mitigate their influence on SD. Bare soil pixels were masked using an NDVI threshold of 0.3, while shadowed pixels were identified and removed through an Expectation Maximization (EM) unsupervised classification. Moreover, the presence of flowering plants within the plots was assessed visually from an RGB composite and attributed to each plot (i.e., a plot was classified as flowering given >10% flower cover). Finally, we rescaled the orthomosaics to 5-cm spatial resolution (using bilinear resampling) to test if coarsening the spatial resolution can mitigate the effect of intraspecific (and intra-individual) variability of optical traits.

6.2.3 Spectral diversity metrics

As there is no consensus on the best-performing method to quantify SD, we applied six different SD metrics within the 1 m × 1 m core area of each 1.5 m × 1.5 m experimental plot. Specifically, we computed six continuous SD metrics, namely: the standard deviation of NDVI (sdNDVI), the Rao's Q entropy index (RaoQ), the mean pairwise distance of reflectance values (MPD), the coefficient of variation of the full spectral range reflectance (CVrefl), and the convex hull volume (CHV). We also computed one categorical metric, spectral species richness (SpSpR) (see Table 6.1 for further details on the metrics used). For the spectral species mapping we

used the `biodivMapR` R package (for a complete description of the method please see Féret and de Boissieu, 2020). To perform the mapping, the number of k clusters was set to 50 (a realistic number of the spectral species present based on ground data and as a trade-off between performance and computational efficiency). The unsupervised clustering of a random subset of pixels was repeated eight times and the mean SpSpR value calculated from these repetitions was assigned to each respective plot.

Table 6.1. Description of the spectral diversity metrics used in this study.

Spectral diversity metric	Description	Reference	Dedicated package
Standard deviation of NDVI (sdNDVI)	The square root of the variance in the NDVI values	(Wang et al., 2016)	
Rao's Q entropy index (RaoQ)	This index quantifies the difference in reflectance values between two pixels drawn randomly with replacement from a set of pixels by considering their abundance and their pairwise distance	(Rocchini et al., 2021a)	`rasterdiv` R package, v. 0.3.2 (Rocchini et al., 2021c)
Mean pairwise distance (MPD)	Mean pairwise Euclidean distance between pixels in the space defined by the first two principal components of the spectral data	(Rocchini et al., 2004)	
Convex hull volume (CHV)	The smallest possible convex volume encompassing all pixels, using the first three principal components of the spectral data	(Dahlin, 2016)	

Coefficient of variation of reflectance (CVrefl)	Average coefficient of variation over all available wavelengths	(Wang et al., 2016)	
Spectral species richness (SpSpR)	The number of spectral species within each plot. Spectral species are identified based on k-means clustering of a random subset of the first three components of the UAV image and then applied to the whole PCA image to assign a cluster to each pixel.	(Féret & Asner, 2014)	`biodivMapR` R package, v.1.9.4 (Féret and de Boissieu, 2022, 2020)

6.2.4 Statistical analyses

To test the relationship between SR and each of the metrics tested, we modelled the variation in SD through Generalized Linear Mixed Effects Models (Mcculloch and Neuhaus, 2014) (Gamma family, log link) using the `lme4` R package *v.1.1–33* (Bates et al., 2015). In our models, SR and the binary variable of flowering (presence/absence) were used as fixed-effect predictors. At the same time, the type of grassland community (i.e., monoculture, low/high functional diversity, low/high phylogenetic diversity, fertilized/unfertilised) was included as a random effect to account for the interdependence among communities in our dataset. To assess the goodness of fit for our models, we calculated the marginal (R^2_m) and conditional (R^2_c) pseudo-R squared (Nakagawa et al., 2017) for each model. These metrics quantify the proportion of variance explained by fixed effects and the complete model (i.e., both fixed and random effects), respectively. We calculated R2m and R2c using the `r.squaredGLMM()` function of the `MuMIn` R package, *v.1.43.17*. Data and scripts are provided at https://github.com/MichelaPerrone/SVH_Benesov.git under CC-BY license.

6.3 Results

When comparing the spectra of two sample plots (i.e., one with and one without flowering), significant differences were observed in the distribution of reflectance values in all six spectral bands (Kolmogorov-Smirnov Test p-values <0.01) at both spatial resolutions tested. Fig. 6.2 shows the spectra and pixel values distributions for the 2-cm orthomosaics; the same information for the 5-cm ortho-mosaics can be found in Supplementary material 6.A. The strongest differences (i.e., larger effect sizes, or higher Kolmogorov's D values) in the distribution of values between the experimental plots were observed for the Green, Red, and NIR bands (Table 6.2), indicating that flowering affects both the visible and NIR regions of the spectrum. Besides, we observed that coarsening the spatial resolution from 2 to 5 cm did not impact the results above. At both the tested spatial resolutions, the models showed a significant and positive relationship between SR and SD only when SD was measured using categorical metrics (i.e., spectral species richness) (Table 6.3; Fig. 6.3). Conversely when the SD response variable was calculated using continuous metrics, flowering was the only variable significantly (positively) associated with SD (Table 6.3; Fig. 6.3). In such models, we observed relatively high R^2_m values, ranging between 0.24 (sdNDVI, 2-cm spatial resolution) and 0.51 (CVrefl, 2-cm spatial resolution). In contrast, models based on spectral species richness had very low R^2_m values (Table 6.3; Fig. 6.4), with no evident differences observed between the two spatial resolutions. Despite the significant relationship between SD and SR, the low variance explained by the fixed effects in the spectral species richness models suggests that other factors play a more prominent role at this ecological scale and within these settings. Moreover, we observed that very fine-spatial resolution data, such as data with a 2-cm resolution, are not beneficial when using categorical metrics. Indeed, with such a fine spatial resolution, we observed that a high number of spectral species are detected in most of the plots, regardless of the actual ground species richness (Fig. 6.4).

Table 6.2. D statistic values of the Kolmogorov-Smirnov tests evaluating the differences between the reflectance values in the two experimental plots shown in Fig. 2.
*Significance codes: *** (p-value <0.001), ** (p-value <0.01), * (p-value <0.05).*

	Blue	Green	Red	Red Edge	NIR1	NIR2
Spatial resolution: 2 cm	0.12^{***}	0.43^{***}	0.43^{***}	0.28^{***}	0.37^{***}	0.39^{***}
Spatial resolution: 5 cm	0.12^{***}	0.48^{***}	0.53^{***}	0.32^{***}	0.40^{***}	0.41^{***}

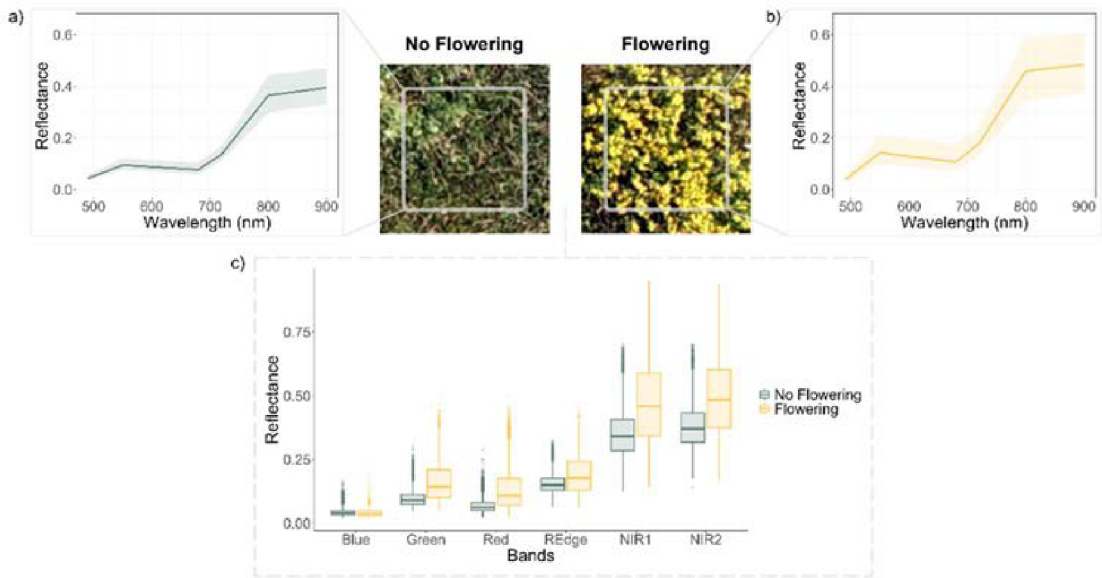

Fig. 6.2. Sample spectra of experimental plots without (a) and with (b) flowering from the 2-cm resolution ortho-mosaic after masking. Bold lines represent the median spectra within the 1 m × 1 m core area of each plot (after masking). The shadowed area represents the interval of the pixel values between the 1st and 3rd quartiles for each band. (c) Box plot of the reflectance values within the two sample experimental plots selected.

*Table 6.3. Summary of the models' results. The columns refer to the SD metric used as the response variable; rows refer to the coefficient estimates (coeff. est.) of the fixed-effect explanatory variables (log-transformed values) and the models' marginal and conditional R^2 values. Significance codes: *** (p-value <0.001), ** (p-value <0.01), * (p-value <0.05).*

Spatial resolution: 2 cm						
	sdNDVI	RaoQ	MPD	CHV	CVrefl	SpSpR
SR coeff. est.	$-4.99e^{-3}$	-0.02	-0.02	0.06	$-1.89e^{-5}$	0.02^{*}
Flowering coeff. est.	0.12^{***}	0.34^{***}	0.30^{***}	0.65^{***}	0.22^{***}	-0.02
R^2_m	0.24	0.39	0.37	0.35	0.51	0.05
R^2_c	0.29	0.50	0.48	0.44	0.58	0.13

Spatial resolution: 5 cm						
	sdNDVI	RaoQ	MPD	CHV	CVrefl	SpSpR
SR coeff. est.	$-5.94e^{-3}$	-0.02	-0.02	0.05	$4.66e^{-3}$	0.04^{**}
Flowering coeff. est.	0.15^{***}	0.34^{***}	0.32^{***}	0.78^{***}	0.21^{***}	$1.46e^{-3}$
R^2_m	0.28	0.37	0.36	0.41	0.38	0.06
R^2_c	0.29	0.49	0.47	0.48	0.50	0.16

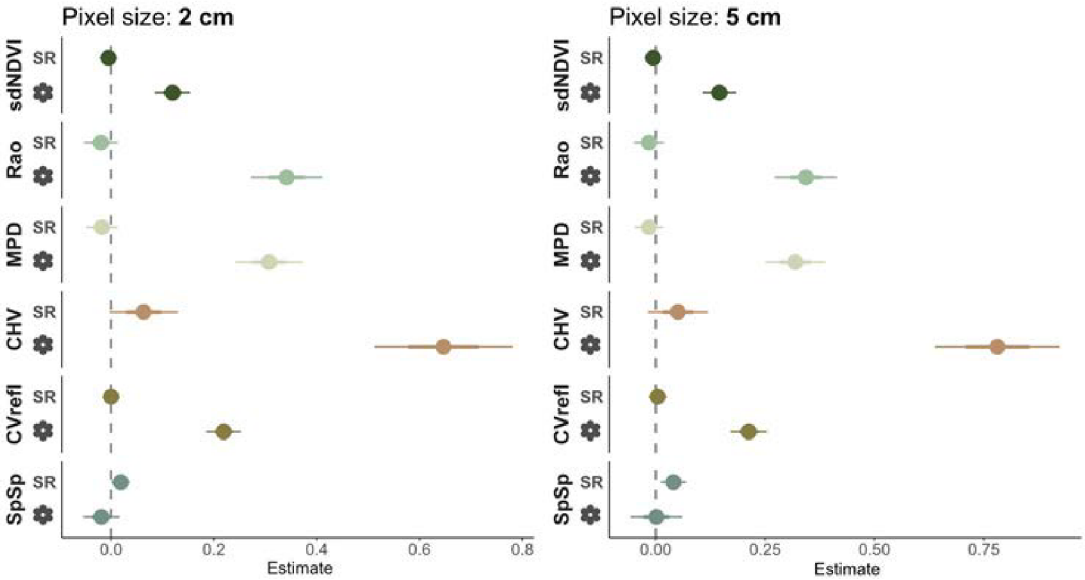

Fig. 6.3. Coefficient plots of the mixed models illustrating the estimated (log-transformed) values for each explanatory variable, along with their corresponding 50% (inner error bars) and 95% (outer error bars) confidence intervals. Colours refer to the individual SD metrics used as the response variable.

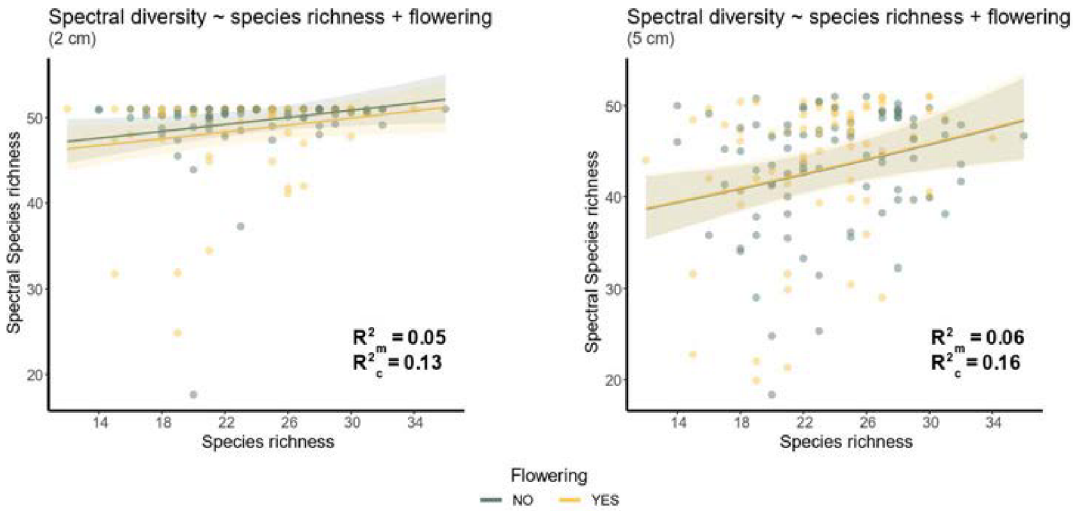

Fig. 6.4. Predicted relationships between SD (calculated as spectral species richness) and species richness derived from the mixed-effect models for the two spatial resolutions tested based on the presence of flowering (see legend).

6.4 Discussion

6.4.1 SD metrics and flowering

The community's phenological pattern impacts the effective application of SD for biodiversity monitoring as plant species exhibit distinct physiological and structural characteristics at different phenological stages, causing changes in their spectral signatures. The presence of blooms (that are markedly different in their spectral characteristics from the plant green organs) impacts the use of continuous SD metrics as such metrics are highly sensitive to extreme reflectance values. On the contrary, our results confirm that by using categorical SD metrics, extreme pixel values are less likely to have a disproportionate influence on the estimated SD, since they would represent distinct categories alongside others of equal importance (Wang and Gamon, 2019). Notably, increasing the range of spectral information considered, i.e., from bands at specific wavelengths (sdNDVI) to all available spectral bands (RaoQ, MPD, CHV, CVrefl), did not substantially improve the performance of the continuous metrics, thus indicating that using only a subset of the available spectral information is not what limits the successful application of SD. To use any of the tested continuous SD metrics, the spectral data acquisition timing turned out to be relevant. Indeed, the asynchrony in phenology among species present in the observed community presented an additional challenge to the applicability of the SVH for estimating biodiversity, as the number of co-present phenological stages (both at the leaf- and flower-level) in a plot confounds the observed SD (Fassnacht et al., 2022; Thornley et al., 2022). Thus, the timing of data acquisition is paramount in identifying possible associations between SD and species diversity. For this reason, categorical metrics are highly advantageous in this context, as they ideally enable overcoming the issue of seasonal change in the optical properties of plant species due to their phenology. Indeed, this type of metric could allow the identification of spatial units with consistent spectral homogeneity through time (Perrone et al., 2023).

Despite their advantages, the successful use of categorical metrics for estimating spectral diversity can be challenged by the necessity of selecting appropriate settings by the user, in particular, the optimal number of clusters into which the spectral space should be partitioned. While it is possible to use virtual dimensionality to get the number of clusters in the case of hyperspectral data, the situation is different in the case of multispectral data; there, it requires going through a time-consuming trial-and-error procedure that should consider the specific plant communities observed, the reliability of the results, and the computation intensity (Féret and de Boissieu, 2020; Perrone et al., 2023; Rocchini et al., 2021b).

The critical role played by the spatial resolution of the data used should be noted as well. Previous studies on SD highlighted how pixel size affects the relationship between spectral and plant diversity, which becomes considerably weaker with progressively coarser resolutions (Gholizadeh et al., 2018, 2019; Wang et al., 2016). However, the dependence of the relationship on pixel size is contingent on the SD metrics used (Gholizadeh et al., 2018) and sampling plot size, as well as on the specifics of the study site (Gholizadeh et al., 2022). Thus, we argue that when relying on very fine spatial resolutions that allow capturing individual objects, the risk is to introduce noise (e.g., due to shadows) into the data (Conti et al., 2021), which could lead to exceeding the number of clusters (i.e., of spectral species) identified within each area unit (e.g., plot) (Fig. 3). Therefore, users must strike a balance between spatial resolution and the desired level of spectral discrimination to avoid this issue and obtain meaningful results.

6.4.2 Confounding factors

The complexity of the herbaceous communities' vertical structure can lead to a negative relationship between SD and plant diversity due to the "occlusion effect" caused by taller species (Conti et al., 2021). Given such previous knowledge, we applied a shadow and bare soil masking on the original ortho-mosaics to improve the correlation and focus on the specific issues we wanted to test (i.e., the influence of flowering on SD). Indeed, as shown by Gholizadeh et al. (2018), filtering out pixels that capture information from non-vegetation sources improves the performance of SD

metrics, allowing a (partial) correction for such confounding factors. In principle, such correction is possible when relying on data with fine spatial resolution (e.g., proximal or UAV-borne sensors) since the spectral signature of individual pixels is more likely to belong to a single object type. Moving to coarser spatial resolutions, such as with airborne and spaceborne sensors, spectral unmixing would be required to correctly identify mixed pixels and correct for bare soil presence, which allows estimating the per-pixel percentage of constituent spectra, or endmembers (Asner and Heidebrecht, 2002; Gholizadeh et al., 2018; Rossi and Gholizadeh, 2023).

In light of the low explanatory power of the models based on spectral species richness, additional confounding factors may have played a role in the computed SD. As highlighted by Rossi et al. (2021a), the presence and ratio of live and dead biomass, together with the total biomass (Villoslada et al., 2020), may lead to higher spectral variability. The impact varies depending on ecosystem type (Rossi et al., 2021a) and specific plant community characteristics, particularly at fine spatial resolutions (Villoslada et al., 2020), emphasizing the contextual dependence of the spectral-plant diversity relationship (Fassnacht et al., 2022). Variables such as species composition, life forms (e.g., graminoids, forbs, legumes), and their prevalence within the community may also affect SD metrics (Gholizadeh et al., 2019; Wang et al., 2018b; Rossi et al., 2021a). As an example, Imran et al. (2021) observed a stronger SD-plant diversity link in artificial, species-poor ecosystems compared to species-rich natural grasslands. Despite being an experimental site, our study area has undergone partial re-naturalisation due to the spontaneous colonisation by local species, increasing species richness within each plot. Such a decrease in the strength of the SD-plant diversity link in high species richness habitats further hinders the operational applicability of SD for biodiversity monitoring purposes in natural and semi-natural habitats.

6.4.3 Limitations

In the present study, we were interested in assessing if the simple presence of flowering has a confounding effect on the relationship between plant and spectral diversity measured through different metric types.

Therefore, flowering was included in the analyses as a binary (presence/absence) variable. We did not attempt a qualitative or quantitative estimation of the flowering presence, as it would have diverted from our original aim. While we acknowledge that gathering information on the specific flower colour, size, and spatial cover would help characterize the presence of flowering within each plot, such information could not be obtained given the data available (both in terms of ground and spectral data). Nevertheless, characterizing and assessing the presence of flowering based on specific flower types is a promising topic for future research, which could include combining hyperspectral data with species-level ground data on flowering plants. This could help in acquiring further insight into the confounding effects of flowering on SD.

Moreover, the experimental setup on which our study is based would have determined the impossibility of further testing the influence of spatial resolution. Indeed, due to the small core plot size (1 m × 1 m) and pixel masking to reduce the impact of bare soils and shadowed areas, further rescaling (i.e., over a 5-cm spatial resolution) would have resulted in few pixels available for SD computation and, thus, would have introduced a major source of error (i.e., small sample size). Besides, our aim was to assess the direct link between SD and plant diversity, which implies the matching between pixel and individual size. Thus, coarsening the spatial resolution further would have been in contrast with our assumptions. Nevertheless, according to what has been previously shown by Fassnacht et al. (2022), we suppose that, at resolutions coarser than the ones tested here, the smoothing effect on extreme values would have resulted in lower SD values. However, we argue that (given the sensitivity of continuous SD metrics to extreme values) coarsening the spatial resolution would reduce, but not resolve, the overestimation of ground plant diversity when using such metrics in the presence of flowering. Additional analyses testing the impact of further coarsening the pixel size on the ability to map plant diversity of flowering communities using SD could be beneficial; however, given the small size of individual plots in our setting, this was not possible to perform within the frame of this study.

Additionally, we did not consider abundance-based indices (e.g., Shannon's H) for both plant and spectral diversity due to the possible mismatch between the actual field-sampled species abundance and the retained spectral information after pixel masking. However, while species richness is the most widespread species diversity metric in SD studies, we acknowledge that abundance-based metrics have proven to be more strongly related to SD on several occasions (Oldeland et al., 2010; Torresani et al., 2019; Wang et al., 2018b). Finally, due to the unavailability of total and relative (live, dead) biomass data, as well as data on life forms abundance, we were unable to take this type of confounding factors into account in our study. To gain a deeper understanding of how all the factors identified so far (i.e., bare soil, phenological features, biomass, vertical complexity, community composition) and their potential interactions affect the plant-spectral diversity relationship, future experiments should be designed to consider them simultaneously and assess their impact on different types of grasslands.

6.5 Conclusions

The reliability of using SD to monitor plant diversity is a matter of controversy and may need more consistency in specific settings, especially in dynamic ecosystems such as grasslands. In this study, we investigated the SD-biodiversity relationship in mesic grassland communities by testing how flowering may influence the estimation of plant species richness using different SD metrics. According to our results, the presence of flowering proved to impair the ability of continuous SD metrics to reflect plant diversity, with flowering likely being the main source of spectral variance within plots. On the contrary, categorical SD metrics appear less influenced by flowering, confirming the better suitability of this type of metrics observed in previous studies (Rossi et al., 2021a). Nevertheless, when calculating SD using categorical metrics, species richness only explains a small portion of the variability in spectral heterogeneity at both spatial resolutions tested. We hypothesise that such a low explanatory power should be ascribed to the presence of additional confounding factors (e.g.,

dead biomass, community composition) that have previously proven to interfere with the estimation of grassland diversity (Gholizadeh et al., 2019; Rossi et al., 2021a; Schweiger et al., 2015; Villoslada et al., 2020). Thus, we encourage future investigations to systematically consider all possible confounding factors when testing the spectral diversity-biodiversity relationship in different types of grasslands. Finally, to define the actual possibilities and technical constraints of the relationship, future research should aim at identifying the optimal trade-off between the spatial and spectral resolutions of the remote sensing data used to assess plant diversity in grasslands while incorporating the temporal variations in the spectral signal. In this framework, comparing spectral signatures over an entire growing season (spatio-temporal spectral diversity) could be critical in estimating plant diversity.

Supplementary materials

Supplementary materials to this article can be found in the online version at https://doi.org/10.1016/j.ecoinf.2024.102589.

7

Discussion and Summary

This thesis addressed the intricate relationship between spectral and plant diversity, shedding light on the complexities underlying the possibility of plant diversity estimation through remotely sensed differences in reflectance. By delving into the interplay of the key factors influencing the link, novel insights have emerged, offering valuable insights for future biodiversity monitoring efforts.

The objective of this thesis was threefold. First, a comprehensive and systematic review of the spectral diversity concept was provided in Chapter 4 by highlighting the contexts and data characteristics for which the SVH has been tested so far. Secondly, the relationship between spectral and plant diversity was explored at the landscape scale by evaluating the effectiveness of three categories of spectral diversity metrics in predicting both plant species richness and functional diversity while considering the influence of habitat types (Chapter 5). Finally, the relationship was assessed at the community scale by evaluating six spectral diversity metrics and accounting for phenology (i.e., flowering) as a potential factor influencing the relationship (Chapter 6).

Given that comprehensive discussions and conclusions specific to each of the studies were presented in the previous chapters, they will not be repeated here. Instead, in this final chapter, I synthesise the key findings of each chapter, discuss their general implications in the spectral diversity framework, and propose avenues for further investigation, underscoring the significance of this work in filling knowledge gaps about the spectral diversity concept and in advancing the field of plant diversity monitoring and conservation.

7.1 Lights and shadows of spectral diversity

The review presented in Chapter 4 allowed us to identify current knowledge gaps about the spectral diversity concept and its applicability for biodiversity estimation and monitoring. The need for an up-to-date review of the ever-increasing body of work on the spectral-plant diversity relationship stemmed from the context-dependent nature of such a link. Indeed, inconsistent findings on the effectiveness of spectral diversity in relating to plant diversity were found across the numerous investigations on the topic, calling for a more systematic consideration of the key factors that influence the relationship (Fassnacht et al., 2022; Gamon et al., 2020). Thus, Chapter 4 was dedicated to describing the contexts in which the SVH has been tested and evaluating its validity across the available literature.

From this review work, it emerged that forest ecosystems comprised the largest share of the studies testing the SVH, with most of these studies relying on spaceborne multispectral and reporting high goodness of fit, showcasing the potential of coarser spatial resolution data in such ecosystems (Gillespie, 2005, Torresani et al., 2019). Grassland research makes up a substantial portion of studies which tend to report improved fits studies when using UAV and field optical data due to higher spatial resolution (Gholizadeh et al., 2018; Polley et al., 2019; Wang et al., 2018a; Thornley et al., 2022). On the contrary, airborne and spaceborne studies in grasslands show low to medium goodness (Möckel et al., 2016; Monteiro et

al., 2022), reflecting the importance of high spatial resolution data. In mixed types of ecosystems, spaceborne multispectral studies dominate and generally show high goodness of fit (Aneece et al., 2017; Chitale et al., 2019; Mapfumo et al., 2016; Marzialetti et al., 2020; Taddeo et al., 2021; Tassi et al., 2022; Warren et al., 2014), although some report lower fits (Chraibi et al., 2021; Fassnacht et al., 2022; Villoslada et al., 2020). All other types of ecosystems individually contribute to less than 10% of the studies. Marine ecosystems, though less studied, show potential for high goodness of fit when relying on airborne hyperspectral data (Herkül et al., 2013). In agricultural systems and savannahs studies, spaceborne multispectral studies dominate and consistently show high goodness of fit, while wetlands reported medium to high goodness.

Moreover, Chapter 4 showed how the variability in findings when investigating the influence of spatial resolution on the relationship between spectral diversity and biodiversity emphasises the need to carefully align remote sensing data scale with the ecological phenomena under study. Consequently, specific attention should be given to field data collection to better match field observations to the pixel size of remote sensing data and develop standardised field protocols (Pacheco-Labrador et al., 2022). Moreover, the spectral range covered can also impact the relationship between spectral and plant diversity (Gholizadeh et al., 2018). However, spatial resolution emerged as the main constraint rather than spectral resolution. Rossi et al. (2021) explained the lesser significance of high spectral resolution with the redundancy resulting from compressing information from highly correlated spectral bands, which likely introduces biases towards certain spectral features. Additionally, several studies underscored the significance of daily and seasonal variations in plant optical traits (related to phenology) on the relationship with spectral diversity, thus highlighting the importance of the temporal resolution of data acquisition. Indeed, acquiring time series of remote sensing data, and not just single acquisitions, is advantageous for detecting temporal variations among species and communities (Rossi et al., 2021), especially during the growing season.

The review also revealed high variability across studies in the metrics used to quantify spectral diversity, stressing that the choice of the metric applied relies on the data available, the ecological goal, and the analytical approach used to assess the relationship between spectral and plant diversity. Specifically, the most frequently used metrics in the considered studies are the coefficient of variation and Rao's Q index. Notably, 16% of the publications present metrics that have been used only once in the literature. Similarly, a wide variety of plant diversity metrics was observed, with species richness and Shannon's H index standing out as the most frequently used. However, several studies indicate that plant diversity metrics based on abundance show a stronger correlation with spectral diversity compared to metrics based solely on species richness (Oldeland et al., 2010; Torresani et al., 2019; Wang et al., 2018b; Xu et al., 2022. Moreover, various studies have extended the application of spectral diversity beyond alpha diversity to gamma and, especially, beta diversity (i.e., species turnover in space). According to most of these studies, methods based on spectral diversity proved to effectively capture vegetation physiological changes, species turnover, and habitat diversity.

Overall, this review allowed us to identify current challenges in the study of the spectral-plant diversity relationship, as it showed that interpreting such a relationship across ecosystems is influenced by multiple interacting factors, including optical data, diversity indices used, and field data acquisition specifics.

7.2 Key factors influencing the relationship between spectral and plant diversity

7.2.1 Spectral diversity metrics

In Chapter 4, the choice of the metrics used to quantify spectral diversity was discussed as a key factor in the ability of spectral diversity to reflect plant diversity. Thus, we tested and discussed the performance of

different types of spectral diversity metrics at the landscape (Chapter 5) and community (Chapter 6) scales.

We observed that both the continuous (i.e., sdNDVI and Rao's Q) and categorical (i.e., spectral communities' richness) metrics tested could explain a similar proportion of variability in ground diversity at the landscape scale, with the continuous ones performing moderately better, depending on the habitat type. Given these results and the computational demands of calculating spectral community-based metrics and Rao's Q index, using simpler metrics like sdNDVI, which have been successful in other studies (Gholizadeh et al., 2019), can be more computationally efficient at this scale. Conversely, at the community scale, we found that categorical metrics (i.e., spectral species richness) are the only ones that show a significant and positive relationship with plant diversity. All the continuous metrics tested at this scale were instead affected by the presence of flowering and didn't show any significant relationship with plant diversity, regardless of the range of spectral information considered.

Overall, estimating spectral diversity through categorical metrics allows summarising the continuous spectral space into discrete spatial objects, likely representing distinct landscape/community features. This approach thus exhibits reduced sensitivity to extreme pixel values that may disproportionately affect the quantification of spectral diversity (Wang & Gamon, 2019). Nevertheless, using categorical metrics for estimating spectral diversity can be challenging because users need to select appropriate settings, particularly the optimal number of clusters for partitioning the spectral space. For hyperspectral data, virtual dimensionality can help determine the number of clusters, but for multispectral data, a time-consuming trial-and-error process is required. This process must consider the specific plant communities, the reliability of the results, and the computational intensity (Féret & de Boissieu, 2020; Perrone et al., 2023; Rocchini et al., 2021b).

7.2.2 Habitat type

Another key factor affecting the relationship between spectral and plant diversity considered in Chapter 4 is the habitat type. By testing in Chapter 5 the relationship at the landscape scale over a variety of habitat types, we observed that its strength varied significantly depending on the habitat type, confirming the influence that such factor has on the spectral-plant diversity relationship. Spectral diversity had a consistently significant and positive effect in areas dominated by arable land, coniferous forests, and transitional woodland-shrubs. Particularly in transitional woodland-shrubs, the spectral diversity effect was notably higher, indicating a stronger association with increased plant diversity, tree cover, or visible understory. Pastures and broad-leaved forests also showed significant positive effects on the relationship, but only in certain models. Finally, negative effects were only observed in artificial surfaces when spectral diversity was calculated using categorical metrics.

The study presented in Chapter 6 focused on one single but challenging type of habitat: grasslands. Previous studies highlighted that the presence of bare soil, with its distinct spectrum, significantly undermines the spectral diversity performance in quantifying plant diversity (Gholizadeh et al., 2018; Hauser et al., 2021b). Additionally, the spectral signal is sensitive to the plant community's vertical structure, where a complex vertical arrangement can cause an "occlusion effect", obscuring shorter species and creating shadowed pixels (Conti et al., 2021). Based on previous findings, we applied shadow and bare soil masking to the original ortho-mosaics to enhance the correlation. However, given the low explanatory power of species richness observed in our results, additional confounding factors specific to grasslands, such as total and dead biomass, life forms presence (e.g., graminoids, forbs, legumes), and their prevalence within the community may have played a role in the computed spectral diversity.

7.2.3 Phenology

The third key factor that was considered is the phenological stage of the vegetation when collecting reflectance data used to calculate spectral

diversity. At the landscape scale, to best capture vegetation cover, smooth out inter-annual variability, and avoid extreme events like floods or fires, we created a "greenest-pixel" composite by selecting pixels with the highest NDVI value over the study period (Chapter 5). The results obtained calculating spectral diversity from a greenest-pixel composite proved to be better than those achieved using a median composite. Therefore, our study confirmed that the relationship between spectral and plant diversity is strongest when photosynthetically active vegetation cover is at its peak (Feilhauer & Schmidtlein, 2011; Thornley et al., 2022; Torresani et al., 2019).

In Chapter 6, we observed that the community's phenological pattern, i.e., the presence of flowering species, affects the relationship between spectral and plant diversity when relying on fine-scale data in grasslands. Indeed, plant species show distinct spectral signatures at different phenological stages, and blooms, with their unique spectral characteristics, influence continuous spectral diversity metrics due to their sensitivity to extreme reflectance values. In contrast, our results indicate that categorical spectral diversity metrics mitigate this issue by treating extreme pixel values as distinct, equally important categories (Wang & Gamon, 2019) and, thus, should be preferred when flowering is present in the area of interest.

7.3 Ways forward

The findings presented in this dissertation shed light on several key aspects of the relationship between spectral diversity and plant biodiversity, yet they also unveil new avenues for further exploration and investigation. This section outlines potential directions for future research that could build upon the findings and insights of this thesis and address remaining questions and gaps in knowledge, providing further insights on the dynamics of the spectral-plant diversity relationship across scales and ecosystems.

As previously highlighted, the relationship between spectral and plant diversity is strongly influenced by the spatial resolution of remotely sensed data, the metrics used to calculate spectral diversity, the temporal variation

in reflectance linked to species phenology, and the type of habitats studied. To achieve a more thorough understanding and develop a robust framework for biodiversity monitoring using optical remote sensing data, future studies should systematically and simultaneously address such key factors that interconnectedly contribute to SVH uncertainty. Furthermore, future investigations should systematically consider all the elements that can have a confounding effect when calculating spectral diversity (e.g., bare soil presence), especially when addressing the direct link with plant diversity (i.e., at fine spatial resolutions). Starting with virtual data that capture the entire optical spectrum and where no confounding factors are present may be beneficial (Hauser et al., 2021b; Pacheco-Labrador et al., 2022), with subsequent experiments using real field data. Additionally, considering various sensors, platforms, data sources, and plant diversity indices will enhance the understanding of the complexities of the SVH and the potential application of spectral diversity as a biodiversity monitoring tool.

Moreover, as revealed by the variation partitioning shown in Chapter 5, the relative importance of spectral diversity accounts for a small fraction of the total variability in plant diversity, regardless of the metrics used. Based on the SVH, we expected that spectral diversity would indirectly serve as a proxy for environmental heterogeneity and thus correlate with plant diversity. Although the indirect relationship between spectral and plant diversity tested at the landscape scale was not strong compared with the other predictors analysed, it was still highly significant. Thus, spectral diversity alone has limited potential as a proxy for taxonomic or functional diversity but can enhance diversity models when combined with other predictors. Future studies should further test the effectiveness of spectral diversity in multivariate models predicting biodiversity (e.g., Kreft & Jetz, 2007; Večeřa et al., 2019) alongside well-established variables influencing diversity, such as productivity, climate, and historical processes (Hawkins et al., 2003; Lomolino et al., 2017; Ricklefs & Schluter, 1994). Additionally, it would be crucial to consider and test how spectral diversity could be integrated with different remotely sensed diversities, such as thermal, structural, and topographical ones. Indeed, recent studies have shown that vegetation height heterogeneity is a good proxy of plant diversity both in

forest (Torresani et al., 2023b) and grassland (Torresani et al., 2024) ecosystems.

The variation in space of spectral reflectance has been mainly proposed to relate to plant biodiversity (Chapter 4). Biodiversity is recognized as a major determinant of ecosystem functions (M.E.A., 2005; Tilman et al., 2014), such as productivity, which proved to be effectively estimated by spectral diversity (Schweiger et al., 2018; Villoslada et al., 2020). Moreover, exploring spectral diversity beyond plant diversity reveals its potential for estimating other taxa's biodiversity, including invertebrate diversity, which correlates with habitat heterogeneity. Indeed, spectral diversity captures various surfaces, aiding assessments of non-vegetated habitats where many invertebrates thrive (Samways et al., 2020). This aligns with the SVH and introduces "surrogacy" in biodiversity estimation, where certain components act as proxies for others, as proposed by Magurran (2021).

Finally, emphasis should be put on the ultimate envisaged application of spectral diversity, which is biodiversity monitoring. In its well-established definition, biodiversity monitoring consists of the periodic and systematic collection, analysis, and interpretation of data to assess the status and highlight trends in the various forms of biodiversity (genes, taxa, ecosystems, etc.) using standardised methods and protocols (Juergens 2009; EEA 2010). Thus, given the intention to apply spectral diversity for biodiversity monitoring purposes, efforts should be increased to include the temporal dimension in future studies. Spectral diversity has been successfully tested for capturing the turnover of species composition between different communities or localities, i.e., beta diversity (Chapter 4), by examining the diversity of spectral patterns in space. In light of these results, if moving from the spatial to the temporal variation in the spectral signal, spectral diversity may hold promise for capturing within the same communities/localities the variation over time in species composition and other facets of biodiversity.

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Curriculum Vitae & List of Publications

Personal

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Affiliations

2020 – present
Department of Spatial Sciences
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Czech University of Life Sciences Prague (CZ)

Education

2020 - present
Department of Spatial Sciences
Faculty of Environmental Sciences
Czech University of Life Sciences Prague (CZ)
PhD studies in Environmental Sciences
Thesis topic: Assessing plant biodiversity by remote sensing at different ecological scales

2017 – 2019
Department of Sciences
Roma Tre University (IT)
Master's degree in Biodiversity and Ecosystem Management
Thesis topic: Monitoring chlorophyll-a concentration in three volcanic lakes of central Italy by remote sensing

9/2018 – 1/2019
Faculty of Sciences
Université de Liège (BE)
Erasmus+ study abroad

2014 – 2017
Department of Sciences
Roma Tre University (IT)
Bachelor's degree in Biological Sciences
Thesis topic: Relictualism and climate change: effects on *Fagus sylvatica* low altitude populations

Participation in Research Projects

2023 – present
EarthBridge - Building Bridges between Earth observation and Environmental Sciences
HORIZON WIDERA – Twinning
Team member

2024 – Present
Impact of open cast mining on Earth's surface physiographic characteristics
Internal Grant Agency of the Faculty of Environmental Sciences
Team member

2022 – 2024
SPACES: testing the SPectral variation hypothesis ACross Ecological Scales
Internal Grant Agency of the Faculty of Environmental Sciences
Project leader

2021 – 2022
Linking spectral heterogeneity and plant diversity across scales: a Czech Republic
experience
Internal Grant Agency of the Faculty of Environmental Sciences
Project leader

Awards

2023
Czech University of Life Sciences Prague
1st place in Rector's Award for the best publication outputs of doctoral students

Internships

4 – 6/2023
Swiss National Park (CH)
Erasmus+ Traineeship

2 – 3/2023
Alma Mater Studiorum Università di Bologna (IT)
Erasmus+ Traineeship

6 – 8/2020
Laboratory of Biodiversity and Ecosystem Services, ENEA (IT)
"Torno Subito" ("Be Right Back") grant of the Regione Lazio European Social Fund

2 – 5/2020
Czech University of Life Sciences Prague (CZ)
"Torno Subito" ("Be Right Back") grant of the Regione Lazio European Social Fund

International Conferences

6/2024
Chronicles of spectral diversity: unravelling plant alpha and beta diversity in grasslands through a multitemporal lens
ECCB 2024 - 7th European Congress of Conservation Biology, Bologna (IT)
Talk

1/2024
"Flower power": how flowering affects spectral diversity metrics and their relationship with plant diversity
11th Biennial Conference of the International Biogeography Society, Prague (CZ)
Poster

9/2023
Biodiversity monitoring from above: linking spectral to local plant diversity
65th IAVS Annual Symposium, Coffs Harbour (AU)
Talk

6/2022
Linking spectral and plant diversity at the landscape scale: disentangling lights and shadows of different metrics
64th IAVS Symposium 2022, Madrid (ES)
Talk

9/2021
Linking spectral heterogeneity and plant diversity across scales and time: a Czech Republic experience
63rd IAVS Symposium 2021, Online
Talk

Editorial Services

Rewiever for the following Journals:

- International Journal of Applied Earth Observation and Geoinformation
- Ecological Informatics
- Journal of Vegetation Science
- Remote Sensing in Ecology and Conservation

Publications in Journals with Impact Factor

Torresani, M., Rossi, C., **Perrone, M.**, Hauser, L. T., Féret, J. B., Moudrý, V., ... & Rocchini, D. (2024). Reviewing the spectral variation hypothesis: Twenty years in the tumultuous sea of biodiversity estimation by remote sensing. *Ecological Informatics*, 102702.

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between remotely-sensed spectral heterogeneity and bird diversity is modulated by landscape type. International *Journal of Applied Earth Observation and Geoinformation*, 128, 103763.

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Teaching Experience

2020 – 2024
Department of Spatial Sciences
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Seminars of GIS I; *GIS II*; *Remote Sensing II*