

Remote Sensing of Grassland Biodiversity

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Summary

Biodiversity is declining globally at rates unprecedented in human history. In particular, grassland biodiversity is threatened by destruction, degradation, and fragmentation due to urban development, intensive farming, and climate change. The loss of grassland biodiversity negatively impacts the function of ecosystems, which are essential not only for the survival of plant and animal species but also for sustaining human life. With the ceaseless destruction of grasslands and associated loss of biodiversity, monitoring effective management practices for biodiversity conservation in grasslands remains a high priority.

As a result, large efforts have been undertaken to monitor plant diversity in the field and coalesce the information into several global databases. Furthermore, remote sensing has emerged as a potential approach that can provide a straightforward, large-scale, and continuous estimation of biodiversity from unmanned aerial vehicles (UAV), airplanes, and satellites. In particular, remotely measuring the sunlight reflected by plants at a specific wavelength, allows for an efficient and rather inexpensive collection of baseline data related to biodiversity. Despite all efforts in field surveys and remote sensing, large-scale information on plant diversity remains scarce with almost no temporal coverage. The measurement of plant diversity across large scales in the field requires a high investment of human and financial resources. Remote sensing of biodiversity is impeded by a unique set of challenges presented by grasslands such as small size of individual plants and high degree of temporal variation due to phenology and land management. Furthermore, field-observed biodiversity metrics do not align well with remote sensing products. To tackle these challenges and to quantify biodiversity in differently managed alpine grasslands, this thesis investigated the use of different remote sensing methods, platforms, and sensors.

It was necessary to comprehend the particularities of grassland ecosystems being observed as well as the ramifications of temporal, spectral and spatial resolutions of optical remote sensing on plant diversity estimations to bridge the work of both ecologists and remote sensing specialists. Commencing with the resolution of satellite sensors (tens of meters in general), the alpine grasslands' spectral responses reflected the diversity between communities (β -diversity). More specifically, the optimized inversion of a radiative transfer model with remotely-sensed reflectance data made it possible to quantify the community-weighted mean of plant traits, thereby elucidating the effect of management types on β -diversity over large areas. In order to estimate the plant diversity in a community (α -diversity), the potential of UAVs and airborne data was explored in a natural grassland experiment. In this context, spatial resolution,

the awareness of confounding factors, such as biomass, and choice of diversity metrics were critical factors to successfully evaluate the richness of plant species. Furthermore, the combination of different sensors allowed to address the intrinsic requirements of high spatial and spectral-resolution for the remote estimation of biodiversity. Finally, this thesis entailed the development of a novel method to estimate plant diversity that accounts for the spatio-temporal variation of spectral diversity. This new method allows for the quantification of the contribution of varied spatial (e.g., communities) and temporal (e.g., phenology) components of spectral diversity. The proposed approach, coupled with the utilisation of multi-temporal satellite data, allowed for the improved estimation of β -diversity in grasslands.

As done in this thesis, the combination of investigating and developing different methods provides the basis for evaluating and monitoring the diversity of plants in differently managed grassland. As a case in point, comparing different management types underscored the significance of a non-intervention policy (i.e., a long-term protection endeavour, which enables natural processes to unfold) endeavouring to enrich different facets of a region's grassland biodiversity.

Zusammenfassung

Die Biodiversität nimmt weltweit in einem noch nie dagewesenen Ausmaß ab. Insbesondere die Diversität von Grasländern ist bedroht. Dies durch Zerstörung, Degradierung und Fragmentierung aufgrund von Stadtentwicklung, intensiver landwirtschaftlicher Nutzung und durch den Klimawandel. Der Diversitätsverlust von Grasländern wirkt sich negativ auf die Funktion von Ökosystemen aus, die nicht nur für das Überleben von Pflanzen- und Tierarten, sondern auch für die Erhaltung des menschlichen Lebens unerlässlich sind. Angesichts der unaufhörlichen Zerstörung von Grasländern und des damit verbundenen Verlusts an Biodiversität hat die Beobachtung wirksamer Bewirtschaftungsmethoden zur Erhaltung der Graslandbiodiversität weiterhin hohe Priorität.

Infolgedessen wurden große Anstrengungen unternommen, um die Pflanzendiversität vor Ort zu bestimmen und die Informationen in mehreren globalen Datenbanken zusammenzufassen. In diesem Zusammenhang hat sich die Fernerkundung als vielversprechender Ansatz herauskristallisiert. Sie ermöglicht eine großflächige und kontinuierliche Schätzung der Pflanzendiversität von Drohnen, Flugzeugen und Satelliten aus. Insbesondere die Messung des von Pflanzen bei einer bestimmten Wellenlänge reflektierten Sonnenlichts bietet eine effiziente und relativ kostengünstige Erhebung von Grundlagendaten zur Biodiversitätsschätzung.

Trotz aller Bemühungen im Bereich der Felderhebungen und Fernerkundung sind großflächige Informationen über die Pflanzenvielfalt nach wie vor spärlich und decken fast keine unterschiedlichen Zeiträume ab. Die Bestimmung der Pflanzendiversität in großem Maßstab erfordert einen hohen Einsatz an personellen und finanziellen Ressourcen, wenn diese Daten direkt im Feld erhoben werden müssen. Die ressourcenschonendere Fernerkundung der Pflanzendiversität hingegen wird durch eine Reihe von Herausforderungen erschwert, die Graslandschaften mit sich bringen, wie z. B. geringe Größe der Pflanzen und starke zeitliche Schwankungen aufgrund von Phänologie und Bewirtschaftung. Hinzu kommt das Problem, dass die im Feld beobachteten Biodiversitätskennzahlen nur unzureichend mit den Fernerkundungsprodukten übereinstimmen. Um diese Herausforderungen zu meistern und die Biodiversität in unterschiedlich bewirtschafteten alpinen Graslandschaften zu quantifizieren, wurde in dieser Arbeit der Einsatz verschiedener Fernerkundungsmethoden, Plattformen und Sensoren untersucht.

Um eine Brücke zwischen der Arbeit von Ökolog/-innen und Fernerkundungsspezialist/-innen zu schlagen, war es notwendig, die Besonderheiten der beobachteten Graslandökosysteme sowie die Auswirkungen der zeitlichen, spektralen und räumlichen

Auflösung der optischen Fernerkundung auf die Schätzung der Pflanzendiversität zu verstehen. Aufgrund der Auflösung der Satellitensensoren (im Allgemeinen einige zehn Meter) spiegelte die Reflektivität der alpinen Graslandschaften die Diversität zwischen den Gemeinschaften (β -Diversität) wider. Die optimierte Inversion eines Strahlungstransfermodells mit Reflexionsdaten aus der Fernerkundung ermöglichte es, den Mittelwert von Pflanzenmerkmalen einer Gemeinschaft zu quantifizieren. Die auf diese Weise ermittelten Pflanzenmerkmale trugen dazu bei, die Auswirkungen von Bewirtschaftungsformen auf die β -Diversität über große Flächen hinweg zu bestimmen. Um die Pflanzendiversität in einer Gemeinschaft (α -Diversität) zu quantifizieren, wurde das Potential von drohnen- und flugzeuggestützten Daten (Auflösung Zentimeter bis wenige Meter) in einem natürlichen Grasslandexperiment untersucht. In diesem Zusammenhang waren die räumliche Auflösung, die Berücksichtigung von Störfaktoren wie die Biomasse und die Wahl der Diversitätskennzahlen entscheidende Faktoren für eine erfolgreiche Bewertung der Anzahl Pflanzenarten. Die Kombination verschiedener Sensoren ermöglichte es, die hohen Anforderungen bzgl. räumlicher und spektraler Auflösung für die Fernerkundung der Pflanzendiversität zu erfüllen. Schließlich wurde im Rahmen dieser Arbeit eine neue Methode zur Schätzung der Pflanzendiversität entwickelt, welche die räumlich-zeitliche Variation der spektralen Diversität berücksichtigt. Diese neue Methode ermöglicht die Erfassung des Beitrags verschiedener räumlicher und zeitlicher Komponenten der spektralen Diversität (z.B. unterschiedliche Gemeinschaften resp. Phänologie). Der vorgeschlagene Ansatz erzielte eine verbesserte Schätzung der β -Diversität in Grasländern, indem multitemporale Satellitendaten genutzt wurden.

Die vorangetriebene Kombination von Untersuchung und Entwicklung verschiedener Methoden bildet die Grundlage für die Bewertung und Überwachung der Pflanzendiversität in unterschiedlich bewirtschafteten Graslandschaften. Der Vergleich von verschiedenen Bewirtschaftungsformen in dieser Arbeit hat die Bedeutung von Gebieten mit einem ausgeweiteten Schutz, welche es ermöglichen, dass sich natürliche Prozesse frei entfalten können, aufgezeigt. Solche Gebiete bereichern die verschiedenen Facetten der Biodiversität von Grasländern einer ganzen Region.

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Abbreviations

ALA	Mean leaf inclination angle
ANOVA	Analysis of variance
ANCOVA	Analysis of covariance
ARTMO	Automated Radiative Transfer Models Operator
a.s.l.	above sea level
AVIRIS-NG	Next generation airborne visible/infrared imaging spectrometer
BRDF	Bidirectional reflectance distribution function
Cab	Leaf chlorophyll a + b concentration
CAI	Cellulose absorption index
Cbrown	Brown pigment content
Car	Leaf carotenoid content
CHV	Convex hull volume
CV	Coefficient of variation
Cw	Leaf water mass per unit area
CWM	Community-weighted mean
FD	Functional diversity
FDi	Functional diversity indices
GCP	Ground control points
GEO BON	Global Earth Observation Biodiversity Observation Network
GNSS	Global Navigation Satellite System
hot	Hot spot size parameter
IUCN	International Union for Conservation of Nature
LDMC	Leaf dry matter content
LAI	Leaf area index
LMA	Leaf dry mass per area
LU	Livestock units
LUT	Lookup table
MSI	Multi-Spectral Instrument
MTCI	MERIS terrestrial chlorophyll index
NDVI	Normalized Difference Vegetation Index
NHG	Federal act on the protection of nature and cultural heritage
N	Leaf structural parameter
NIR	Near-infrared
PCA	Principal component analysis
psoil	Soil brightness

RaoQ	Rao's quadratic entropy
RF	Random forest
RGB	Red green blue
RTM	Radiative transfer model
SD	Spectral diversity
SKYL	Ratio of diffuse to total incident radiation
SLA	Specific leaf area
SNP	Swiss National Park
SS	Sum of squares
SVH	Spectral variation hypothesis
SWIR	Short-wave infrared
TGI	Triangular greenness index
UAV	Unnamed aerial vehicle
VH	Vegetation height
VI	Vegetation index
VIS	Visible

1

Introduction

Biodiversity is the totality of all inherited variation in the life forms of Earth, of which we are one species. We study and save it to our great benefit. We ignore and degrade it to our great peril. Today, in the urgent need of comprehensive biodiversity monitoring, remote sensing has the potential to continuously capture plants and their diversity at different spatial and temporal scales. This chapter expresses the motivation and relevance of this thesis and provides a brief overview of the state-of-the-art in remote sensing of grassland biodiversity.

"Many eyes go through the meadow, but few see the flowers in it."

RALPH WALDO EMERSON

1.1 Importance of grassland biodiversity

Grasslands are areas in which a nearly continuous cover of grasses dominates the vegetation. With a coverage of 40% of the Earth's terrestrial surface, grasslands are the largest and the most exploited biome on Earth (Gibson, 2009) that provide an extensive range of ecosystem services including forage production, carbon sinks, climate control, genetic resources, water quality and recreation (Hein et al., 2006; Lamarque et al., 2011). In addition, grasslands are home to the most iconic animals on Earth (e.g., elephants, bison and lions). Unique from most other biomes, grasslands are relatively simple in structure but rich in many species. Besides the functioning and services provided, the grassland diversity demonstrates consequences for different trophic levels, for ex-

ample by influencing an increase in diversity of insects and their predators (Dinnage et al., 2012). Nevertheless, grasslands remain the least protected ecosystems on the planet.

1.1.1 The decline of grassland biodiversity

Biodiversity is declining globally at unprecedented rates in human history (Barnosky et al., 2011; Ceballos et al., 2017; Díaz et al., 2019). Switzerland is no exception, and the statistics show that biodiversity has declined significantly since 1900, with 35% of approximately 10,000 species studied considered to be at risk (Gattlen et al., 2017). Among the main drivers of this decline is the defining attribute of our time, that is, the global change manifested through habitat destruction, pollution, intensive agriculture, and forestry (Newbold et al., 2016; Steffen et al., 2011). In particular, nitrogen deposition due to combustion of fossil fuels and agricultural fertilisation has been shown to reduce grassland biodiversity (Clark and Tilman, 2008). The evidence available indicates that the loss of grassland biodiversity impacts ecosystem productivity and stability (Hautier et al., 2014; Tilman et al., 1996, 2006, 2012), carbon storage capacity (Ward et al., 2016), and the number of pollinators (Batary et al., 2010) negatively. As such, losing grassland biodiversity means jeopardising ecosystem functions that are essential for the survival of plant and animal species (Tews et al., 2004) and vital in sustaining human life (Díaz et al., 2006; Gómez-Baggethun et al., 2010; Manning et al., 2018).

Although the worldwide loss of grassland biodiversity and the associated decline of ecosystem services call for effective biodiversity policies and management practices, scientific evidence (Secretariat of the Convention on Biological Diversity, 2020) and authorities - such as the European Environment Agency - indicate that current instruments to help determine such practices are far from sufficient. Therefore, comprehensive monitoring of plant biodiversity is necessary. The primary limitations in increasing knowledge, the science base, and technologies related to biodiversity monitoring are described in the following sections.

1.2 A sparse sampling of biodiversity

Access to information about biodiversity from field-based studies is limited. Measuring plant diversity in the field needs to be based on a robust sampling design, and

demonstrates a high demand for human and financial resources and is exposed to biases due to environmental conditions and the person in charge (Bonar et al., 2011; Löhmus et al., 2018). Furthermore, governments are notoriously reluctant to share data and information that exposes their resource use and policy priorities (Ustin and Middleton, 2021). This reluctance and high resource demands lead to areas where biodiversity remains poorly sampled, especially in developing countries (Kattge et al., 2020).

A growing body of research highlights the role of the functional facet of plant biodiversity (i.e., functional diversity), expressed by the variation in plant traits within or between plant species and communities, rather than species diversity in linking biodiversity to the functioning of ecosystems (de Bello et al., 2010; Díaz et al., 2007a; Grigulis et al., 2013; Lavorel et al., 2011). Traits are heritable characteristics of an organism that potentially affect performance, fitness, or resource acquisition strategies (Díaz and Cabido, 2001; Díaz et al., 2016; Loreau, 2000; Musavi et al., 2015). Environmental properties such as climate, agricultural management or biotic interactions determine which traits and ecosystem functions prevail at a particular location (Díaz et al., 2006; Westoby, 1999). Thus, being able to quantify traits efficiently is essential to understand the impact of land-use, climate change and the provided ecosystem services across the landscape (Díaz et al., 2006; Garnier et al., 2007; Grigulis et al., 2013; Laliberté et al., 2012; Laughlin, 2014; Socolar et al., 2016; Sonnier et al., 2012; Westoby, 1999). Furthermore, in the context of the Global Earth Observation Biodiversity Observation Network (GEO BON) species traits are considered an Essential Biodiversity Variable to inform policy regarding biodiversity change (Kissling et al., 2018; Pereira et al., 2013). The availability and accessibility in appropriate quantity and quality of plant traits, therefore, provides a crucial basis for quantitative and predictive ecology and the global change science–policy interface (McGill et al., 2006; Westoby and Wright, 2006). However, traits suffer from spatially and temporally limited data availability and on average, only around 2% of vascular plant species have any trait measurements available across landscapes (Jetz et al., 2016).

1.3 The overwhelming emphasis on localness

Our perception of biodiversity is affected by the unit of observation, i.e., the number of observations included or the size of the community, and the spatial extent over which plant biodiversity is quantified (Field et al., 2009). Based on the given unit and extent, plant biodiversity is calculated over a certain number of sampling units. Delineating the size and shape of these units generally takes into account the hierarchical

structure of biodiversity (Kolasa, 1989) as proposed by Whittaker (1960): α -diversity (within-community diversity) and β -diversity (between-community diversity). The nature, form, and structure of data quantifying biodiversity can therefore differ significantly between large and small scales. As such, research has often focused on one scale to the exclusion of others, which in turn, has particularly neglected the investigation of large-scale effects in the function of an ecosystem (Fischer et al., 2014). These large-scale effects are crucial in ensuring ecosystem functions and stability (Oehri et al., 2020; Tälle et al., 2016; Thompson et al., 2018) and essential for land use planning and policy-making (Nelson et al., 2009). In ecology, there is rarely a single scale that identifies how specific processes drive biodiversity (Anderson, 2018). Furthermore, the definition of a community is the subject of considerable debate. Ricklefs (2008) indicated the community concept as a major obstacle in the progress towards an exhaustive understanding of biodiversity at local to regional scales. Estimating plant biodiversity from species or/and traits on a few discrete and arbitrary sampling units results in an overwhelming emphasis on localness, which leads to insufficient data coverage across landscapes and high variability in the shapes of areas being sampled. On the contrary, replacing discrete local-community boundaries with a time-space continuum of plant biodiversity estimations on multiple scales is what ecologists should embrace. Moreover, being able to quantify biodiversity continuously on different spatial scales efficiently is essential to understand the plant assembly processes that generate and maintain biodiversity and ecosystem functioning (Münkemüller et al., 2012).

1.4 Conservation needs support

The efforts to protect biodiversity are generally insufficient, as the failure to achieve the UN's biodiversity targets shows: By 2020, at least 17 % of terrestrial and 10 % of marine areas were to be protected (Aichi Target 11), but only 15 % and 7 % respectively have been achieved (Secretariat of the Convention on Biological Diversity, 2020). Furthermore, this percentage of protected areas is far from sufficient to stop mass extinctions and secure the livelihoods and well-being of people in the long term (Dinerstein et al., 2017; Noss et al., 2012). Establishing new protected areas is however challenging and the nature conservation negotiations complex as demonstrated by the recent park project failures in Switzerland (Michel and Backhaus, 2019). Conservation and management actions are usually limited in scope and effectiveness by numerous interacting financial, logistical, cultural, and political factors. Moreover, the success of various practices in restoring or maintaining biodiversity is largely unknown. All

the more important is to investigate the impact of long-term protection endeavours on biodiversity and concurrently identify the location and essential components of high-value conservation targets.

1.4.1 A strict nature reserve

An area where human interference is minimised (e.g. visitors are not allowed to leave the marked paths, as well as, hunting and livestock grazing are forbidden) can be found in the Swiss National Park (SNP) in the Grisons. The park and its surroundings offer an ideal place to study the effect of management practices on plant biodiversity. Founded in 1914, the SNP is the oldest national park in Central Europe and the country's only national park. The park is designated as a category Ia nature reserve (highest protection level - strict nature reserve, IUCN), where nature has been left to itself for over a century.



Figure 1.1: In the middle of the image, a typical pasture in the Swiss National Park (Stabelchod) transitioned from grazing by domestic livestock to agricultural abandonment towards grazing by red deer. ©SNP/Andi Hofstetter

Vegetation ecology research has a long tradition in the SNP. The first long-term observation plots were established by Josias Braun-Blanquet in 1917. Since then, measuring plants and their diversity has undergone different stages from very detailed point data recorded in the field to large extents of the SNP covered using airborne data (Schweiger et al., 2015a). Despite the legacy, vegetation studies were often limited to the boundaries of the SNP, to species count, neglected in favour of ungulate ecology, difficult due to remoteness of the area and partially restricted to walkways (Wipf et al., 2021). These restrictions have led to a limited understanding of the long-term differences between non-intervention policy in the park, i.e., protected grasslands, and managed grasslands in the surrounding cultural landscape. In literature, the response of plant biodiversity due to agricultural abandonment of grassland as experienced in the park is controversial. Both increase (Mason et al., 2011) and decrease (Peco et al., 2012) in plant biodiversity have been encountered within 5-10 years abandoned grassland. In addition, the strict protection in the park has favoured the recovery, comeback and behaviour of different herbivores. On a small scale, Schütz et al. (2003) found a higher species number after the exclusion of livestock and the re-population of the red deer (*Cervus elaphus* L., Fig. 1.1). These findings are evidence that the research in the SNP suffers from the same limitations related to plant biodiversity described in the previous sections. Furthermore, it is essential to move beyond considering biodiversity as the only number of species, and approaches looking at the different facets of biodiversity (i.e., genetic, species, function, and ecosystem structure) are necessary. Therefore, investigating the impact of long-term protection endeavours on grassland biodiversity and monitoring plant biodiversity on different scales in the years to come need to be deepened and facilitated by integrating new technologies. In addition, identifying sites over large areas, unique in their genetic, species, and/or trait composition would guide and prioritise conservation or restoration efforts.

1.5 A global database of plant traits

Efforts have been made to increase the representativeness and accessibility of worldwide plant trait measurements and species information through great data-sharing platforms like the TRY and sPlotOpen databases (Kattge et al., 2020; Sabatini et al., 2021). Data from this thesis have been contributed to the TRY databases (Kattge et al., 2020). In the TRY program, the success of calls to the scientific community for data in the 12 past years resulted in over 765 data contributors with almost 12 million trait records from 280000 species distributed over more than 20000 sites. The TRY database

now provides an unprecedented number of consolidated plant trait data easily accessible under an open access data policy. Besides the huge amount of data coverage, however, a general bias towards certain traits and temperate biomes was observed. Long-tail distributions characterise data coverage across traits: A small number of traits is well covered by records and species, while the majority of traits have only very low coverage of records and species. Apart from Europe, all continents contain major regions that are very sparsely represented in TRY and sPlotOpen. Furthermore, trait variations in time are almost not covered in TRY. However, they are relevant to characterise the seasonal variation of plant and ecosystem function (Xu and Griffin, 2006; Xu and Baldocchi, 2003) and long-term trends to inform policy about biodiversity change (Kissling et al., 2018). For example, in the context of GEO BON, collection and repeated trait measurements from the exact location or population to monitor biodiversity change and inform policy are needed. It clearly emerges from the above that global databases of field data alone cannot fully solve the problem of sparse and discrete coverage of the world's plant diversity.

1.6 Remote Sensing: The solution?

Measuring reflected radiation at a distance (i.e., remote sensing) entails more detail and looking at more processes and variables than ever before. Differences among individual plants and communities result from contrasting evolutionary histories, genetic backgrounds, and environmental conditions (Cavender-Bares et al., 2020). Because these differences are expressed in physiology, biochemistry, and structure, many of these properties can be detected using spectral reflectance from leaves and plant canopies (see Section 1.6.1). Thus, spectral signatures, patterns, and heterogeneity obtained from remote sensing are proxies of the diversity of plant species and traits. Thereby, providing profound opportunities to quantify different facets of plant biodiversity at extended spatial and temporal scales (Cavender-Bares et al., 2017; Gholizadeh et al., 2020; Jetz et al., 2016; Lausch et al., 2016; Oldeland et al., 2010; Pettorelli et al., 2018; Rocchini et al., 2018b; Rossi et al., 2021; Schneider et al., 2017; Schweiger et al., 2018; Ustin and Gamon, 2010; Wang and Gamon, 2019). In particular, the era of openly available satellite data at a high revisit time offers new opportunities for measuring and modelling large-scale biodiversity from space (Randin et al., 2020; Rocchini et al., 2018a; Rossi et al., 2020; Schneider et al., 2020; Ustin and Middleton, 2021). In addition, the increasing availability of cheap unmanned aerial vehicles (UAVs) is revolutionising the way field data is collected and plot-scale biodiversity is quantified (Aasen and Bolten, 2018;

Schweiger et al., 2020; Zhao et al., 2021). In the coming decade a new level of quantitative information about plant biodiversity will therefore be remotely retrieved. Instead of relying on a few single measurements covering the region of interest, remote sensing products continuously cover the entire region. Thus allowing to move away from an overwhelming emphasis on localness and efficiently map traits and species even in less accessible areas. Remotely sensed data presents the strong potential to complement field plot data, fill knowledge gaps, reduce uncertainties and undoubtedly lead to significant advances and unexpected breakthroughs in understanding plants, their diversity, and functions.

So far, however, grasslands present a unique set of challenges that complicate the assessment of plant biodiversity using remote sensing. As done in this thesis, addressing these challenges and understanding the dependencies of the remotely sensed biodiversity will pave the way for applying new technologies in monitoring plant biodiversity. The following sections briefly introduces principles, sensors, platforms, opportunities, and challenges of remote sensing of grassland biodiversity.

1.6.1 Principles of optical remote sensing

This thesis investigates the most well-known technique to estimate plant biodiversity in grassland, i.e., optical remote sensing. Other techniques such as Light Detection and Ranging (LiDAR) and Radio Detection and Ranging (radar) play an important role in remote sensing. However, they are mostly limited to biomass and soil moisture estimations in grasslands (Bartsch et al., 2020).

Optical remote sensing makes use of sensors to form images of the Earth's surface by recording the fraction of solar radiation reflected by an object in a non-destructive manner (Clark et al., 1999). The sun emits continuous electromagnetic radiation predominantly in wavelengths between 200 nm and 2500 nm with a peak at around 483 nm (Fig. 1.2a). Although a significant fraction of the radiation never reaches the Earth's surface, it is scattered and absorbed in the atmosphere (Ollinger, 2011), a large part of it does and interacts with matter on the surface. In particular, the interactions with plants are diverse: The reflection of light is dependent on the wavelength and incidence of radiation for the plant but also on a range of structural and biochemical properties of plant leaves such as pigment content, leaf thickness, leaf water content, and leaf dry matter content. The reflected light of the plant can be plotted against the wavelength, which is referred to as the reflectance spectrum (see Fig. 1.2b). The incoming radiation in the visible part of the spectrum (VIS, 400–700 nm) is absorbed (i.e., low reflectance)

by light-absorbing pigment, i.e., the chlorophyll, causing electrons in the chlorophyll molecules to change from one energy state to a higher state. As they return to their original state, heat or fluorescence gets emitted and the energy gained can be coupled to chemical reactions, such as photosynthesis (Jones and Vaughan, 2010). On the contrary, the energy level in the near-infrared (NIR, 700–1400 nm) and short-wave infrared (SWIR, 1400–2500 nm) is not high enough to drive photosynthesis but could cause overheating and damage to plant tissues and thus incident radiation gets predominantly scattered and reflected diffusely. Given the large number of cells and cell wall surfaces in leaves, leaf structural characteristics play an important role in scattering light in the NIR and SWIR regions of the spectrum. Furthermore, similar to water absorption in the atmosphere, the direct effects of liquid water in leaves include distinct absorption features at 1450 and 1950 nm. The more general rotation-vibration features of water molecules cause additional absorption that begins at 1400 nm and increases at longer wavelengths. This absorption causes the characteristic pattern of declining reflectance at wavelengths beyond the maximum values in the NIR plateau (Fig. 1.2b). It follows that characteristic combinations of these leaf traits in individual species allow them to be distinguished based on reflected radiation. But not only do the leaf traits govern the reflected radiation, rearrangement of leaves in a canopy substantially modifies the reflected light. The canopy reflection is a result of radiation scattering and secondary and tertiary interactions between the leaves in the canopy, as well as the underlying soil. Last but not least, atmospheric interactions must be considered in the propagation of sunlight to the plant and from the plant to the sensor (i.e., atmospheric correction is needed). Following atmospheric correction, scene-dependent corrections are often required, including corrections for different illumination and reflectance due to the sun- target- sensor geometry, i.e., the bidirectional reflectance distribution function (BRDF).

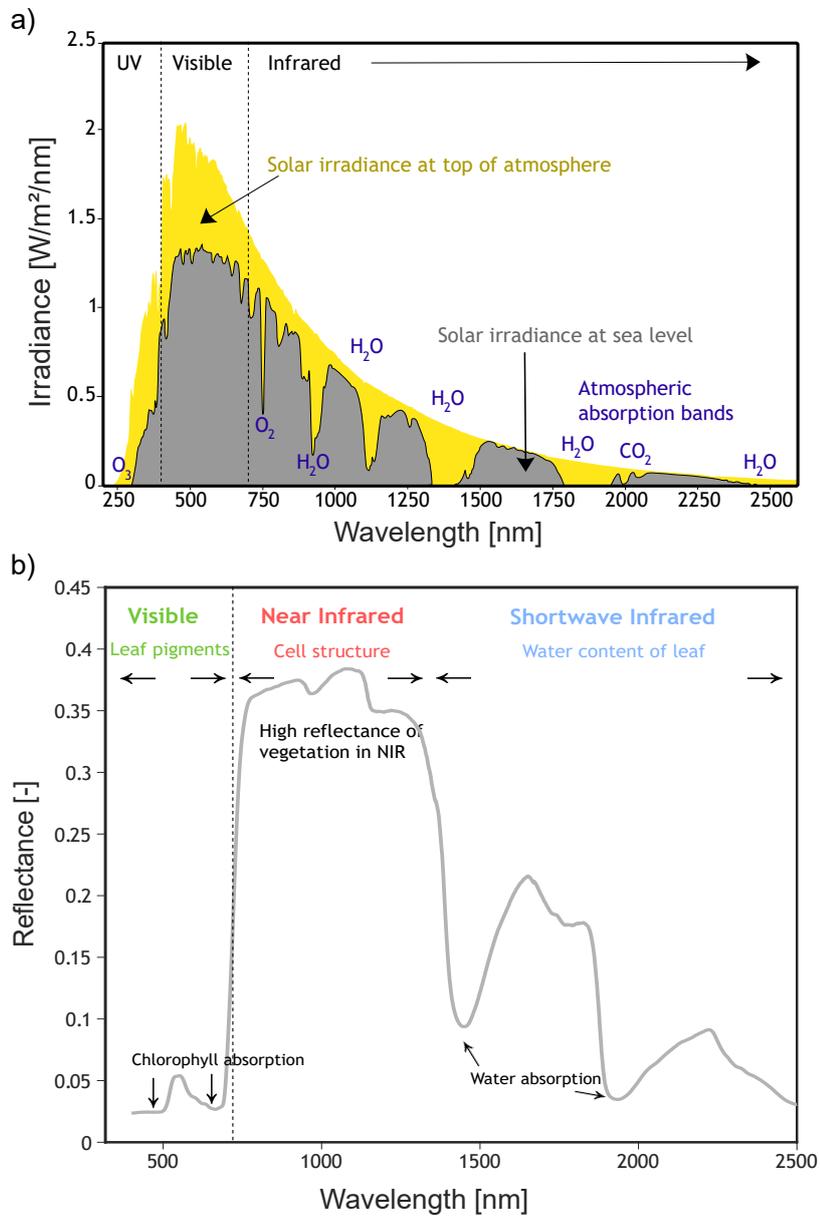


Figure 1.2: a) The solar radiation spectrum above (yellow) and below the atmosphere (grey), and b) typical reflectance spectra of vegetation with key structural and chemical absorption features that are associated with the physiological and biochemical properties of plants.

1.6.2 Remote sensing sensors and platforms

The recording of the reflected solar radiation can be achieved using different sensors mounted on different platforms. Each combination of sensor and platform differs in the number of spectral wavelengths, the spatial resolution (i.e., pixel size), the spatial extent and temporal frequency (i.e., temporal resolution) at which reflectance is recorded. Depending on the spectral resolution, optical sensors can be divided into multispectral sensors and imaging spectrometers (or hyperspectral sensors). Imaging spectrometers record data in several spectrally contiguous, narrow, registered bands (resulting in a reflectance spectrum for each pixel), while multispectral sensors record data in fewer bands (typically up to 15 bands) with a coarser spectral resolution. The spatial resolution and extent depend highly on the distance at which reflected radiation from an object is measured, ranging from few millimetres up to thousands of kilometres (Fig. 1.3). Close-range, airborne, and spaceborne remote sensing can be distinguished with their characteristics, capabilities and limitations. Close-range remote sensing encompasses UAVs, which record images with a very high spatial resolution (<5 cm) depending on the sensor system. Compared to airborne and spaceborne platforms, it is much easier to plan and conduct an image acquisition campaign. However, the efficient use of UAVs is limited to areas of less than a couple of square kilometres. Therefore, their main application in the context of biodiversity assessments is at the scale of field observations (e.g., plots). On the contrary, spaceborne sensors cover the entire planet at moderate to coarse spatial resolutions (3-1000m). Besides commercial satellites, a whole palette of openly available satellite data offers a way to investigate biodiversity on a landscape level (Moreno-Martínez et al., 2018). Furthermore, spaceborne sensors demonstrate a high temporal resolution capable of quantifying variation of traits in time and improving the differentiation between species or most likely plant communities. Nevertheless, satellites and UAVs are still mostly limited to multispectral sensors due to financial and technical limitations. In the future, a range of high-resolution imaging spectrometers onboard satellites will be available in operational missions for systematic spectral measurements (Cawse-Nicholson et al., 2021), offering unprecedented data to scientists and decision-makers. Novel lightweight imaging spectrometers with consumer-grade data processing software will boost the capabilities of UAV platforms. So far, however, imaging spectrometers remain mostly limited to airborne platforms. The typical spectral range of an airborne imaging spectrometer is 400–2500 nm with a wavelength sensitivity in the range of a few nanometres for every single band. Multiple airborne imaging spectrometers have been used worldwide, while, in contrast, their use and access remain relatively limited to single acquisitions

in time of a limited area. In terms of pixel size (a couple of meters) and extent, airborne platforms are a bridge between UAV and satellite applications. Furthermore, it is imperative to consider multiple platforms and sampling scales because the spatial and temporal resolutions of different remote sensing platforms do not always match the operational scale of the ecological process of interest. Therefore, the different platforms are and will be not mutually exclusive and the combined use offers many opportunities to determine plant biodiversity on different scales. In this thesis, the potential of remote sensing in estimating grassland biodiversity with data provided by multispectral spaceborne sensors (Chapter 2 and 4) and with multispectral UAV and hyperspectral airborne data was investigated (Chapter 3).

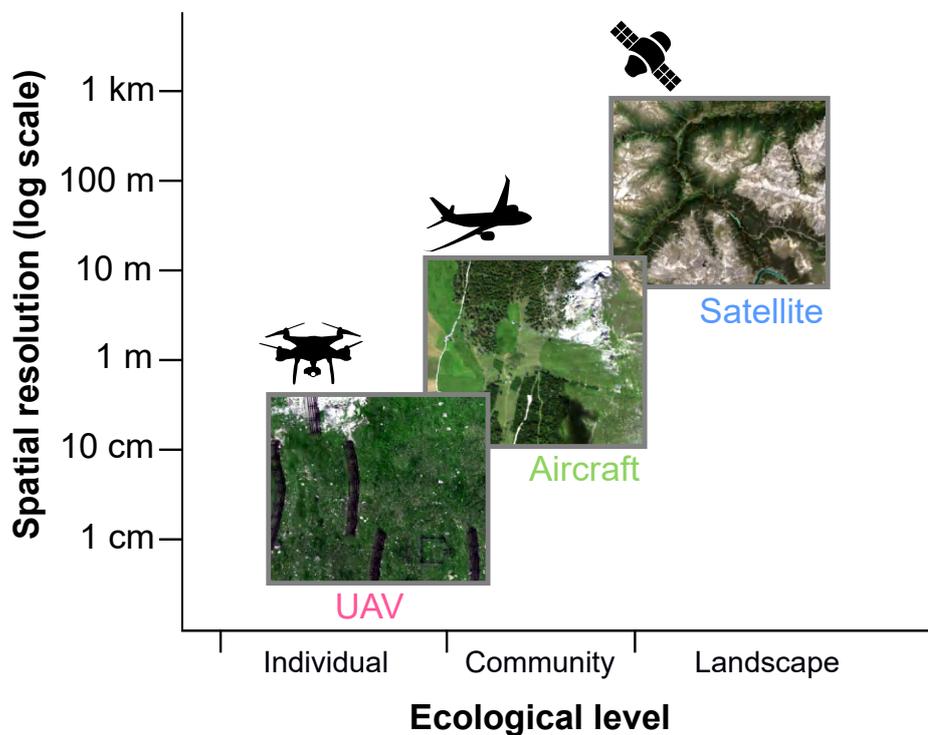


Figure 1.3: Remote sensing platforms and the provided spatial resolution of spectral datasets, which can be used to estimate plant biodiversity for different ecological levels. The spatial scale associated with various platforms spans roughly six orders of magnitude.

1.6.3 Remote sensing of biodiversity

Over the last five decades, starting with the advent of the first civilian satellite observations of Earth (i.e., 1972 with the launch of Landsat 1), optical remote sensing has been

used to characterise ecosystems and species (Al-Mufti et al., 1977; Curran, 1980). Especially, from the 1990s a larger number of studies on biodiversity using remote sensing started to emerge (Debinski et al., 1999; Innes and Koch, 1998; Menon and Bawa, 1997; Stoms and Estes, 1993). Remote sensing techniques for biodiversity can be categorised into four classes: i) direct mapping of species distribution, ii) habitat mapping for modelling the species distribution, iii) estimating functional diversity through plant traits, and iv) establishing a direct relationship between biodiversity and remote sensing spectral data.

The early applications of remote sensing in biodiversity estimation mainly focused on mapping habitats and their heterogeneity. Already with a few spectral bands, it is possible to separate vegetation types (i.e., grasslands, forests, marshes, etc.). In particular, spectral vegetation indices, such as the normalised difference vegetation index (NDVI) derived from the red:near-infrared reflectance ratio, have been used to capture land cover, land surface phenology, potential productivity and changes through time of an ecosystem (e.g., Gillespie et al., 2008; Pettorelli et al., 2005; Townshend et al., 1991). Moreover, remotely sensed land cover classifications and NDVI have been widely used as an integral part of modelling habitat suitability for animals and plants (He et al., 2015). Similar to blood pressure for humans, NDVI is a biomarker of the ecosystem. In the case of NDVI, high values reflect healthy and productive vegetation, where low values could indicate water scarcity in leaves.

Recent advances in the close-range to spaceborne sensors (Aasen et al., 2018; Drusch et al., 2012), machine learning (Brodrick et al., 2019; Kattenborn et al., 2021) and cloud computing (Gorelick et al., 2017) have made it possible to improve plant diversity estimation capabilities over the widely used NDVI. Although it is typically impossible to distinguish every grassland species using remote sensing, it is often feasible to differentiate dominant species or community types using spectral differences. For example, high spatial resolution data combined with machine learning approaches can be used to map single plant functional types (Lu and He, 2017) or target species such as invasive weeds (Wijesingha et al., 2020). Furthermore, sensors recording reflectance at multiple wavelengths are capable of estimating different leaf traits and consequently functional diversity (Rossi et al., 2020; Schneider et al., 2017). Compared to NDVI, traits offer a gathering point between measurements undertaken *in-situ* and remotely, i.e., between ecology and remote sensing, needed to improve our understanding of global functional and plant biodiversity. In remote sensing, plant traits are inferred by studying their spectral properties using empirical or physical models based on statistical relationships or radiative transfer theories (Homolová et al., 2013; Jacquemoud et al., 2009; Ollinger, 2011).

The establishment of direct relationships between biodiversity and spectral data has, however, recently permitted bypassing the use of these empirical or physical models (Cavender-Bares et al., 2020). The so-called spectral variation hypothesis (SVH) was firstly introduced by Palmer et al. (2002). This hypothesis suggests that the diversity in spectral reflectance (i.e., spectral diversity) of an area is representative of plant diversity (Cavender-Bares et al., 2017; Rocchini et al., 2010). Central to the SVH is the radiative transfer theory on plant-light interaction described in Section 1.6.1 and the surrogacy hypothesis. The surrogacy hypothesis suggests that a higher spectrally observable landscape heterogeneity will host more species, thereby propelling plant diversity. Direct links between different facets of plant biodiversity and spectral diversity have been established on different spatial scales (Rocchini et al., 2004; Schweiger et al., 2018; Wang et al., 2018a). Moreover, spectral diversity is emerging as an important component of biodiversity, alongside taxonomic, functional and genetic diversity. Thus, besides trait mapping, spectral diversity approaches are investigated in this thesis.

1.6.4 Challenges and gaps in remote sensing of grassland biodiversity

Estimating plant biodiversity with remote sensing has developed rapidly in the last decade, but some key challenges in grasslands remain (Fig. 1.4).

First, individual plants in grasslands are usually much smaller compared to the grain size of remotely sensed data. The smallest unit of observation that can be observed through remote sensing are pixels that are typically defined by the spatial resolution based on technical specifications of the sensor used (see Section 1.6.2). A key challenge lies in matching the scale of the remote sensing measurement to the ecological levels of organisation (i.e., individuals, communities, ecosystems). If individual plants are not captured, pixels of grassland most likely represent ecological communities. However, the translation of pixels to ecological communities is not straightforward and as such, it is imperative to make scaling decisions regarding the number of pixels representing a community. Pixels could contain a mix of within- and between-community diversity. The larger the individual plants under study, the more likely the pixel-based diversity will lean towards an α -diversity. In contrast, for smaller individual plants pixel-based diversity tends to be dominated by β -diversity. In particular, there is much uncertainty as regards to what extent the satellite remote sensing derived diversity will translate into ecological α - or β -diversity. Furthermore, the measured pixel value, containing

multiple individual plants, results from leaf traits as well as a complex interaction between individual plants and/or the soil (Section 1.6.1). To what extent do these complex interactions affect our ability to quantify community properties and biodiversity remain an open methodological question. Notably, there is a lack of research directed toward linking trait metrics at the community level that are typically related to ecosystem processes and services, the community-weighted mean (CWM) and trait diversity indices (i.e., functional diversity indices), with remotely sensed data (Abel-leira Martínez et al., 2016).

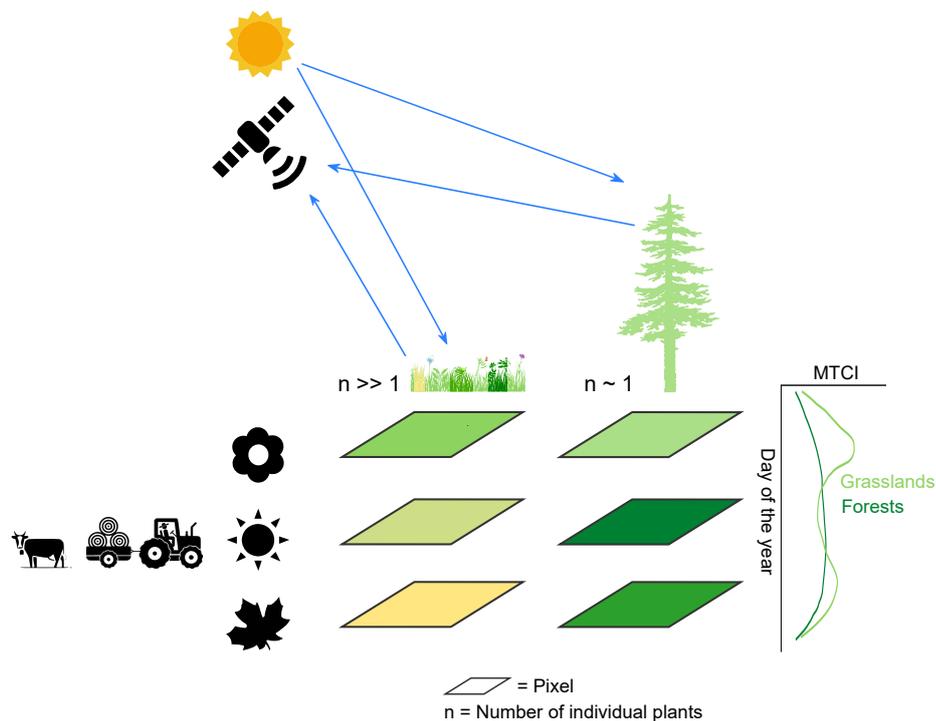


Figure 1.4: The main challenges in optical remote sensing of biodiversity in grasslands compared to forests are: i) the multiple individual plants per remote sensing pixel, and ii) the high variations in time of remotely sensed data due to phenology and most importantly land management, such as grazing and mowing. Here, remotely sensed data is represented by the MERIS terrestrial chlorophyll index (MTCI, Dash and Curran, 2004).

Second, even with spatial resolutions of less than 1 cm, species identification of individual plants in grasslands is challenging and might only work under favourable conditions such as low structural complexity, low spatial overlap, and low number of species (Lopatin et al., 2017). In contrast, in line with the spectral diversity approach (Section 1.6.3), detection of individual plants is no longer needed to monitor

different aspects of biodiversity. Species that are not spectrally distinguishable may be redundant in their ecosystem function and/or closely related (Cavender-Bares et al., 2017), making their differentiation marginal for the estimation of genetic and functional diversity. However, the estimation of biodiversity through spectral diversity still depends on the spatial and spectral resolution of the available remote sensing data (Gholizadeh et al., 2019; Rocchini, 2007; Wang et al., 2018a). Very high spatial resolution offers the potential to quantify α -diversity and an increased spectral resolution enhances the capabilities to differentiate between species. Unfortunately, the available remote sensing sensors and platforms have to trade-off between spatial and spectral resolution, often constrained by engineering requirements and physical laws. In addition, different studies have reported both positive correlations as well as ambiguous relationships between spectral diversity and field-measured plant diversity (Dahlin, 2016; Lucas and Carter, 2008; Villoslada et al., 2020; Wang et al., 2018b). Especially in grasslands that are artificially composed of a limited species pool, the spectral diversity approach has showed promising results (Schweiger et al., 2018), but notably, different issues have to be expected for an application in naturally assembled systems. For example, confounding effects of the spectral diversity-biodiversity relationship such as biomass or soil (Gholizadeh et al., 2019) limit our capabilities to estimate biodiversity and thus, necessitate attention.

Third, highly dynamic ecosystems such as grasslands with high land-use intensities, phenology, and land management demonstrate high variations in remotely sensed data and therefore remotely estimated plant diversity. Thus, the ability to detect biodiversity using spectral diversity can vary significantly over time (Gholizadeh et al., 2020). In contrast, capturing the full temporal dynamics of plant species and traits can provide better insights into the function and composition of communities (Schwinning and Kelly, 2013). Nevertheless, the temporal dimension is rarely considered in most remote sensing applications. Several remote sensing studies on plant biodiversity are based on a single overpass (e.g., a single airborne or satellite image), limiting the opportunities for examining temporal effects. This low consideration seems to be heretical since remote sensing is the only means that offers the opportunity to efficiently address the effect of temporal variations on the retrieval of plant biodiversity. However, this construct is missing a framework for quantifying spectral diversity over time alongside spectral diversity in space.

1.7 Scope and research questions

This thesis is a cross-disciplinary collaboration conducted at three different institutions: the Remote Sensing Laboratories at the Department of Geography of the University of Zürich, the Plant-Animal Interactions group at the Swiss Federal Institute for Forest, Snow and Landscape Research and the Swiss National Park. Thus, this thesis is characterised by a strong interdisciplinary spirit, which pervades all of its parts and will manifest well in the research publications that stem from it.

The overarching scope of this thesis is to widen remote sensing applications in grassland ecology and address challenges disrupting the remote sensing of grassland biodiversity. A particular focus lies on alpine grasslands and the impact of different management practices on plant diversity, ranging from intensively managed to protected with a non-intervention policy. In line with the objectives to be truly exhaustive, biodiversity estimations need to consider the data's spatial, spectral and temporal dimensions. In the following chapters of the thesis, remote sensing capabilities with different spatial, spectral and temporal resolutions are therefore explored. The knowledge gained exploring different dimensions of remote sensing will be summarised and linked in the synthesis, thus creating a perspective on the integration of different sensing platforms. Overall, this dissertation is framed by three fundamental challenges of grassland remote sensing transmuted into the following research questions:

Research Question I:

What component of functional diversity is captured with remote sensing as we move to coarser spatial resolutions?

Individual plants in grasslands are much smaller in comparison to the grain size of remotely-sensed satellite data. Although a coarse spatial resolution can capture environmental heterogeneity and a related within-community plant diversity, spectral responses at a resolution of satellite sensors (typically tens of meters) in grassland reflect most likely the diversities between the communities. This hypothesis is tested with the application of a radiative transfer model used to link functional trait metrics, the community-weighted mean and functional diversity indices, with remotely sensed data in Chapter 2.

Research Question II:

What are the key ingredients for the successful estimation of plant species richness from remotely measured spectral diversity in species-rich grasslands?

Due to technical constraints, available sensors have to trade-off between spatial and spectral resolution, limiting remote sensing estimation of grassland species richness via spectral diversity. Similarly, the spectral diversity-biodiversity relationship might be confounded by diverse factors such as the amount of death and live biomass in a community. Moreover, depending on the metric used to calculate spectral diversity confounding effects could be mitigated. A multi-sensor and data fusion approach is used to tackle sensor constraints and dependencies of the spectral diversity-biodiversity relationship are investigated in Chapter 3.

Research Question III:

How important is the temporal resolution for remote sensing of plant biodiversity?

Phenology and land management, such as mowing or grazing in grasslands lead to variations in remotely sensed data and, in turn, remotely estimated plant diversity. Nevertheless, our knowledge on how to use datasets sampled at multiple points in time to quantify biodiversity is scarce, although such an approach might extend the accuracy and informative power way beyond the use of a dataset obtained for a single point in time. A novel methodology to approach this research gap is proposed in Chapter 4.

1.8 Structure

Three fundamental research questions resulted in three main chapters of this thesis, namely Chapter 2, 3, and 4. Additionally, an introduction to the thesis and corresponding synthesis in Chapter 1 and 5 are provided.

Chapter 1 provides the relevance and the motivation of the dissertation followed by current opportunities and challenges of remote sensing grassland biodiversity and the main research questions.

- Chapter 2** corresponds to the peer-reviewed article published in *Remote Sensing of the Environment* (Rossi et al., 2020). It addresses the first research question by describing and investigating the use of the radiative transfer model to estimate plant functional trait metrics from space. The spatial diversity and magnitude of remotely sensed traits provide new knowledge of the functional diversity of the Swiss National Park and its surroundings.
- Chapter 3** addresses the second research question with an article currently under review in *Remote Sensing of Ecology and Conservation*. It addresses the association between spectral diversity and species richness in a species-rich alpine grassland ecosystem by investigating i) the trade-off between spectral and spatial resolution in remote sensing by data fusion, ii) the suitability of three different spectral metrics to describe spectral diversity, and iii) the importance of confounding effects of biomass, dead biomass and plant life forms on the spectral-biodiversity relationship.
- Chapter 4** addresses the third research question with the peer-reviewed article published in *Ecological Indicators* (Rossi et al., 2021). This chapter presents a new methodological approach to account for spatio-temporal spectral dissimilarities between plant communities. Through the medium of a case study the paper demonstrates that accounting for temporal variations in spectral diversity improves the estimation of plant biodiversity through remote sensing in grasslands.
- Chapter 5** summarises and discusses the main findings of the thesis and provides an outlook on possible future research.

2

From local to regional: Functional diversity in differently managed alpine grasslands

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and has been modified to list all cited references
in the Bibliography chapter.*

Description of author's responsibilities

CR: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Project administration. Mk: Conceptualization, Validation, Writing - review & editing. MS: Conceptualization, Investigation, Writing - review & editing. MES: Conceptualization, Writing - review & editing, Supervision. RMH: Conceptualization, Funding acquisition. ACR: Conceptualization, Validation, Writing - review & editing, Supervision.

2.1 Abstract

Increasing evidence suggests that ecosystem functions are strongly linked to morphological plant traits, like specific leaf area (SLA) and its variability, which serve as a proxy of functional diversity (FD). Functional diversity is rarely studied at regional scales, and its scale dependence is poorly understood. Capturing trait variations at distinct spatial scales and in differently managed grasslands remains challenging, mainly because a limited number of trait measurements are available and field campaigns are time-consuming. Here, we derived α - and β -FD indices based on SLA measured in the field and estimated from optical satellite data by using molecular absorption profiles of leaves in canopies. We inverted the 1-D columnar radiative transfer model PROSAIL using Sentinel-2 reflectance data at canopy level. From the inversion we were able to distinguish different alpine management types based on retrieved SLA. Model uncertainties were mainly related to the different local plant communities, here represented by functional diversity indices and community-weighted means of traits. Thus, successful PROSAIL application was affected by management type. Management categories displaying lower α -FD, like mowed and fertilized, delivered the most reliable results. Further, we compared FD (i.e., richness, evenness, divergence) from local to regional scales. Locally, management determines the magnitude of FD, whereas on a regional scale, parcel size and the uniformity of agricultural practices control trait diversity. Our results highlight the importance of quantifying β -FD from space as it delivers additional information on the impact of management types, differing from locally measured α -FD values.

2.2 Introduction

With a coverage of 40% of the earth's terrestrial surface, grasslands are the largest and most exploited biome worldwide (Gibson, 2009). Grasslands provide a range of ecosystem functions at local, regional, and global scales (Hein et al., 2006; Lamarque et al., 2011). These functions are essential for the survival of plant and animal species (Tews et al., 2004) and vital in sustaining human life (Gómez-Baggethun et al., 2010; Manning et al., 2018). Ecological functions are particularly important at regional scale, as it is at this scale, resource management decisions, crucial in ensuring ecosystem functions (Tälle et al., 2016), are generally made (Nelson et al., 2009). A number of studies have shown that locally, ecosystem functions are strongly linked to plant traits and their variations, called plant functional diversity (de Bello et al., 2010; Díaz et al.,

2007b; Grigulis et al., 2013; Lavorel et al., 2011). This relationship is explained by an increased partitioning of the total resources available (Cadotte et al., 2011). As functional diversity increases, a greater range of functional traits are present, providing opportunities for efficient resource use (Loreau, 2000). In addition, a higher functional diversity leads to a higher probability that some species will respond differently to perturbations and therefore are able to maintain ecosystem functioning (Díaz and Cabido, 2001). At a regional scale, faster recovery of a disturbed area depends on the availability of surrounding areas with certain ecosystem functions (Lavorel, 1999; Loreau et al., 2003). Plant traits are subject to environmental filters that determine which traits and ecosystem functions can survive at a particular site (Díaz et al., 2007a; Westoby, 1999). Filters such as climatic properties, management types and biotic interaction, tend to act at different spatial scales (Díaz et al., 1999a). For example, different management types such as grazing by large herbivores or mowing impact local functional diversity by altering both plant species composition and traits (Bouchet et al., 2017; Chapin Iii et al., 2000; de Bello et al., 2011). Consequently, the relationship between functional diversity and ecosystem functions is also likely to be scale dependent (Thompson et al., 2018), as functions operate across a range of scales (MEA, 2005). As individual plants and plant traits are expected to respond differently along environmental and management gradients, regional plant functional diversity is assumed to be related to landscape composition, which, in turn, is affected by land use and land cover at a regional scale (Uuemaa et al., 2013). Functional diversity displays contrasting relationships with spatial scale, i.e., it can i) increase following a species-area law, ii) be scale invariant or iii) decrease (Karadimou et al., 2016; Schneider et al., 2017). Generally, it is necessary to understand relationships between plant functional diversity and ecosystem functions and be aware of discrepancies between regional and local plant functional diversity in order to extrapolate them from local to regional scales (Messier et al., 2017). However, getting a better understanding requires to capture trait variations at distinct spatial scales and in differently managed grasslands, which remains challenging, mainly because only a limited number of trait measurements are available and field measurements of plant traits are time consuming (Jetz et al., 2016). Morphological plant traits such as the specific leaf area (the ratio of leaf area to leaf dry mass; SLA) or its inverse, leaf dry mass per area (LMA), have unique properties: for example, they i) have an impact on ecosystem functioning (Table 2.1), ii) respond to land use, and iii) are quantifiable across a wide range of spatial scales in a cost- and time-efficient manner. In particular, SLA enables an assessment of how plant species utilize their resources and interact with one another (Garnier and Navas, 2012). Specific leaf area is a key feature in capturing leaf economics, reflecting a trade-off between carbon gain and longevity of a plant

(Díaz et al., 2016; Wright et al., 2004). Depending on land use intensity, traits suited for either fast or a more conservative resource capture can be identified (Garnier et al., 2007). Fertilization can favour traits associated with rapid growth, resulting in higher SLA (Laliberté et al., 2012; Schellberg and Pontes, 2012). In contrast, a conservative plant strategy has to be expected for undisturbed, low-productive habitats that are associated with lower SLA (McIntyre, 2008). Similarly, grazing favours plant attributes that limit nutrient losses to herbivores (Schütz et al., 2003) and results in plants adopting strategies against animal grazing. Examples are avoidance, which is reflected in small plant height and leaf size, and tolerance with high growth rate that is positively correlated to SLA (Díaz et al., 1999a; Westoby, 1999).

Table 2.1: Individual ecosystem functions and their correlation with SLA in grasslands based on literature review (+ = positive, - = negative correlation).

Ecosystem functions	SLA	References
<i>Standing litter</i>	-	Garnier et al. (2007), Grigulis et al. (2013), Lavorel et al. (2011)
<i>Litter decomposability</i>	+	Cornelissen et al. (1999), Fortunel et al. (2009), Garnier et al. (2004)
<i>Peak green biomass</i>	+	Grigulis et al. (2013)
<i>Above net primary production</i>	+	Garnier et al. (2004), Violle et al. (2007)
<i>Microbial biomass N</i>	-	Grigulis et al. (2013)
<i>Soil organic matter</i>	-	Garnier et al. (2007), Grigulis et al. (2013), Lavorel et al. (2011)
<i>Soil water content</i>	+	Díaz et al. (2007b)

Optical remote sensing that measures ground reflected solar radiation (Clark et al., 1999) is commonly used to assess biochemical (e.g., pigments, leaf water content, dry matter content; Ustin et al., 2009) or structural (e.g., leaf area, angle, leaf structure) leaf characteristics (Ollinger, 2011; Ustin and Gamon, 2010). Consequently, scattering and absorption features of the measured reflectance spectra are associated with different leaf characteristics (Curran, 1989). At the canopy-scale, multiple scattering effects in dense vegetation or low scattering at certain wavelengths by canopy structural variations can enhance the signature of leaf characteristics. This is particularly true for SLA (Asner and Martin, 2008b; Asner et al., 2011; Baret et al., 1994; Kokaly et al., 2009). To retrieve plant traits from multispectral and imaging spectroscopy data, radiative transfer models (RTMs) can be inverted (Botha et al., 2007; Feret et al., 2008; Jacquemoud et al., 2009; Laurent et al., 2013, 2014; Shiklomanov et al., 2016). These models describe canopy reflectance as a function of canopy, leaf and soil background characteristics using physical laws (Houborg et al., 2015) and directly connect vegetation biophysical and chemical properties with canopy reflectance measured by a sensor (Houborg et al., 2007). The RTMs have the advantage of not being site-specific (Verrelst et al., 2015a). Model transferability to remote sensing data collected at different sites under different conditions is therefore better than using statistical approaches. Thus,

it is possible to cover a wide range of conditions intrinsic to vegetation (e.g., phenological stage) and environmental conditions (e.g., atmospheric conditions), while at the same time minimizing the dependency on field observations (Dorigo et al., 2007). By using RTMs, it is also possible to directly compare remotely sensed canopy reflectance and community-weighted means (CWM) of plant traits, i.e., plot-level trait values weighted by species abundances collected in the field (Lavorel and Garnier, 2002). The reflectance of a “pixel” measured by an air- or spaceborne sensor is only comparable with the CWMs of that pixel if the CWMs collected at the leaf level are scaled to the canopy level, e.g. by multiplying CWMs with plant biomass. Otherwise physical scaling from canopy to leaf level, or vice versa through an RTM is required (Homolová et al., 2013; Lausch et al., 2013; Malenovsky et al., 2007). The disadvantage of an RTM is the simplification of the model itself and the equifinality of the model inversion, because several sets of input variables can yield almost identical spectra (Combal et al., 2002). The equifinality can be mitigated against by using a priori information, considering multiple model solutions and adopting temporal and spatial constraints (Baret and Buis, 2008). Using complex three-dimensional RTMs (e.g., DART) is computationally expensive and may not be appropriate for many operational applications at a regional scale (Gastellu-Etcheberry et al., 2015; Kimes et al., 2002). Simpler RTMs reduce the amount of data and computational requirements through approximations. However, understanding when these approximations render RTMs ineffective remains an open methodological question. Currently, there is a knowledge gap in estimating CWM and functional diversity indices (FDi; Mason and de Bello, 2013; Mason et al., 2005) from remotely sensed data (Abelleira Martínez et al., 2016). Community-weighted means have hardly been considered when comparing traits measured in the field with traits derived from remote sensing data. In particular, SLA remains poorly investigated with modest results (Colombo et al., 2008; Riaño et al., 2005), and has only been retrieved for forest ecosystems (Ali et al., 2017; Lymburner et al., 2000) or at the leaf scale (Ali et al., 2016; Féret et al., 2018). Similarly, FDi retrieved from remotely sensed plant traits have only been analysed in forest studies (Asner and Martin, 2008a; Schneider et al., 2017) considering one individual tree for one pixel or the aggregation of several pixels to one individual. Functional diversity index application to heterogenous grasslands is still lacking, mainly because in grasslands, one remotely sensed pixel always includes several plant species. We will fill this knowledge gap by deriving regional FDi from remotely sensed CWM of SLA. More specifically, we will assess

- i) the accuracy of using a physical based model with remotely sensed data to describe local grassland CWM of LMA and SLA,

- ii) the consistency of remotely sensed SLA to distinguish between grassland management type at regional scales, and
- iii) whether the impact of grassland management on FDi is correlated at local and regional scale.

Since SLA and LMA are simple reciprocals of one another, we use them in an interchangeable way throughout the paper. In relation to the RTM, we will use LMA since it is a direct input of the model. However, for the assessment of management types we prefer to use SLA due its linear and positive scalability with relative plant growth and its widespread use in functional ecology (Table 2.1). We estimated CWM of LMA and the resulting SLA by optimizing the RTM trait retrieval, and assessed the physical model accuracy. We expected RTM based trait retrieval uncertainties to depend on local trait composition, because uncertainty in determining canopy variables using RTMs increases with violation of model assumptions, e.g., homogeneity is violated with increasing numbers of plant species present. Also, uncertainties in retrieving LMA will depend on trait composition as traits are correlated with the spectral response of plant communities (Lausch et al., 2016). In addition, we estimated FDi at three different spatial scales, from local to regional, based on field measurements and remote sensing derived SLA. We expected to find higher redundancy in trait values among grassland communities at a regional scale, and higher trait turnovers at a local scale (de Bello et al., 2009). Nevertheless, it is difficult to predict how the results of the three different scales compare due to the dependence of functional diversity on grassland management (Niu et al., 2014) and the influence of landscape composition on regional FDi values.

2.3 Methods

2.3.1 Study area

The study encompasses an approximately 900 km² area of differently managed grasslands, i.e., protected grasslands and grasslands subject to organic as well as traditional agricultural management in the canton of Grisons, Switzerland (latitude 46°34' to 46°54'N, longitude 9°58' to 10°25'E). The area is characterised by a dry inner-alpine climate with mean annual temperatures of 1°C at 2000 m a.s.l., and 6 °C at the valley floor (1300 m a.s.l.), and mean annual precipitation of around 800 mm (MeteoSwiss, 2018). Protected grasslands were located within the Swiss National Park (SNP) that

extends over 170 km². The park is designated as a category Ia nature reserve (highest protection level - strict nature reserve, IUCN). Elevation ranges from 1350 to 3170 m a.s.l.. The underlying parent material is mainly dolomite. The plant growing season is short, extending from mid-May to mid-September. About 36 km² of the park area consists of subalpine and alpine grasslands. Due to different grazing regimes during former agricultural land use (until 1914), short- and tall-grass vegetation developed, differing in soil nutrient content (Schütz et al., 2006). Today, grasslands in the SNP are grazed by wild ungulates with stocking rates in livestock units (LU) varying between 0.15-0.5 LU/ha (based on SNP population counts and surveys of spatial distribution in 2016 and 2017). Managed grasslands were selected adjacent to the SNP in Val Müstair and the Lower Engadine valley. Large parts of the subalpine grasslands are hay or silage meadows, fertilized with manure. Some grasslands are additionally irrigated. Alpine pastures grazed by livestock cover roughly 25% of the area. Conglomerates, coarse sandstones and gneisses characterize the geology of the Engadine valley and gneisses and amphibolites dominate the bedrock in Val Müstair.

2.3.2 Selection of reference plots for plant trait measurements in the field

We defined seven management types: 1) protected, 2) mowed and fertilized multiple times per year with manure or mineral fertilizer, 3) mowed and never, once per year or every second year fertilized with manure, 4) grazed or grazed and mowed, 5) summer grazed by cattle, 6) summer grazed by sheep, and 7) summer grazed by cattle and sheep. None of the grazed grasslands (categories 4, 5, 6, 7) are fertilized. The seven management types were chosen to cover most of the agricultural practices in the region with a priori information available from landscape quality data (Federal act on the protection of nature and cultural heritage, NHG) available from the canton of Grisons and the Swiss federal office for agriculture. A total of 39 plots, i.e., 5 to 6 replicates within each management type, were established based on a clustered-stratified random sampling approach (Fig. 2.1). Stratified sampling was applied to agricultural parcels in three cluster regions with a diameter of 10 km in the municipalities of Scuol and Fuldera, and in the SNP/Il Fuorn area. Each of the 39 plots was 20 m x 20 m in size and chosen to be located in a homogeneous area (i.e., same management type and high fractional vegetation cover) of at least 1 ha to avoid edge effects in the remotely sensed data.

2.3.3 Plant trait measurements

In each plot, we collected plant trait data once during the growing season with field-work being split into four campaigns, i.e., 21 July 2016, 9 September 2016, 26 June 2017 and 6 July 2017. During each field campaign we sampled data in each management type. We collected plant traits in 25 equidistant locations along a georeferenced 10-m-long transect in each plot (Gaucherand and Lavorel, 2007). All leaves in physical contact with a vertically positioned metal rod were counted, collected, stored in sealed plastic bags, and kept at low temperatures (2-6°C) until further processing. On average, 70 leaves were sampled per plot. We quantified SLA, its inverse LMA and leaf water mass per unit area (C_w) from collected leaves, as well as vegetation height from the corresponding plant (VH; Cornelissen et al., 2003). Leaf area was determined using an image analysis software (ImageJ v1.50i) on photos taken with a leaf area meter (prototype 1.0 SNP, Appendix Fig. 2.9). Fresh and dry leaf mass were determined with a high precision scale for each sampled leaf. Identification and names of plant species followed Hess et al. (2015, Appendix Fig. 2.8). Community-weighted means and FD metrics were calculated using frequency-based relative abundances of each plant species, which corresponds to the number of contacts for a given species divided by the total number of contacts per transect (Leps et al., 2006). In this study, plant communities define a collection or association of plant species within a designated geographical unit (i.e., plot or pixel).

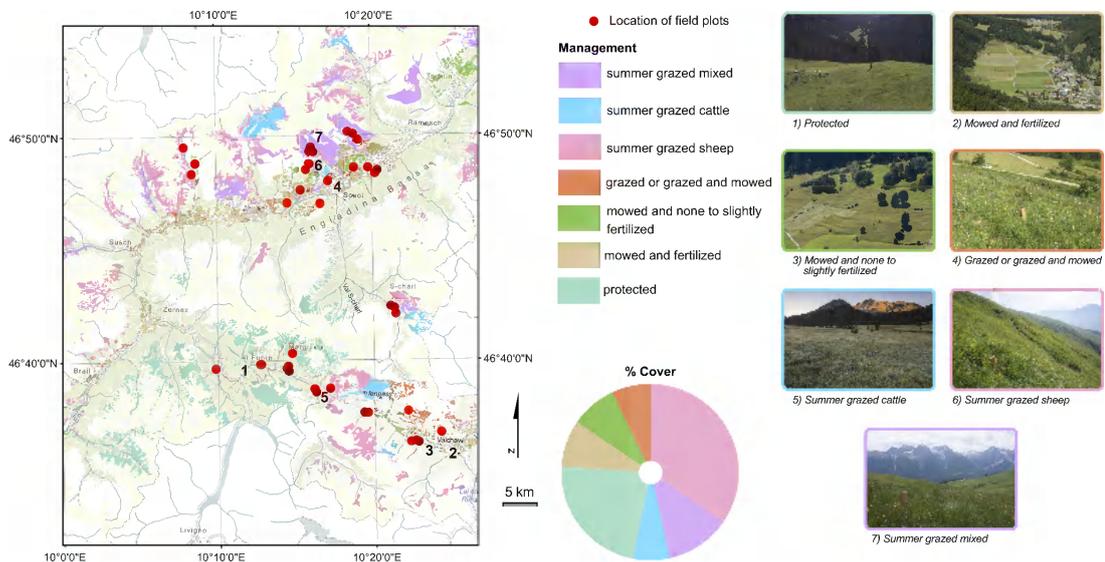


Figure 2.1: Study region with the seven different management types containing the 39 plots. Numbers (1-7) in the map indicate locations of pictures.

2.3.4 Remote sensing data

We used open access Copernicus Sentinel-2 data to quantify CWM (i.e., plot-level trait values weighted by species abundance) and FDi at a regional scale (Berger et al., 2012; Drusch et al., 2012). The Multi-Spectral Instrument (MSI) onboard of both Sentinel-2 satellites provides a set of 13 spectral bands spanning from the visible and near infrared (NIR) to the shortwave infrared (SWIR), with four bands at 10 m, six bands at 20 m and three bands at 60 m spatial resolution. The latter three are used for atmospheric correction and cloud detection. Near infrared and SWIR bands are most useful for retrieving SLA as shown by our sensitivity analysis of the PROSAIL model (Appendix Fig. 2.10). We used Sentinel-2 data (part of tile 32 TNS) atmospherically corrected by the sen2cor (v2.3 Muller-Wilm et al., 2013) procedure with the 90 m digital elevation model from the NASA's shuttle radar topography mission, converting top-of-atmosphere reflectance to top-of-canopy reflectance with 20 m spatial resolution and 10 bands (Fig. 2.2). The datasets were acquired for the day the field data were collected. The 10 m spectral bands were resampled to 20 m spatial resolution based on nearest neighbour interpolation. Pixels not classified as vegetation and not belonging to the predefined grassland layer obtained by the cantonal data were masked out. Further, we applied a random forest supervised classification to distinguish between recently mown and unmown meadows in each dataset (Appendix Fig. 2.11). Mown meadows were removed from the analysis to separate long-term management effects from a single mowing event.

2.3.5 Physical based model approach

To predict CWM of SLA and LMA from the remotely sensed Sentinel-2 data across our study area we inverted the combined PROSAIL RTM (Jacquemoud et al., 2009), a model that combines the 4SAIL (Verhoef and Bach, 2007) canopy bidirectional reflectance model and the PROSPECT-5b leaf optical model (Feret et al., 2008, Fig. 2.2, green simulated PROSAIL reflectance spectra). The PROSPECT-5b model calculates leaf transmittance and reflectance as a function of six input parameters: 1) leaf structural parameter N (unitless), 2) leaf chlorophyll $a + b$ concentration C_{ab} ($\mu\text{g}/\text{cm}^2$), 3) leaf carotenoid content C_{car} ($\mu\text{g}/\text{cm}^2$), 4) brown pigment content C_{brown} (unitless), 5) leaf dry mass per unit area LMA (g/cm^2), and 6) leaf water mass per unit area C_w (g/cm^2). The trait of interest, i.e., SLA (mm^2/mg), can be derived from the inversion of the PROSPECT parameter LMA ($SLA = 1/LMA$; Ali et al., 2016). The leaf reflectance and transmittance values generated by PROSPECT-5b are then fed into the 4SAIL model. Besides leaf reflectance and transmittance, 4SAIL requires eight input par-

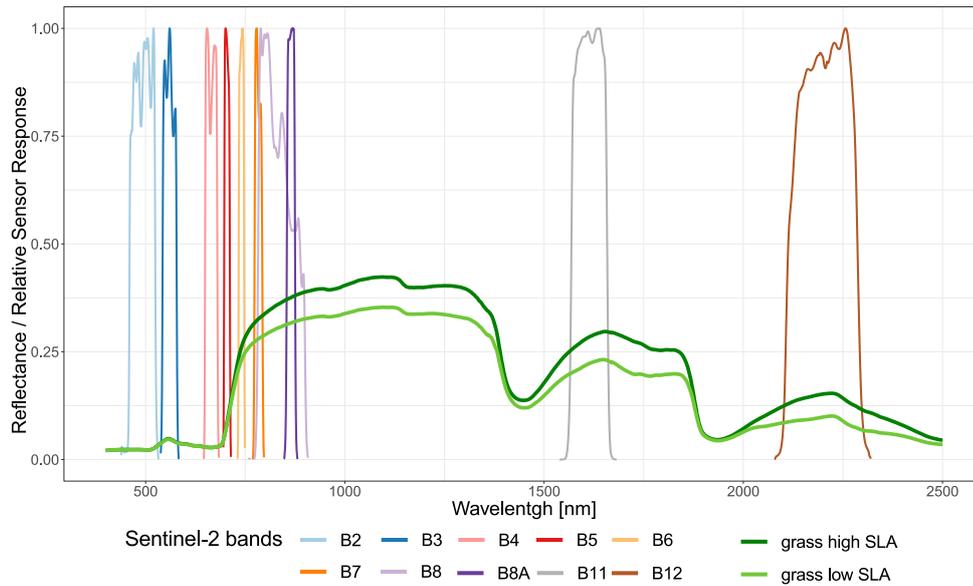


Figure 2.2: Spectral response functions of the 10 bands (B2 through B12) used in this study from the MSI on the Sentinel-2 satellite (European Space Agency, 2018). Two simulated PROSAIL reflectance spectra of grass with high and low SLA are shown in green.

ameters to simulate the top-of-canopy bidirectional reflectance, i.e., sun zenith angle, sensor viewing angle, relative azimuth angle between sensor and sun, fraction of diffuse incoming solar radiation, soil reflectance, leaf area index, average leaf inclination angle and the hot spot size parameter (see Table 2.2). Leaf dry matter content (LDMC, Wilson et al., 1999; $LDMC=LMA/(LMA+Cw)$) was retrieved in a similar way. However, due to the high negative correlation of LDMC with SLA (Garnier et al., 2001), we only report the results for LDMC in the Appendix (Appendix Fig. 2.12). As the PROSAIL model is one-dimensional and treats the canopy as a turbid medium, several sets of input variables can yield almost identical spectra (Combal et al., 2003). These issues were mitigated against by i) using a lookup table (LUT) based inversion strategy with addition of gaussian noise to account for model and measurement uncertainties, ii) calculating a mean of multiple solutions in the inversion and iii) constraining the input variables to the field measurements (Meroni et al., 2004; Rivera et al., 2013).

2.3.6 LUT generation

LUT-based inversion requires simulations of the reflectance spectra for a wide range of RTM parameters. The goal of the inversion is to identify a spectrum or a group

Table 2.2: Specific ranges of variable input parameters of the PROSAIL model used to generate the LUTs.

Parameter	Symbol	Unit	Minimum value	Maximum value
Leaf area index	LAI	m ² /m ²	0.3	7.5
Mean leaf inclination angle	ALA	deg	40	70
Hot spot size parameter	hot	m/m	0.05	0.1
Soil brightness	psoil	-	0	1
Ratio of diffuse to total incident radiation	SKYL	-	0.25	0.25
Leaf structural parameter	N	-	1.5	1.9
Chlorophyll a+b content	Cab	µg/cm ²	5	75
Carotenoid content	Car	µg/cm ²	2	60
Equivalent water thickness	Cw	g/cm ²	0.005	0.02
Leaf dry mass per area	LMA	g/cm ²	0.002	0.015
Brown pigments content	Cbrown	-	0	0

of spectra that resembles the remotely measured spectrum. In our study, five parameters, i.e., sensor viewing angle, azimuth angle, sun zenith angle, fraction of diffuse incoming solar radiation and brown pigment content, were kept constant to generate LUTs of the 14 model input parameters. Cbrown was set to zero as no senescent leaves were visible at the time of field data collection (Jay et al., 2017). We also kept the fraction of diffuse incoming solar radiation fixed to a mean value of 0.25 for all datasets across all wavelengths. The fraction of diffuse radiation was estimated using a model that included global horizontal and extra-terrestrial irradiance and solar altitude angle (Reindl et al., 1990). We calculated separate LUTs for the June/July and September Sentinel datasets to account for differences in sensor and sun zenith and azimuth angle. For the remaining PROSAIL input parameters (i.e., LAI, ALA, psoil, hot, N, Cab, Car, LMA and Cw), 100'000 parameter sets were selected randomly. The constrained ranges for the uniformly varying model parameters to generate the LUTs are reported in Table 2.2. LMA and Cw ranges were selected based on our field measurements. Soil reflectance was retrieved from bare moist and dry soil pixels identified in the remotely sensed data. Psoil takes soil brightness as a function of these two soil types into account and was varied over the full range of theoretically possible values. The other model parameters were set to values derived from prior studies conducted in similar grassland ecosystems (Darvishzadeh et al., 2008; Feilhauer et al., 2018; Verrelst et al., 2015b). Look-up tables of simulated spectra were generated by varying the input parameters in each model run. 100'000 parameter combinations for each LUT were found to be a good compromise between computation time and accuracy (He et al., 2012; Weiss et al., 2000). In order to find the best solution of the inverse approach, each forward-modelled reflectance spectrum based on the LUT had to be compared to the remotely sensed spectrum. Therefore, the simulated PROSAIL spectra were resampled

using the spectral response function of Sentinel-2 (European Space Agency, 2018). We then selected the modelled spectrum providing the smallest deviation, evaluated by a cost function. Leaf dry mass per area values generating the selected spectrum through the PROSAIL simulations, as well as the resulting SLA, are the solutions of the model inversion. Similar to Rivera et al. (2013) and Verrelst et al. (2015b), we constrained the inversion process by testing multiple solutions and cost functions, and added gaussian noise to simulated canopy reflectance to optimize the inversion results. We used one third of the field data, selected randomly, to calibrate the inversion process. We tested cost functions from three mathematically different families (Leonenko et al., 2013; Rivera et al., 2013): i) information measures, ii) M-estimates and iii) minimum contrast method. All the 18 different cost functions proposed by Rivera et al. (2013) were used. *Information measures* are based on minimization of distances between two probability distributions. Remotely sensed and modelled reflectances have to be rewritten as a probability distribution function by a simple normalization. *M-estimates* can be described by a non-linear regression function to find a relationship between one or more independent variables, and a dependent one. The widely used least squares estimator belongs to this class. Such cost functions are consistent, but can give misleading results if the assumption of a gaussian density function of errors is violated. The third family tested, *minimum contrast estimator*, minimizes the distance (contrast) between a parametric model and a non-parametric spectral density. The modelled reflectance is interpreted as a spectral density of a stochastic process. We applied a range of 0–35% gaussian noise (with steps of 1%) to the simulations to account for uncertainties due to measurement error and model (Baret et al., 2007), and evaluated a mean of multiple solutions of best matching simulated spectra with a range of 0–10% (with steps of 1%) to improve model inversion. An overall model validation was performed against the CWM of SLA field measurements for all four Sentinel-2 datasets together. We evaluated a linear model and predictive accuracy by calculating the coefficient of determination (R^2) and the normalized (with the mean of measured data) root mean square error (nRMSE). The modelling and optimization process was carried out using the ARTMO (Automated Radiative Transfer Models Operator) GUI toolbox in Matlab (v3.23 Verrelst et al., 2011).

2.3.7 Functional diversity

The inversion of PROSAIL with Sentinel-2 data allowed us to estimate traits as the CWM of pixel-sized plant communities, and thus mean values at a regional scale. Total

functional diversity (FD) was partitioned into different spatial components (Ricotta, 2005). We quantified the *local* within-pixel community (i.e., 20x20m) trait diversity as α -FD for each of the 39 plots from traits measured in the field. The *regional* among-pixel diversity equals β -FD and was derived from pooling the remotely sensed CWM of different pixels (Féret and Asner, 2014; Rocchini et al., 2018b; Siefert et al., 2013). Consequently, α -FD represents the variance of a given trait in a community and β -FD accounts for variability in mean trait values between pixel-sized communities. We calculated β -FD at two different spatial scales, i.e., i) neighbourhood by using a moving window approach on adjacent pixels (3x3 pixels, scale=0.36 ha, β -FD_{0.36}; Rocchini et al., 2015), and ii) landscape by pooling together a subsample of pixels subject to the same management types (15'000 pixels, scale=600 ha, β -FD₆₀₀). We calculated three one-dimensional FDi (equations 2.1 to 2.3) to represent FD (Schleuter et al., 2010). A one-dimensional approach based on SLA links the variation in environmental gradients to ecosystem functions and captures the species response to the environment (Butterfield and Suding, 2013; Pakeman, 2011). For all equations, x_i denotes trait values, w_i species abundance and S total number of species or communities. For β -FD calculation, the abundance term (w_i) can be neglected. We used the same indices for all three spatial scales as proposed by de Bello et al. (2009) for functional divergence. The Rao's quadratic entropy index used by Rocchini et al. (2018b) summarizes both functional richness and divergence (Mouchet et al., 2010). Consequently, we preferred to use three distinguishable FDi for a better interpretation of relationships between diversity and ecosystem or assembly processes. The functional range index FR_R (equation 2.1, Mason et al., 2005) is a measure of functional richness that indicates how much of the niche space is occupied by species or communities present:

$$FR_R = \frac{\max_{i \in S}(x_i) - \min_{i \in S}(x_i)}{\max_{i \in US}(x_i) - \min_{i \in US}(x_i)} \quad (2.1)$$

The functional regularity index FRO (equation 2.2, Mouillot et al., 2005) is a measurement of functional evenness that indicates whether mean species or community traits are distributed regularly within the occupied trait space:

$$FRO = \sum_{i=1}^{S-1} \min \left(\frac{\frac{|x_{i+1}-x_i|}{|w_{i+1}+w_i|}}{\sum_{i=1}^{S-1} \frac{|x_{i+1}-x_i|}{|w_{i+1}+w_i|}}, \frac{1}{S-1} \right) \quad (2.2)$$

The functional divergence index FD_{VAR} (equation 2.3, Mason et al., 2003) is a measure of variance of species or community functions and the position of their clusters in trait space:

$$FD_{VAR} = \frac{2}{\pi} \arctan \left(5 \sum_{i=1}^S w_i (\ln(x_i) - \overline{\ln x})^2 \right) \quad (2.3)$$

The next step was to test how CWM of SLA differed between our seven management types at a regional scale using Welch's ANOVA. A post-hoc Games-Howell test was conducted when significant differences between management types were detected. Further, we investigated what proportion of the CWM and FDi variance of SLA at a regional scale could be explained by management type or elevation. Elevation was included to detect a potential confounding effect on management. We used a linear model to evaluate the relationships between the independent variable (management type or elevation) and the dependent variables (CWM or FDi). To account for spatial autocorrelation in the regression analysis, we used a randomly selected subsample of pixels ($n = 15'000$). Correlations between FDi at different spatial scales and management types were computed using the Pearson correlation coefficient (ρ) and tested for statistical significance. For this analysis the α -FD per plot and β -FD_{0.36} per pixel were averaged per management type. Each mean value per management of β -FD_{0.36} was derived from a random subsample of 2'500 pixels.

2.3.8 Comparison between model uncertainty and local trait composition

Exploiting the multiple solutions of the inversion procedure of the PROSAIL model allows to quantify the uncertainty of the trait retrieval on a per-pixel basis. The standard deviation of multiple solutions is considered an indicator of the uncertainty range around the mean estimate (Rivera et al., 2013). For each plot we compared measured CWM and α -FD from three traits (LMA, Cw, VH), as well as number of species S and Shannon index H locally (i.e., at plot level) with the standard deviation of multiple model inversion solutions of LMA using Pearson correlation coefficient (ρ). Statistical analyses and diversity indices were computed in R 3.4.1 (R Core Team, 2017) with the use of the raster package (v2.5-8 van Etten, 2012). Graphs were generated with the ggplot2 (v3.1.0 Wickham, 2016) and ggcorrplot packages (v0.1.1) in R.

2.4 Results

2.4.1 Inversion of physical model

Following model inversion optimization for the two LUTs, we found that the minimum contrast estimator cost functions with 1% of multiple solutions were most effective among the three different families of functions in retrieving LMA (Table 2.3). It consistently provided robust results by displaying one of the highest R^2 and lowest RMSE. The percentage of added gaussian noise was dataset specific, with generally higher noise for the September dataset independent of the cost function.

Table 2.3: Cost function, percentage of gaussian noise, multiple solutions, R^2 and RMSE providing the best four model inversion results of LMA for June/July datasets.

Cost function	Gaussian noise [%]	Multiple solutions [%]	R^2	RMSE
Minimum contrast				
$K(x)=\log(x)+1/x$	0	1	0.55	0.0017
M-Estimates				
Geman and McClure	7	0.001	0.3	0.0018
Least square estimator	35	10	0	0.0024
Information Measures				
Neyman chi-square	0	0.001	0.63	0.0023

The estimated LMA ($R^2 = 0.53$, $nRMSE = 0.27$) and SLA ($R^2 = 0.57$, $nRMSE = 0.27$) values from the model correlated with the field measurements (Fig. 2.3), but tended to be lower (SLA) or higher (LMA). The estimated LDMC values showed low accuracies (Appendix Fig. 2.12, $R^2 = 0.21$, $nRMSE = 0.22$) due to the limited Cw sensitivity of the model (Appendix Fig. 2.10).

2.4.2 Dependence of model uncertainties on local trait composition

The standard deviation of the LMA model inversion (measure of model uncertainties) was primarily correlated with field-measured CWMs (Fig. 2.4). Community-weighted mean vegetation height (VH) and model uncertainties were negatively correlated ($\rho = -0.56$, $p < 0.001$, $n=39$), while CWM of LMA and model uncertainties were positively correlated ($\rho = 0.5$, $p < 0.001$, $n=39$). The strongest positive correlation between model uncertainties and local community diversity was found for the *FRO* of LMA ($\rho = 0.46$,

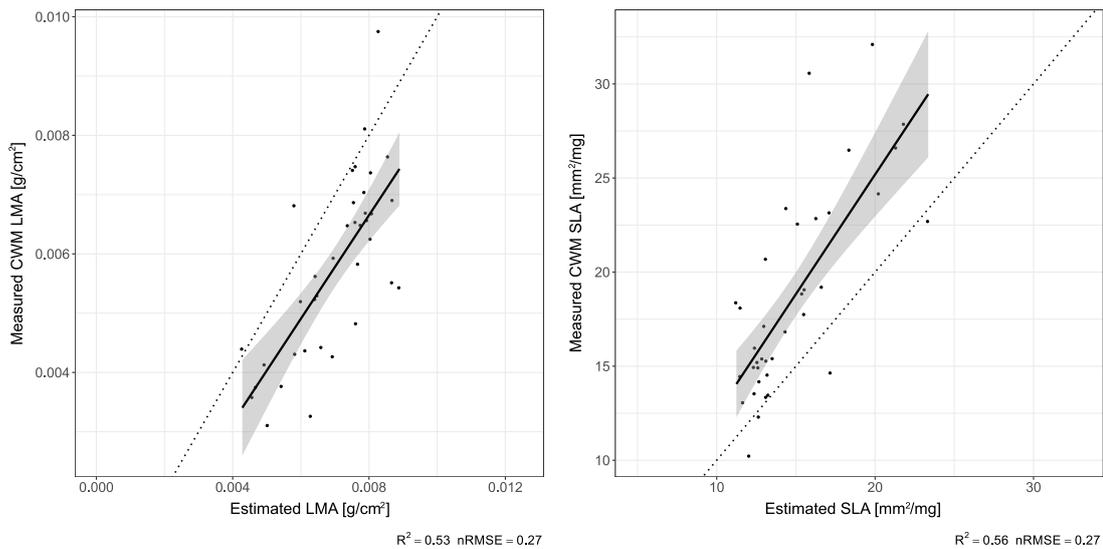


Figure 2.3: Estimated LMA and SLA from four Sentinel-2 datasets versus measured CWM LMA and SLA of the field plots (dotted line is 1:1 line). Grey areas of the regression line indicate 95% confidence intervals for predictions from the linear regression.

$p < 0.001$, $n=39$). A significant positive correlation with uncertainties was also detected for FD_{VAR} of LMA ($\rho = 0.44$, $p < 0.001$, $n=39$) and a negative correlation for VH ($\rho = -0.58$, $p < 0.001$, $n=39$). However, FD_{VAR} was highly correlated with the respective CWM ($\rho_{VH} = 0.67$, $\rho_{Cm} = 0.57$, $\rho_{Cw} = 0.67$, $p < 0.001$, $n=39$). As a result, management types that featured extreme trait values or high functional regularity at a local scale were accompanied by higher model uncertainties in retrieving SLA from space.

2.4.3 CWM in grasslands of different management types

A pre-analysis of the average reflectance per management type revealed land use specific differences in the spectral response (Fig. 2.5a). Reference plots in fertilized meadows had the highest reflectance in the NIR. High reflectance in the SWIR was found in pastures and dry meadows. Both CWM of SLA (Fig. 2.5b) based on the individual Sentinel-2 datasets, as well as those measured in the field differed between the seven management types (Welch's ANOVA, $p < 0.01$, $n=21000$ regional, $n=39$ local). Post-hoc tests revealed that the mean CWM of SLA trait values at a regional scale significantly differed for all datasets between management types that used only mowing and those subject to grazing. Discrimination ability between pasture categories varied among the observed dates; on 06 July 2017, *summer grazed by sheep* and *protected grassland*, as well

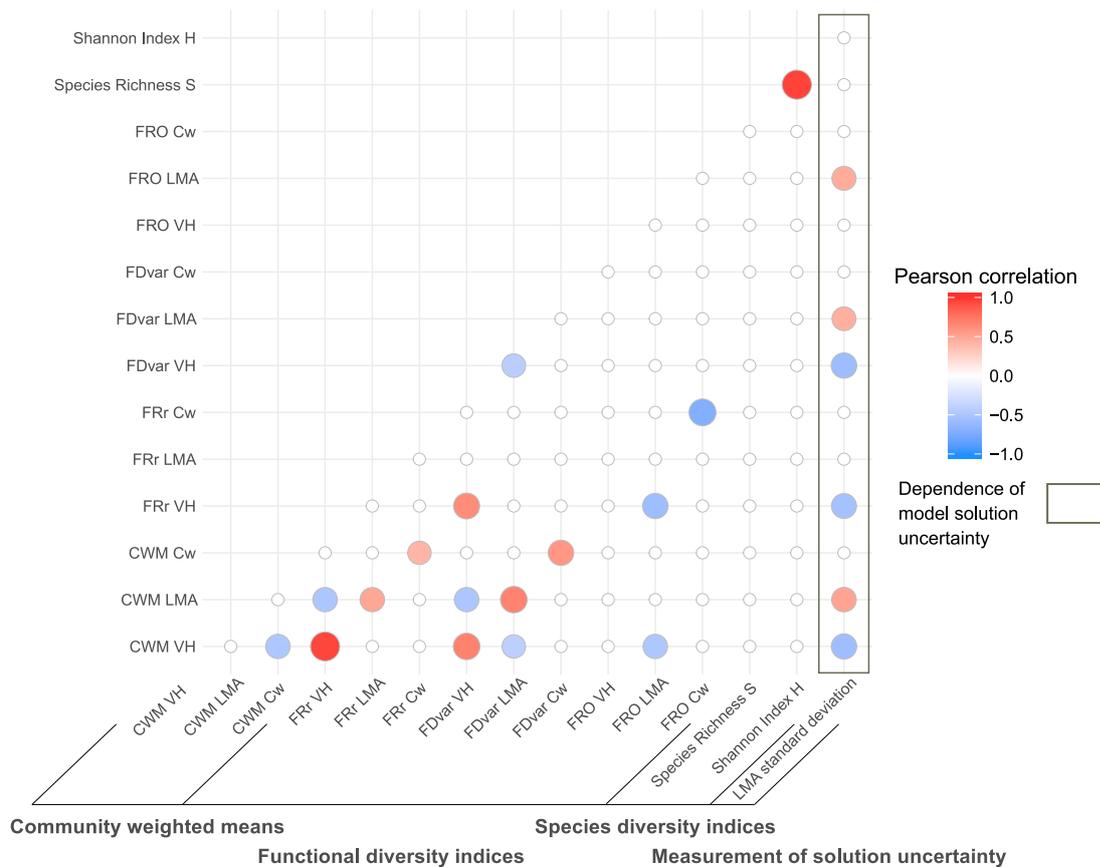


Figure 2.4: Correlation matrix of measured local CWM, α -FD based on functional diversity indices (FR_R , FRO , FD_{VAR}) from three different traits, species diversity (Species richness S, Shannon index H) and model inversion uncertainty represented by the standard deviation of multiple solutions of LMA for the 39 plots. Size and shade of each circle represent the strength of the relationship, while the colour indicates if the relationship is negative (blue) or positive (red). Correlations with a confidence interval of 99% are displayed.

as *summer grazed by cattle* and *summer mixed grazed* showed no statistical difference. On 21 July and 09 September 2016, all *summer grazed pastures*, independent of type of livestock, differed from protected grassland (Fig. 2.5d and Appendix Fig. 2.6). Overall, management type explained 41% of the variance in CWM of SLA averaged over the four datasets at the regional scale. By comparison, elevation explained only 30% of the variance (Appendix Table 2.5). Besides differences in management types, plant traits also showed different variability dependent on management (cf., degree of dispersion in the boxplots of Fig. 2.5c,d). High variability occurred in plots that were mown and fertilized due to high variability in mowing date, mowing frequency, and the amount of fertilizer applied. In protected grasslands, the trait variabilities were large when we

sampled former cattle resting areas usually located close to stables. Here, we generally found high CWM values for SLA compared to the surrounding areas where cattle historically did not graze, mainly due to a high occurrence of *Aconitum napellus* (Fig. 2.6). Former stables were identified from the Topographic Atlas of Switzerland (1870-1926). Overall, protection produced intermediate levels of mean trait values in July for both the remotely sensed and field data compared to all other management types.

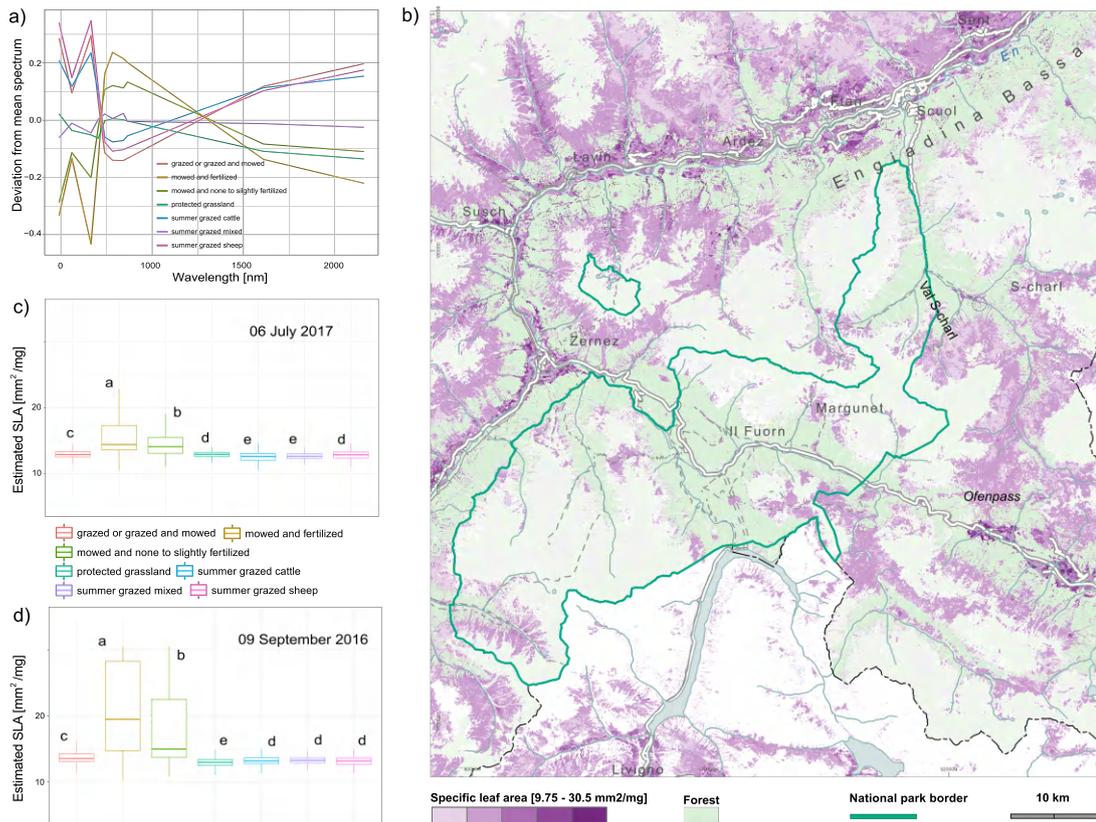


Figure 2.5: a) Relative deviation for surface reflectance per management type in the reference plots from the average spectrum (dataset: Sentinel-2 part of tile 32 TNS of 06 July 2017); b) CWM of SLA of the study area mapped from 26 June and 06 July 2017 through PROSAIL inversion. SLA ranges from 9.75 to 30.47 mm²/mg (13.36 ± 1.90 mm²/mg ; mean \pm standard deviation); c,d) Boxplots showing the CWM of SLA for the different management types for 06 July 2017 and 09 September 2016. Same letters indicate no statistically significant differences based on post-hoc Games-Howell tests. The central bar shows the median, the box represents the interquartile range (IQR) and the whiskers show the location of the most extreme data points still within 1.5 IQR \pm the upper or lower quartiles.

2.4.4 Functional diversity per management type

Community-weighted means of SLA retrieved from remote sensing data correlated between the four Sentinel-2 datasets ($\rho = 0.6-0.80$, $p < 0.001$, $n=30000$, Appendix Fig. 2.14). Variation originated from different mowing dates across the region, as well as the different growing seasons the datasets were collected in. Functional diversity results at a regional scale were averaged over all datasets excluding 21 July 2016, due to its widespread cloud cover.

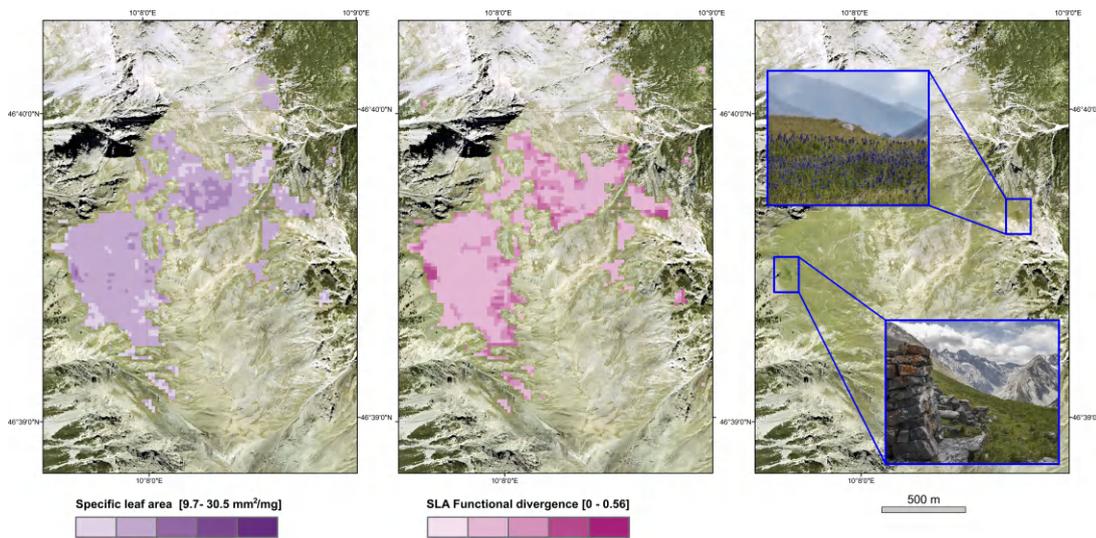


Figure 2.6: CWM of SLA (left) and functional divergence on a neighbourhood scale (β -FD_{0.36}) of SLA (middle) mapped for Murter (Plan dals Poms) in the SNP (protection), based on the 06 July 2017 Sentinel-2 dataset. High CWM of SLA values in former cattle resting areas with high occurrence of *Aconitum napellus* are visible in the subsetted images (right). Differences from surroundings are highlighted by a higher neighbourhood functional divergence.

Table 2.4: Pearson correlation coefficient between functional diversity indices in different management types across spatial scales ($n=7$), and between α -FD and β -FD_{0.36} for all reference plot ($n=39$). * Correlation is significant at 0.05, ** Correlation is significant at 0.01.

	α -FD - β -FD ₆₀₀	α -FD - β -FD _{0.36}	β -FD _{0.36} - β -FD ₆₀₀
Functional richness FR_R	-0.05	0.18	0.72
Functional evenness FRO	-0.75 *	0.08	-0.91**
Functional divergence FD_{VAR}	-0.77 *	-0.30	0.86 **

Functional richness measured at a local scale (α -FD) was higher in our mowed management types compared to management with livestock, but not where wild ungulates

grazed (Fig. 2.7a). The opposite was found for functional divergence and evenness, where lowest values were detected for mowed and fertilized management types (Fig. 2.7b,c). β -FD₆₀₀ showed no or a negative correlation with α -FD per management category ($\rho_{FRr} = -0.05$, $p = 0.9$; $\rho_{FRO} = -0.75$, $p = 0.05$; $\rho_{FDvar} = -0.77$, $p = 0.04$, $n = 7$; Fig. 2.7a,b,c, Table 2.4). Mowing proved to be the most successful promoter of FD at a large spatial scale (i.e., β -FD). For β -FD_{0.36}, little functional differentiation and magnitude were found due to spatial autocorrelation of remotely sensed SLA (Moran's I = 0.85). Yet, Figure 2.6 shows the potential of mapping β -FD_{0.36} divergence, as we found substantial differences in CWM of SLA at a relatively small spatial scale. Management categories explained 32% of the variance for β -FD_{0.36} richness (Appendix Table 2.5). Less variance was explained for functional evenness (8%) and for functional divergence compared to richness (21%). No correlation was found between α -FD and β -FD_{0.36} in measured reference plots ($\rho_{FRr} = 0.18$, $p = 0.3$, $\rho_{FRO} = 0.08$, $p = 0.62$, $\rho_{FDvar} = -0.3$, $p = 0.07$, $n=39$, Table 2.4). The two β -FD scales were positively correlated for divergence and richness ($\rho_{FDvar} = 0.86$, $p = 0.01$, $\rho_{FRr} = 0.72$, $p = 0.06$, $n = 7$, Figure 7a,c), and negatively for evenness ($\rho_{FRO} = -0.91$, $p < 0.01$, $n=7$).

2.5 Discussion

2.5.1 PROSAIL inversion accuracy

The performance of a physical model based on Sentinel-2 data to retrieve local grassland CWM of SLA performed similarly or even better compared to similar attempts that used imaging spectroscopy data from protected grassland and cotton plantations ($nRMSE > 0.3$; Casas et al., 2014; Thorp et al., 2015). This was surprising, as the input of Sentinel-2 used for RTM inversion is limited compared to imaging spectroscopy data, which should increase uncertainties in retrieving traits (Shiklomanov et al., 2016). However, various vegetation properties are related to relatively broad spectral regions (Verrelst et al., 2016). Therefore, even a limited number of broader bands covering spectral features of designated plant traits seem to be sufficient to quantify such traits. Féret et al. (2018) also showed that $nRMSE$ can be reduced by 55% when estimating LMA without including spectral domains with strong water absorption (1800 to 2100 nm) or the NIR domain between 900 and 1300 nm in the RTM inversion. The Sentinel-2 bands used in our study excluded these two spectral domains, which likely also helped to accurately estimate SLA. In addition, Lepine et al. (2016) revealed that the actual limiting factor in trait retrieval from multispectral data is not the broader spectral resolution,

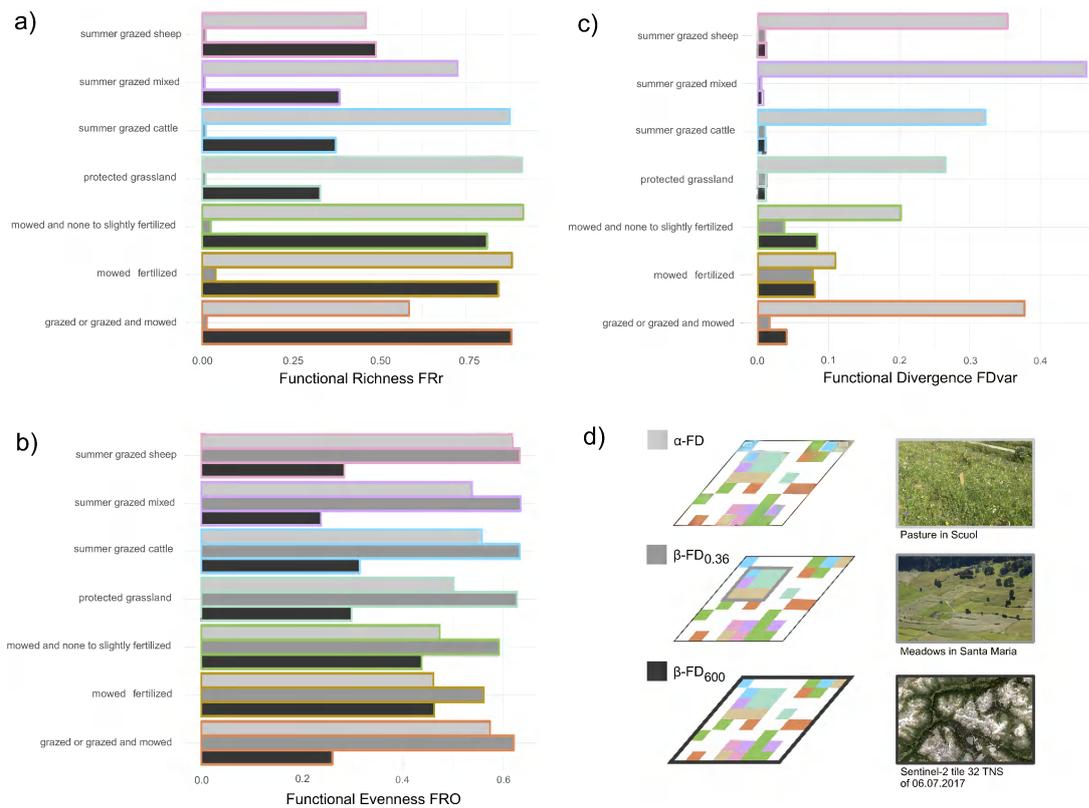


Figure 2.7: Three measures of mean α and β functional diversity, represented by a) richness, b) evenness and c) divergence dependent on scale and grassland management. d) Representation of the different spatial scales: α -FD as calculated from trait measurements in the reference plots; β -FD derived from remotely sensed SLA calculated at two different scales, i.e., neighbourhood (0.36 ha) β -FD_{0.36}, and landscape (600 ha) β -FD₆₀₀.

but the spatial resolution and loss of sensor fidelity. The spatial resolution provided by Sentinel-2 is close to that used in Casas et al. (2014). In contrast, lower accuracy of retrieving LDMC indicates some limitations of Sentinel-2 data. There is a lack of bands located around water absorption spectral regions at 1450 and 1950 nm where Cw strongly influences reflectance (Jay et al., 2016). A further aspect to consider is that plant trait measurements used for calibration and/or validation in other studies often represent individual pixels inaccurately due to a lack of standardised field sampling (McCoy, 2005). Using CWM (i.e., plot-level trait values weighted by species abundances) to represent field conditions is a clear improvement towards successful model application. According to the mass ratio hypothesis (Grime, 1998), ecosystem properties (e.g., spectral response of a plant community) should be predicted by CWM. In general, the full optimization of the PROSAIL inversion process (i.e., constraining the

input variables, testing different cost functions, multiple solutions and adding gaussian noise) explains the good performance of our method. Simplified model assumptions and uncertainties arising from different sources such as instrument calibration lead to mismatches with asymmetric, biased or heavy-tailed distributions between observations and simulated reflectances. Therefore, testing cost functions to better estimate error distributions instead of assuming a gaussian error distribution can result in better estimates of SLA. We found a reduction in nRMSE by 0.25 between the best and worst performing cost functions. This is in agreement with the accuracy levels achieved by Rivera et al. (2013) using a model inversion optimization for retrieving leaf chlorophyll content from Sentinel-2 data (reduction of nRMSE by up to 0.20). The optimization procedure tackles the equifinality of the model by reducing or averaging between possible model solutions. The disadvantage of model optimization is that it requires considerably more trait measurements collected in the field to split the data into calibration and validation sets. Moreover, one strength of the physical based approach is weakened, as the optimization is partially site and dataset specific and therefore less general. However, including a priori knowledge based on field measurements to calibrate the inversion clearly improved the inversion performance in our study. This supports previous work employing prior information or Bayesian approaches to improve model accuracy (Combal et al., 2003; Shiklomanov et al., 2016). Two major issues arose when comparing model uncertainties, i.e., the standard deviation of multiple inversion solutions, with CWM, α -FD and species diversity indices measured in the field. First, PROSAIL underestimated extreme trait values, i.e., values close to the upper limit of the model range. For example, in case of high LMA, the model solutions converged less and resulted in larger uncertainties in resource-poor environments. The saturation effect of PROSPECT at higher LMA values plays a major role in explaining such uncertainties (Feret et al., 2008). However, resource-poor environments are most likely characterized by lower vegetation densities and spectra thus affected by bare ground reflection (Roberts et al., 2004). The higher uncertainties we found for low vegetation heights supports this. Moreover, model assumptions in which the only canopy components are small and flat leaves were violated when large leaves were found in a short canopy (Verhoef, 1984). Similarly, Schweiger et al. (2015b) found that a low percentage of non-photosynthetic vegetation (i.e., dead or dry biomass), characteristic of resource-poor environments, strongly influenced the spectral response of a pixel leading to difficulties in remotely retrieving biophysical variables. Trying to improve model accuracy by varying “brown pigment content” in the PROSPECT model failed (not reported), resulting in drastically reduced accuracy in retrieving SLA (nRMSE = 0.35). Thus, using an older version of PROSPECT (e.g., PROSPECT-4) without pig-

ment differentiation yielded the same results for SLA (nRMSE = 0.27). As the PROSPECT versions do not differ in the infrared part of the spectrum (Feret et al., 2008), the inversion scheme is more important than the model used (Laurent et al., 2014). Secondly, as expected, we found less accurate trait estimations for areas with higher plant diversity measured in the field due to model assumptions. Yet, plant FD (functional evenness and divergence) rather than plant species diversity more accurately described the adverse heterogeneity for PROSAIL in our study. Heterogeneous species composition is only indicative of high functional diversity when no niche overlap or high variability in niche space occupation are found (Díaz et al., 2007a). The assumption of homogeneity in PROSAIL is violated for canopy architectures showing irregular or clumped distributions (Berger et al., 2018). High evenness of SLA likely indicates an irregular canopy architecture with niches that are equally filled. SLA varies substantially with light availability. Therefore, irregular or structured canopies that provide different light niches result in an even spacing of observed SLA (Bachmann et al., 2018; Bhaskar et al., 2014). Similarly, a clumped architecture may result from a community with relatively high functional divergence, for example, extreme trait values of the most abundant species (Mason et al., 2005). On the other hand, the functional richness index is less representative for the overall heterogeneity of the canopy, as it is strongly affected by outliers (Mouchet et al., 2010). Furthermore, functional richness measures the amount of niche space filled, but does not indicate how the space is filled. The results for functional richness, considered together with functional evenness and divergence, suggest that the manner in which the niche space is filled is representative of canopy architecture, rather than the size of the occupied niche space.

2.5.2 CWM in grasslands of different management types

The regional analysis of CWM for SLA corroborates our inversion results and highlights the consistency of PROSAIL across different datasets. Local variabilities in former land use history, grazing intensities or environmental factors that influence plant traits (Bernard-Verdier et al., 2013; de Bello et al., 2013; Lavorel and Garnier, 2002; Vries et al., 2012) were captured well with PROSAIL. We were able to clearly distinguish between different management types over the course of the growing season. In mowed and fertilized grasslands, plants adapt more acquisitive strategies and have higher SLA's (Bouchet et al., 2017; Fortunel et al., 2009; Knops and Reinhart, 2000). However, we could only partially explain the trait magnitude of our management types due to high within management type trait variability. For example, in the SNP, we know that land

use history and current grazing intensities created a mosaic of patches with high and low soil nutrients that support different plant communities (Schütz et al., 2003, 2006). Thus, the SNP does not mirror typical trait CWM values of abandoned land, i.e., low SLA. Moreover, current numbers of wild ungulates (0.15-0.5 LU/ha) are suitable to maintain the grasslands (Sepe et al., 2011) comparable to extensively managed pastures. Furthermore, elevation was a confounding effect that influenced our trait values. In particular, management types become less important in areas with a strong climatic filtering effect (e.g., high elevation meadows and pastures, Díaz et al., 1999b).

2.5.3 Functional diversity in different management types

Multi-trait approaches capture community assembly processes where single trait approaches fail (Kraft et al., 2015). However, we made use of a single trait approach to quantify functional diversity, as single trait indices are well correlated to ecosystem functioning (Gagic et al., 2015). In particular, ecologically meaningful traits (e.g., SLA) are required to describe functions in different environmental gradients (Butterfield and Suding, 2013). Specific leaf area explains most of the variation in the leaf economic spectrum and the relative growth rate of plants (Poorter et al., 2009; Wright et al., 2004). Caveats of using SLA arise from the potential impact of canopy shading. At productive sites with higher canopy density, more shade-tolerant species with higher SLA are found. In this context, it is therefore not straightforward to predict at which point high SLA ceases to identify the potential for fast growth and begins to represent slow growth under shaded conditions (Hodgson et al., 2011). Nonetheless, in semi-arid grasslands, there is a high correlation between SLA and leaf nitrogen content suggesting a fast versus slow growth strategy (Liu et al., 2017). Furthermore, multi-trait indices may not differentiate between management types if they include traits with contrasting responses to fertilization, mowing and grazing (Spasojevic and Suding, 2012). Our results showed that mowing resulted in higher local richness compared to grazing, which agrees with findings by Catorci et al. (2014). High grazing intensity in managed pastures (0.5 - 3 LU/ha) leads to a dominance of traits related to grazing resistance (Dainese et al., 2015; Niu et al., 2015) and could explain the reduced FD in pastures compared to the one in the protected area. Furthermore, land use history is an important factor influencing FD at small scales (Saar et al., 2017), as found in the SNP (Puorger et al., 2017; Schütz et al., 2003). The result is a dualism of traits related to grazing opposed to undisturbed areas, often missing in managed pastures. Our results for functional evenness and divergence suggest a trait conver-

gence when competition for light is high (e.g., fertilizing), similar to Carmona et al. (2015). Low functional divergence and evenness at the local scale generally represents a low level of niche differentiation, high resource competition and less effective use of available resources, which leads to a reduction in the functioning of the ecosystem. Translated to our PROSAIL application, this means that management categories, such as mowed and fertilized delivered the most reliable results. This is consistent with expected higher canopy densities in meadows, where soil background noise is minimized. At regional scales (neighbourhood and landscape), we found that management type differently affected FD compared to the local scale. On a regional scale, higher FD was found for meadows and an overall lower β -FD compared to the α -FD. Higher FD within local communities compared to between communities was also found by de Bello et al. (2009). Nevertheless, the different impact of management on α - and β -FD detected in our study requires some explanation. More heterogeneous management at the regional scale, for example, time of mowing, or the amount/type of fertilizer used, resulted in higher regional FD (Kessler et al., 2009). The moving window approach on adjacent pixels that we used captures within-community diversity if the plant community extends over a larger area than the pixel itself. However, supported by the high correlation between our two β -FD scenarios and strengthened by the absence of correlation between α -FD and β -FD_{0.36} for the reference plots, the moving window approach captures between-community diversity in alpine grasslands well. The variability of CWMs in our different management types was similar at both our regional scales. This result is in accordance with a small parcel size of mowed and fertilized meadows (mean size is 0.25 ha) and the possibility of higher diversity at field edges (Gabriel et al., 2006). This could also explain the difference to α -FD, with a more heterogeneous landscape for meadows due to the limited extension of parcel size compared to the wider pasture and protected grassland. Our results are also similar to findings by Socolar et al. (2016) who showed that uniformity of agricultural practices and policies over large areas reduces β -diversity. Fertilized and mowed grasslands are influenced by a variety of anthropogenic subjective management decisions due to few legislative constraints compared to all other management types. Alpine pasture and extensive meadows undergo different policies to enhance and preserve local biodiversity. Protection is the most constrained practice with no actual anthropogenic influence. High FD at a small scale is redundant on all pastures in the SNP, resulting in a low regional diversity. However, since differences in SLA and a scale-dependent impact on FD among management types were highlighted we suggest that a patchy landscape with multiple diversified management types enhances both α -FD and β -FD.

2.6 Conclusion

We predicted CWM of SLA from space for differently managed grasslands using the PROSAIL model. More specifically, a combined use of satellite data with field measured CWMs improved the accuracy of the model inversion process and permitted the calculation of β -FD at different regional scales. Such diversity derived from traits at large spatial scales can represent functions and resilience of an ecosystem. If the magnitude of CWMs mirrors the management type typical for a certain area, β -FD quantification delivers a broader picture influenced by policies, parcel size and elevational gradients. The consistency of the approach across different datasets provides a solid base for evaluating management practices on CWM of SLA, and makes a PROSAIL application attractive for incorporation into monitoring schemes and important for conservation and restoration decision-making (Cadotte et al., 2011). Our results also suggest the need to account for scale dependency of FD, which is highlighted by the discrepancy between the impact on β -FD measured from space and α -FD measured locally in plots of different management types. Yet, even though FD quantification is valuable at a regional scale, locally measured FD influences the success of its applications. Through our quantification of model uncertainties, we were able to 1) improve our understanding of cases where model assumptions were violated and 2) define which management types and environmental conditions were more suitable for the application of the PROSAIL model. Furthermore, the correlation between model uncertainties and FD we found suggests that it should be possible to measure functional diversity from space at a local scale by quantifying model uncertainties. However, launching such an approach successfully requires 1) a better understanding of the representativeness of FD indices for the canopy architecture, and 2) incorporating multiple diverging traits simultaneously to more accurately explain community assembly across different ecosystems (Laughlin, 2014).

2.7 Data availability

R code to calculate diversity indices from raster files are publicly available at <https://data.mendeley.com/datasets/4xjcd6dvzg/4>, trait data are available in the TRY database <https://www.try-db.org/TRYWeb/Home.php> upon request.

2.8 Acknowledgments

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2.9 Appendix

Table 2.5: ANOVA table investigating the effect of management and elevation on remotely sensed CWM (community weighted mean) of SLA (specific leaf area) and FDi (functional diversity indices).

	DF	Sum Sq	Mean Sq	F-value	Pr (>F)	R ²
Response CWM SLA						
Management	6	15458	2576.28	1752.4	<0.001	0.41
Residuals	14993	22042	1.47			
Response CWM FDi						
Elevation	1	12559	12558.9	7537	<0.001	0.33
Residuals	14998	24992	1.7			
Response β-FD_{0.36} FRr						
Management	6	1.3131	0.218846	1174.9	<0.001	0.32
Residuals	14993	2.7926	0.000186			
Response β-FD_{0.36} FDvar						
Management	6	5.8846	0.98077	675.87	<0.001	0.21
Residuals	14993	21.7567	0.00145			
Response β-FD_{0.36} FRO						
Management	6	8.77	1.46169	215.7		0.08
Residuals	14993	101.6	0.00678			

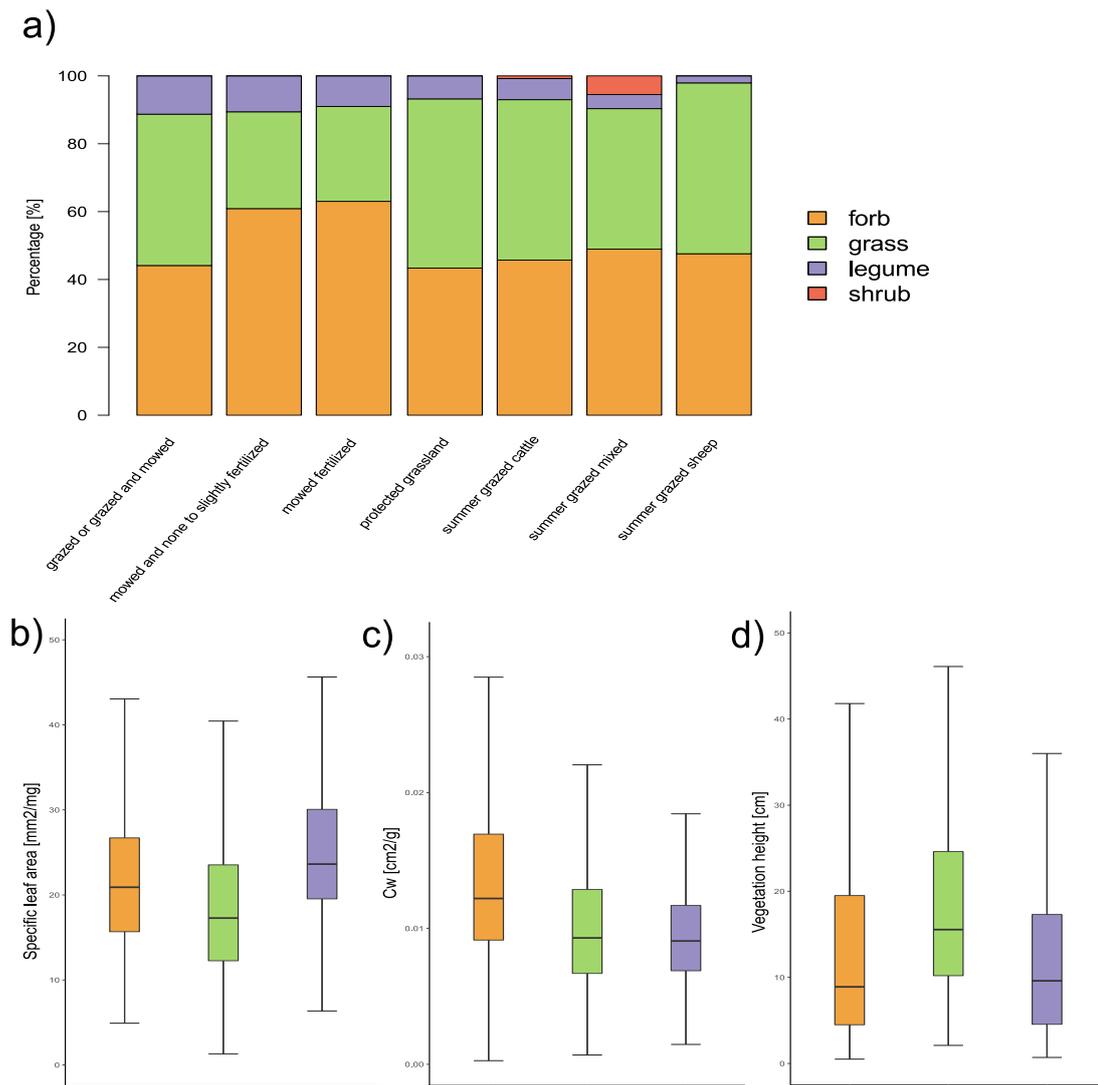


Figure 2.8: a) Percentage of life-forms (forbs, grasses, legumes, shrubs) recorded per management type in the field. Here, we report the most frequent species recorded with the transect method (Gaucherand and Lavorel, 2007) for each management type following identification and names of Hess et al. (2015). *Grazed or grazed and mowed*: *Nardus stricta*, *Hieracium pilosella*, *Briza media*; *mowed and none to slightly fertilized*: *Taraxacum officinale*, *Dactylis glomerata*; *mowed and fertilized* *Taraxacum officinale*, *Trifolium repens*, *Heracleum sphondylium*, *Pimpinella major*; *protected grassland* *Carex sempervirens*, *Leontodon helveticus*, *Alchemilla vulgaris*, *Nardus stricta*; *summer grazed cattle* *Nardus stricta*, *Potentilla aurea*, *Achillea millefolium*; *summer grazed mixed* *Nardus stricta*, *Homogyne alpine*, *Carex sempervirens*; *summer grazed sheep* *Nardus stricta*, *Hieracium pilosella*, *Plantago atrata*. b,c,d) Specific leaf area, leaf water mass per unit area and vegetation height for each life-form measured in all plots.

Figure 2.9: Leaf area meter prototype 1.0 SNP. The device is constructed of wood; gear-wheels were recycled from an old toilette. Images were taken with a Sony DSC-HX90V camera with 18.2 megapixels.

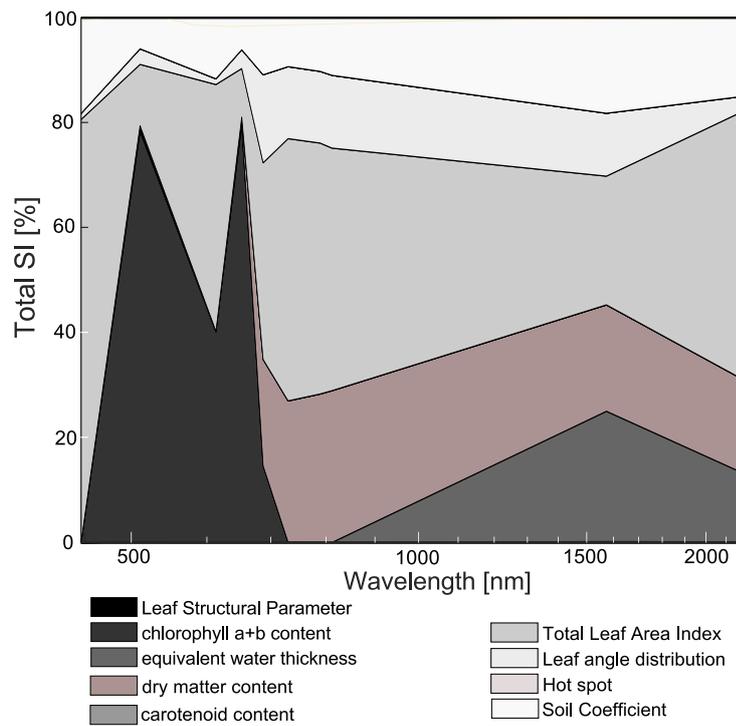


Figure 2.10: Variance-based global sensitivity (Total SI) analysis (Saltelli et al., 2010) of the PRO-SAIL model with the proposed range of input parameters for the ten Sentinel-2 bands used in this study (LMA (leaf dry mass per area)). LMA explains around 30% of the output variance in the NIR (B7 and B8) and 20% in the SWIR (B11).

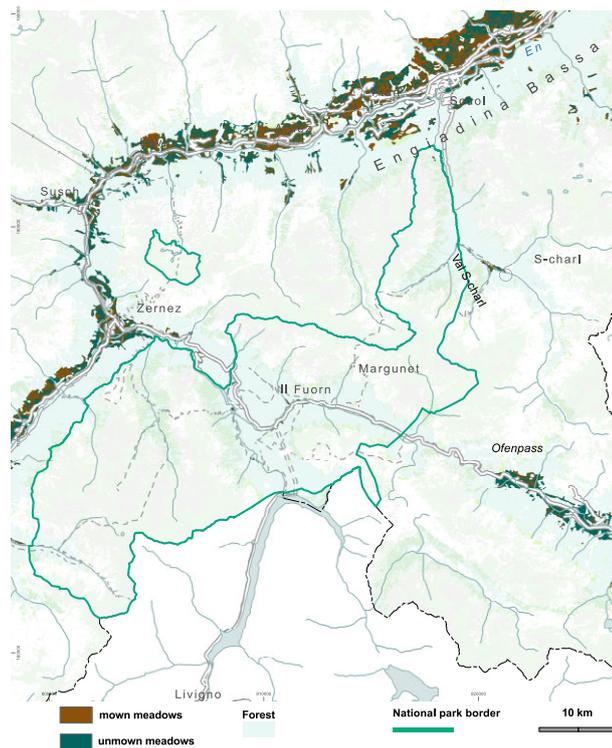


Figure 2.11: Random forest supervised classification of mown and unmown meadows based on reflectance values of B2, B3, B4 and B8 Sentinel-2 bands from the 26.06.2017 dataset. Dataset was classified by using the rminer package (v1.4.2) in R.

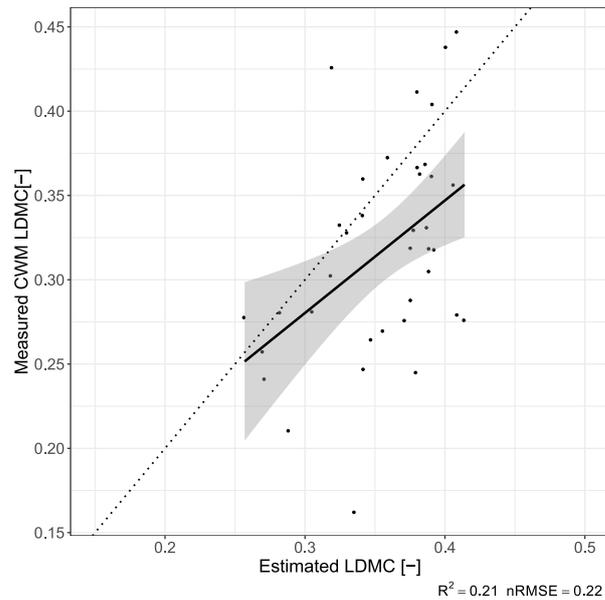


Figure 2.12: Estimated leaf dry matter content (LDMC) from four Sentinel-2 datasets versus measured CWM LDMC of the field plots (dotted line is 1:1 line). Grey areas of the regression line indicate 95% confidence interval for predictions from the linear regression.

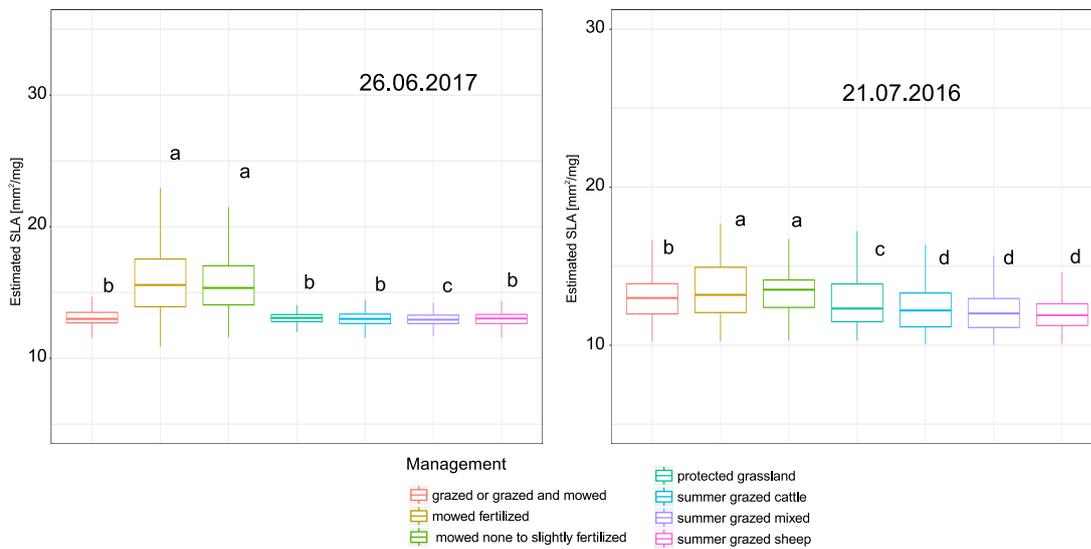


Figure 2.13: Boxplots showing the differences in CWM of SLA for the different management types between the distinct datasets. Same letters indicate no statistically significant differences based on post-hoc Games-Howell tests. The central bar shows the median, the box represents the interquartile range (IQR) and the whiskers show the location of the most extreme data points still within $1.5 \text{ IQR} \pm$ the upper or lower quartiles.

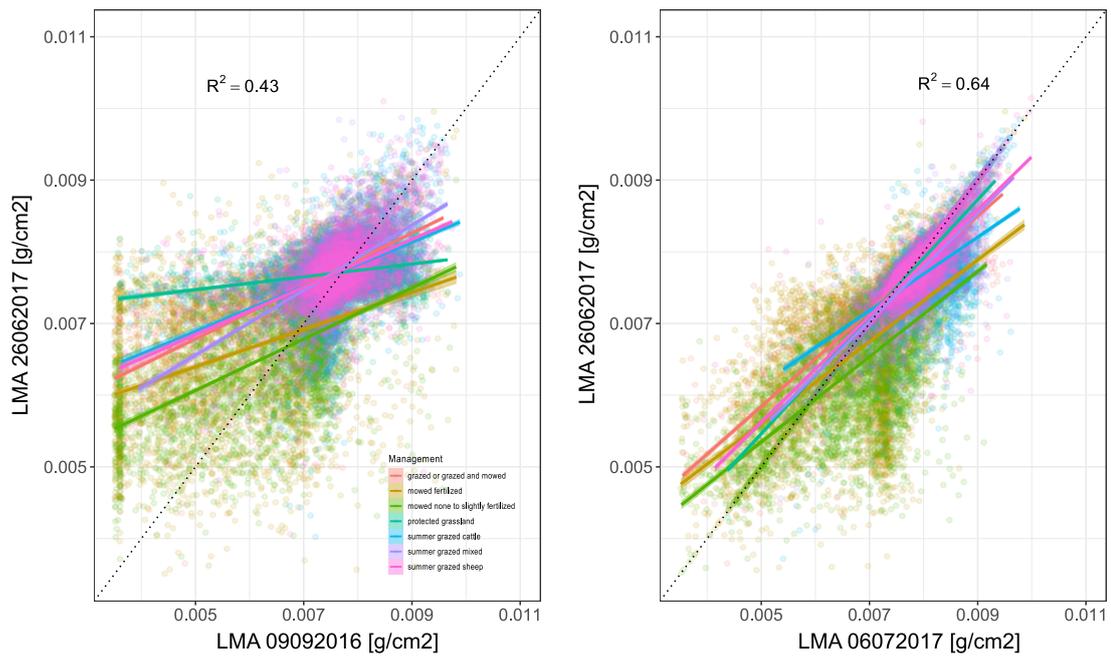


Figure 2.14: Linear regression between estimated LMA from different Sentinel-2 datasets ($n=30000$, dotted line is 1:1 line). Coloured lines show patterns within each management type. R^2 refers to the total linear regression independent of management type.

3

Spatial resolution, spectral metrics and biomass are key aspects in estimating plant species richness from spectral diversity in species-rich grasslands

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in the Bibliography chapter.*

Description of author's responsibilities

CR: Conceptualization, Methodology, Software, Formal analysis, Data Curation, Writing - Original Draft, Project administration. MK: Conceptualization, Validation, Writing - Review & Editing. MS: Conceptualization, Investigation, Writing - Review & Editing. MES: Conceptualization, Writing - Review & Editing, Supervision. RMH: Conceptualization, Funding acquisition. ACR: Conceptualization, Investigation, Validation, Writing - Review & Editing, Supervision

3.1 Abstract

Increasing evidence suggests that remotely sensed spectral diversity is linked to plant species richness. However, a conflicting spectral diversity–biodiversity relationship in grasslands has been found in previous studies. In particular, it remains unclear how well the spectral diversity–biodiversity relationship holds in naturally assembled species-rich grasslands. To address the linkage between spectral diversity and plant species richness in a species-rich alpine grassland ecosystem, we investigated (i) the trade-off between spectral and spatial resolution in remote sensing data; (ii) the suitability of three different spectral metrics to describe spectral diversity (coefficient of variation, convex hull volume and spectral species richness) and (iii) the importance of confounding effects of live plant biomass, dead plant biomass and plant life forms on the spectral diversity–biodiversity relationship. We addressed these questions using remote sensing data collected with consumer-grade cameras with four spectral bands and 10 cm spatial resolution on an unmanned aerial vehicle (UAV), airborne imaging spectrometer data (AVIRIS-NG) with 372 bands and 2.5 m spatial resolution, and a fused data product of both datasets. Our findings suggest that a fused dataset can cope with the requirement of both high spatial- and spectral resolution to remotely measure biodiversity. However, in contrast to several previous studies, we found a negative correlation between plant species richness and spectral metrics based on the spectral information content (i.e. spectral complexity). The spectral diversity calculated based on the spectral complexity was sensitive to live and dead plant biomass. Overall, our results suggest that remote sensing of plant species diversity requires a high spatial resolution, the use of classification-based spectral metrics, such as spectral species richness, and awareness of confounding factors (e.g. plant biomass), which may be ecosystem specific.

3.2 Introduction

Biodiversity is declining globally at rates unprecedented in human history (Díaz et al., 2019). In particular, grassland biodiversity is threatened by destruction, degradation and fragmentation due to urban development, agricultural land-use such as grassland transformation into monocultures, eutrophication, overgrazing, and climate change (Clark and Tilman, 2008; Harrison et al., 2015; Hautier et al., 2014; Mooney et al., 2009). Grassland biodiversity provides a large range of ecosystem services (Hein et al., 2006; Lamarque et al., 2011) essential for the survival of plant and animal species (Dinnage

et al., 2012) and vital in sustaining human life. Lower grassland biodiversity leads to lower stability in plant productivity over time (Hautier et al., 2014), limited carbon storage (Ward et al., 2016), and reduced pollinator abundance (Batary et al., 2010). Therefore, with the worldwide loss of grassland biodiversity and the associated decline of ecosystem services, comprehensive monitoring of grasslands remains a priority (Suding, 2011).

However, assessing grassland biodiversity based on field inventories is highly time consuming, expensive and subjective (Bonar et al., 2011; Löhmus et al., 2018). In contrast, technological developments in passive remote sensing approaches, which measure the sunlight reflected by an object at a specific wavelength, allow for an efficient and relatively inexpensive collection of baseline data related to biodiversity (Cavender-Bares et al., 2017; Frye et al., 2021; Rocchini et al., 2018a; Schweiger et al., 2018) across various spatial and temporal scales (Gholizadeh et al., 2020; Jetz et al., 2016; Pettorelli et al., 2018; Rossi et al., 2021). In particular, the approach known as the spectral variation hypothesis (Palmer et al., 2002) assumes that the remotely measured variation in spectral patterns, i.e., spectral diversity, is related to biodiversity (i.e., plant species richness; Cavender-Bares et al., 2017; Dahlin, 2016; Oldeland et al., 2010; Rocchini et al., 2010). Spectral diversity represents a set of pixels recorded by remote sensing mirroring the spatial heterogeneity of the environment, e.g., vegetation, soil and topography. Vegetation spectral diversity may be based on specific spatial patterns in reflectance (hereinafter spectral metrics) of known vegetation indices (Rocchini et al., 2018a), principal components (Rocchini et al., 2004), or the clustering and classification of reflectance spectra (Féret and Asner, 2014; Schäfer et al., 2016). The measured spectral diversity of vegetated areas is assumed to be shaped by morphological, physiological or phenological features that manifest the life history of a species, like plant leaf traits (e.g., pigments, leaf water content, leaf area and dry matter content), canopy structure, plant functional types and plant phenological state (Asner and Martin, 2008b; Asner et al., 2011; Ollinger, 2011; Schweiger et al., 2017; Ustin and Gamon, 2010; Ustin et al., 2009; Wang and Gamon, 2019). Some of these features represent different environmental adaptations or resource use strategies (Díaz et al., 2016). Therefore, variation in these features indicate the presence of different plant species and hence characterise plant species richness (Pavoine and Bonsall, 2011).

Nevertheless, using remote sensing techniques to estimate plant species richness in grasslands is more challenging than it appears to be (Gholizadeh et al., 2019; Rossi et al., 2020; Schmidtlein and Fassnacht, 2017; Wang et al., 2018a). In general, grassland plants are much smaller than the pixel sizes of remotely sensed data. Several studies estimated grassland species diversities from spaceborne and airborne remote sensing

data and spatial resolutions of several meters (Gholizadeh et al., 2019; Lopes et al., 2017; Möckel et al., 2016; Rocchini et al., 2004). Such unfavourable spatial resolutions of the sensors may lead to pixels containing many individual plants, as well as many plant species. Therefore, it is likely that spectral diversity based on such an approach may only accurately reflect biodiversity at a regional level and between plant communities (Polley et al., 2019; Rossi et al., 2020), but not at a local level in an individual plant community (Lopatin et al., 2017) or an individual plot of an ecological experiment (Wang et al., 2018a).

Furthermore, a range of factors may confound the spectral diversity-biodiversity relationship. For instance, the fraction of bare soil (Gholizadeh et al., 2018) and dead biomass (Schweiger et al., 2015a), size of plants (Conti et al., 2021), phenology, flowering patterns, short-term weather conditions and management (Gholizadeh et al., 2020; Rossi et al., 2021), as well as the amount of biomass (Villoslada et al., 2020) and composition of the plant community (e.g., different life forms such as graminoids, forbs and legumes, Wang et al., 2018b) affect the spectral diversity and thus interfere with the estimation of plant species richness. Such confounding factors may in part be mitigated with an extensive use of spectral information. Using only limited spectral information, e.g., only the Normalized Difference Vegetation Index (NDVI), can weaken the spectral diversity-biodiversity relationship or even result in a negative relationship between the two, due to strong correlations of NDVI with e.g., biomass (Goswami et al., 2015; Villoslada et al., 2020; Wang et al., 2016). In contrast, using imaging spectroscopy data (i.e., hundreds of spectral bands with a wavelength sensitivity in the range of a few nanometers) with a spatial resolution matching the object of investigation was found to result in a positive spectral diversity-biodiversity relationship (Wang et al., 2018a,b). Finally, to date, there is no consensus on the best spectral metrics to be used to quantify plant species richness in grasslands. Spectral metrics based on the information content in the spectral data (spectral complexity) heavily depend on the variance of spectral information, i.e., extreme values that can confound the spectral diversity-biodiversity relationship (Lucas and Carter, 2008). Accordingly, spectral metrics based on classification algorithms (Féret and Asner, 2014) may be better suited to assessing the high small-scale heterogeneity of grasslands. Whether the spectral variation hypothesis works for mapping plant species richness at small spatial scales in grasslands is therefore likely to depend on i) appropriate spatial and spectral resolution, ii) the chosen spectral metrics, and iii) accounting for confounding factors such as bare soil, dead and live biomass.

Previous studies have been performed either in experimental grasslands like Cedar Creek (Gholizadeh et al., 2018; Wang et al., 2018a,b) with communities artificially com-

posed of a limited species pool (i.e., 1, 2, 4, 8, or 16 species per plot) or in naturally assembled grasslands with spectrally (Villoslada et al., 2020) or spatially limited datasets (Möckel et al., 2016). Thus, the interdependencies of the relationship between spectral diversity and biodiversity, as well as possible trade-offs in natural settings still need to be explored. Hence, it is unclear whether the contradicting spectral diversity-biodiversity relationships reported between naturally and experimentally assembled grassland ecosystems result from differences in the spectral information used, or are instead driven more by confounding factors such as, for instance, biomass.

Due to technical constraints, remote sensing devices are usually designed as a trade-off between spatial and spectral resolution (Aiazzi et al., 2012). Unmanned aerial vehicles (UAVs) are remote sensing platforms that can provide imagery with high spatial resolution. Yet, UAVs are primarily used in combination with standard digital cameras providing low spectral resolution (Lu and He, 2017), and UAVs mounted imaging spectrometers of high spectral resolution are still rare, expensive and complex. Furthermore, they are frequently prone to radiometric noise and generally subject to lower spatial resolution in comparison to multispectral cameras with a limited number of wavelength bands (Aasen et al., 2018; Adão et al., 2017). In contrast, space- or airborne imaging spectrometers combine reduced spatial with high spectral resolution.

Here, we studied the controversial spectral diversity-biodiversity relationship in a naturally assembled grassland ecosystem above the timberline with high small-scale species richness of up to 35 plant species per square metre. We used plots from a long-term experiment (Nutrient Network; <https://nutnet.org>), in which small-scale plant species richness was manipulated by the application of fertilisers and the exclusion of plant-feeding animals (see e.g., Borer et al., 2014a). Our objectives were to:

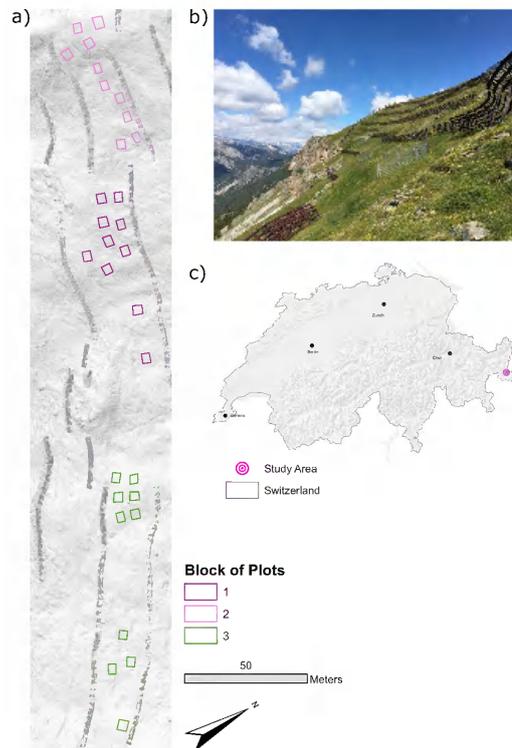
- (i) evaluate the trade-off between high spectral and high spatial resolution when estimating small-scale plant species richness using spectral diversity, in particular by testing image fusion methods (Zhang, 2004),
- (ii) compare three different spectral diversity metrics that have different sensitivities towards extreme values which potentially confound the spectral diversity-biodiversity relationship. Two of these three metrics are based on spectral complexity (convex hull volume, coefficient of variation), and one on a clustering algorithm (spectral species richness)
- (iii) test how far confounding factors such as dead biomass, total biomass or the plant life forms may influence the estimation of plant species richness from spectral diversity.

3.3 Method

3.3.1 Study area

We collected our data in Val Mustair in south-eastern Switzerland in a naturally assembled grassland area above the timberline (2320 m above sea level, latitude 46°37'55" to 46°37'50" N, longitude 10°22'29" to 10°22'18" E, Fig. 3.1). Such alpine grasslands are characterised by high small-scale variability in topography and thus in edaphic conditions. This, in combination with generally nutrient-poor conditions due to low fine earth fractions in the soil, results in high small-scale plant species richness of up to 35 species per square metre on our control plots. The mean annual temperature is 0.3 °C, and the mean annual precipitation amounts to 1098 mm. The parent material underlying the site is a mixture of dolomite and volcanic conglomerates. Soil organic carbon (C) concentration is roughly 4.5%, total soil nitrogen (N) is 0.3%, and the soil C:N ratio is 13.3 (Risch et al., 2019). Soil pH is around 5. The site is part of the globally distributed Nutrient Network (NutNet; Borer et al., 2014a). The network aims to analyse global change effects such as fertilisation and altered herbivore community composition on grassland productivity and biodiversity in a randomised-block design. Three replicate blocks with 10 treatment plots each were established. The 10 plots were randomly assigned to nutrient (7 plots) and fencing (2 plots) treatments, and a control (1 plot) without any experimental treatment. All plots are 5 x 5 m in size. Nutrient additions and herbivore removal treatments started in 2009, hence, were in place for nine years at the time of data sampling in 2018. For the nutrient additions, 10 g N m⁻² yr⁻¹ as time-release urea, 10 g P m⁻² yr⁻¹ as triple-super phosphate, and 10 g K m⁻² yr⁻¹ as potassium sulphate are applied separately, as well as in all possible combinations in each block every year. The vertebrate herbivore removal treatments (fence) were established by fencing two plots, one with full fertiliser application (NPK) and one without fertiliser application. The fences were designed to effectively exclude above-ground mammalian herbivores with a body mass of over 50 g (i.e., ibex, chamois, red deer, marmots and snow hares, Borer et al., 2014a). The fences at the Val Mustair site are 200 cm high and are covered with a 5 cm square mesh with extra cabling support to prevent snow damage. The treatments have, by now, resulted in significant differences in plant species richness and plant biomass. Thus, this experimental setup is well suited for testing the spectral diversity-biodiversity relationship and possible confounding effects in a natural but still controlled setting.

Figure 3.1: a) Study area with location of field plots subdivided into blocks. b) Photo of the study area. c) Location of the study area in Val Mustair in south-eastern Switzerland.



3.3.2 Vegetation data

Plant species richness was assessed in early July 2018. For this purpose, all plant species within a permanently assigned 1 x 1 m square located within each 5 x 5 m plot were identified. Biomass was assessed by clipping two 0.1 x 1 m strips from a 1 x 1 m plot adjacent to each survey square. For each plot, the collected biomass was sorted into three life forms (graminoids, forbs, legumes) and dead biomass, afterwards oven-dried at 60° C and weighed.

3.3.3 Remote sensing data

UAV system, flight mission and image processing

We used a Falcon 8 octocopter (UAV; Ascending Technologies, Krailing, Germany) equipped with a Sony NEX-7 camera (total weigh 2.3 kg). Onboard navigation sensors (Global Navigation Satellite System GNSS, Inertial Measurement Unit, barometer, compass) and an adaptive control unit permitted high positional accuracy and stable flight

characteristics. A laptop installed with a flight control system (AscTec Navigator Flight Planning Software *v3.4.4*) acted as the ground station to control the flight in real-time using communication devices.

We used two different Sony NEX-7 cameras, both with a 24 mega pixel complementary metal-oxide sensor and a small, lightweight Sony NEX 20mm F/2.8 optical lens. One camera recorded red-green-blue (RGB) imagery, the other one had the internal NIR-blocking filter replaced with an 830 nm long-pass filter to record the NIR signal (Bühler et al., 2017; Holman et al., 2019; Lu and He, 2017). The cameras were connected to the Falcon 8 by a gimbal with active stabilisation and vibration damping. Two flights were made over the study area, each collecting 98 images using either the RGB or NIR camera. Both flights were made between 11:03 - 11:33 local time on July 11, 2018 under stable light conditions (i.e., sunny with no clouds and fixed camera settings). The UAV was operated at an altitude of approximately 40 m above ground and at a speed of about 4 metres per second. The images had a spatial resolution of about 1.25 cm, an approximate 85% forward overlap and 60% side overlap. Twelve ground control points (GCPs, 15 x 15 cm in size) were evenly distributed over the entire test site for subsequent georeferencing of the imagery. The locations of the GCPs were measured with a Trimble GeoXR real-time kinematic GNSS with an expected accuracy of < 0.10 m.

Two out of 98 images taken during each flight were eliminated manually due to blurring. The remaining images, i.e., 96 RGB and 96 NIR images, were processed to remove Gaussian noise and optical vignetting by applying a linear filter (Wiener filter) and a flat-field correction, which uses Gaussian smoothing (Matlab *vR2020a* Image Processing Toolbox). The denoised images were subsequently processed in Pix4DMapper (Pix4D *v4.5.6*), which uses structure from motion techniques to generate a dense point cloud, a digital surface model and a mosaicked and rectified reflectance dataset. Detailed radiometric calibration procedures for the UAV data are provided in Appendix 3.8.1. During processing in Pix4D, the twelve GCPs were added for improved georectification of the imagery (root mean square error of GCP localisation around 2 cm). The resulting RGB mosaic and the blue band from the modified camera containing the NIR signal (Holman et al., 2019) were stacked together and resampled bilinearly, resulting in a reflectance dataset consisting of four bands and 10 cm spatial resolution. We chose to resample the original 1.25 cm resolution to 10 cm because of computational constraints and to better reflect an achievable resolution of UAV mounted hyperspectral sensors (Aasen and Bolten, 2018).

Airborne imaging data

We used airborne imaging spectroscopy data was acquired with the next generation airborne visible/infrared imaging spectrometer (AVIRIS-NG; Hamlin et al., 2011) on July 08, 2018 (11:31 - 11:36 local time). The AVIRIS-NG sensor collected reflected radiance at 5 nm intervals covering the spectral range from 380-2500 nm. The geometrically- and atmospherically-corrected datasets are openly available via the AVIRIS-NG Data Portal 2014-2019 (Gao et al., 1993; Thompson et al., 2015). We used the mean reflectance values of two overlapping flight lines (CHNP 25 and CHNP 26) to reduce potential directional effects emerging from a different sun-target-sensor geometry. Due to inaccuracies in georeferencing according to standard data processing, we manually georeferenced the respective datasets using specific objects (e.g., avalanche protection structures) with known coordinates (ArcMap *v10.7.1* Georeferencing toolbar). Subsequently, we bilinearly resampled the data from 2.7 to 2.5 m spatial resolution and applied a mask to match the extent of the UAV data. We used 372 of the 425 AVIRIS-NG bands after removing bands showing low signal-to-noise ratios or strong water absorption (Appendix Fig. 3.6).

3.3.4 Data fusion

The data fusion step combined the available high spatial resolution UAV data with the high spectral resolution airborne data. Since several data fusion techniques have been published that differ significantly in method and performance (Mookambiga and Gomathi, 2016; Yokoya et al., 2017), we tested seven different state-of-the-art fusion methods (Table 3.1). The goal was to find the best method for our application (rather than making a general comparison of fusion methods). For a detailed description of the algorithms of the different methods and their code, we refer to Yokoya et al. (2017) and Appendix 3.8.4. The results of the fusion seven different fusion approaches were compared i) visually, ii) using image entropies, and iii) using image standard deviations (Jagalingam and Hegde, 2015). A high standard deviation indicates high contrast. Similarly, high entropy represents high spectral information content. Furthermore, we assessed how the different methods were able to quantify plant species richness. Consequently, the best fused dataset was selected based on the highest standard deviation, the highest entropy and the strongest relationship with plant species richness.

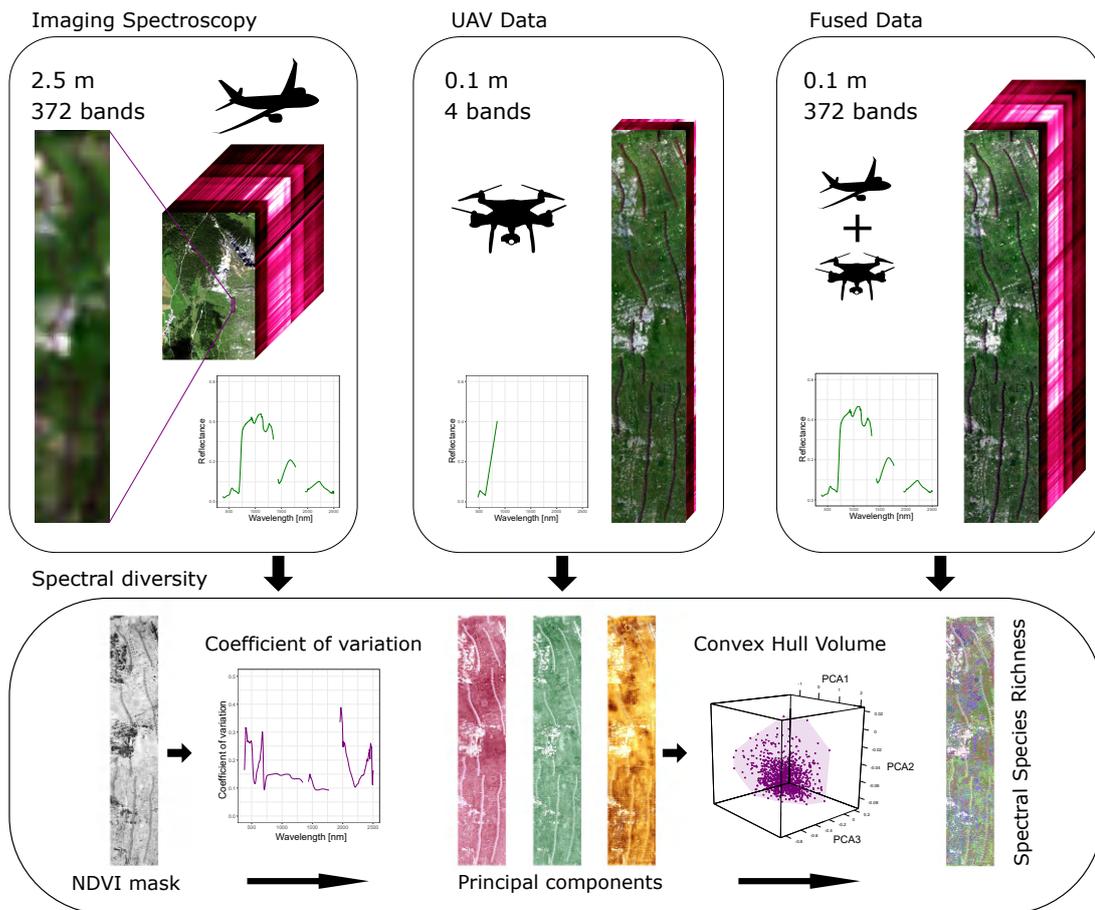


Figure 3.2: Overview of the workflow to calculate three spectral diversity metrics (coefficient of variation, convex hull volume and spectral species richness). Spectral diversity metrics were calculated from airborne imaging spectroscopy (AVIRIS-NG), UAV and fused datasets. We masked all pixels with NDVI values < 0.4 . Convex hull volume was derived from the first three components of a principal component analysis (PCA). The first four PCA components of the reflectance image were used to classify spectral species. The spatial (m) and spectral (number of bands) resolutions of AVIRIS-NG, UAV and fused approach are indicated.

Table 3.1: List of methods used for fusion of multispectral UAV data and AVIRIS-NG data.

Method	Category	Theory	Reference
Gram Schmidt adaptive algorithm (GSA)	Pansharpening-based methods	Component substitution	Aiazzi et al. (2007)
Generalized Laplacian pyramid (GLP)	Pansharpening-based methods	Multiresolution analysis	(Aiazzi et al., 2006)
Smoothing filter-based intensity modulation (SFIM)	Pansharpening-based methods	Multiresolution analysis	Liu (2000)
Coupled nonnegative matrix factorization (CNMF)	Subspace methods	Unmixing	Yokoya et al. (2011)
Maximum a posteriori with stochastic mixing model (MAP-SMM)	Subspace methods	Bayesian	Eismann and Hardie (2004)
Fast fusion based on Sylvester equation (FUSE)	Subspace methods	Bayesian	Wei et al. (2016)
Hyperspectral Superresolution (HySure)	Subspace methods	Bayesian and unmixing	Simoes et al. (2015)

3.3.5 Spectral diversity metrics

We calculated three different spectral diversity metrics for our datasets, namely for the UAV, airborne and the seven fused datasets for each plot (Table 3.2, Fig. 3.2). We chose three of the most commonly used diversity measures in current spectral diversity research (Gholizadeh et al., 2018; Wang et al., 2018a), each with different sensitivities to extreme values. The convex hull volume (CHV) was derived from the first three principal components of the reflectance values (Fig. 3.2). CHV was standardised by subtracting the standard deviation for each dataset across all plots. The coefficient of variation (CV) was calculated as the ratio between the standard deviation and the mean of the reflectance value at a specific wavelength for each plot and was then averaged over all wavelengths. We quantified spectral species richness for the UAV and fused datasets, but not for the airborne dataset due to the limited number of pixels (four) per plot. The spectral species richness approach assumes that the spectral signature of one or several similar species is unique. Spectral species were defined based on the K-means clustering method of a random subset (2500 pixels, with NDVI values > 0.4 and 10 random starts) of the first four principal components of the reflectance image (i.e., UAV or fused dataset) collected across the entire scene (1.7 ha; package `randomForest v4.6-14` and `cluster v2.1.0` in R). The number of clusters was set to 50, which corresponds approximately to the number of plant species recorded in the area. To cluster the 2500 pixels, we used the K-means algorithm on the proximity matrix generated from a Random Forest (RF) model (number of trees to grow = 500) applied on the first four principal components values of the 2500 pixels. The clusters obtained were used to train a subsequent RF model for spectral species classification. In other words, once the 50 spectral species were defined through clustering, each pixel contained in a plot was assigned to one of these spectral species with the trained RF classifier. Due to the random nature of clustering approaches, we repeated this process 20 times for each dataset and averaged the number of spectral species, i.e., spectral species richness. To consider only vegetated pixels, pixels with NDVI values < 0.4 , which were assumed to represent bare soil, were excluded from the UAV and fused imagery analysis for all three spectral diversity metrics. After excluding bare soil, we took a random subsample of 1000 pixels from the centre of each plot to avoid edge effects when calculating the metrics for the UAV and fused datasets.

Table 3.2: Description of the three different spectral diversity metrics used in this study.

Spectral diversity metric	Description	Reference
Convex hull volume (CHV)	CHV calculates the volume of pixels forming a convex hull, using the first three principal components of the reflectance data.	Dahlin (2016)
Coefficient of variation (CV)	CV calculates the ratio between the standard deviation and the mean of the reflectance value at a specific wavelength, averaged over all wavelengths.	Wang et al. (2018a)
Spectral species richness	Defines the number of spectral species based on clustering of the reflectance signal.	Féret and Asner (2014)

3.3.6 Statistical analysis of spectral diversity and plant species richness

First, we assessed the relationship between spectral diversity (i.e., spectral metrics), and *in-situ* plant species richness for each experimental plot for each fused, UAV and airborne dataset using bivariate Spearman correlations (ρ). In addition, we calculated the root mean square error (RMSE) between spectral species richness and plant species richness for each fused (Appendix 3.8.4) and UAV dataset. To further investigate differences between the datasets in estimating plant species richness, we used an analysis of covariance (ANCOVA). An ANCOVA allows to test for differences in slopes and intercepts between different regression lines. We compared those linear regressions between plant species richness and spectral diversity derived for the different datasets and spectral metrics that showed a significant relationship. Second, we modelled the plot-wise relationship between spectral diversity and possible confounding factors of the spectral diversity-biodiversity relationship using linear models without interactions (package `stats` in R 4.0.2). Each spectral diversity metric derived from the three datasets (i.e., UAV, airborne only CHV and CV, fusion) served as a response variable (i.e., 8 linear models). The response variables were log-transformed to improve normality of the residuals. The explanatory variables were i) total biomass (live plus death), ii) the ratio of dead biomass to total biomass, and iii) the ratio of different life forms (grass, forb, legume) to live biomass. We assessed the independence of the explanatory variables, i.e., multicollinearity, by computing the variance inflation factor (R package `car v3.0-10`). For each model, residuals were inspected visually for their randomness and normal distribution. Note that two plots in block 2 (see Fig. 3.1a) had to be removed from the datasets due to blurred UAV images, resulting in 28 out of 30 experimental plots.

3.4 Results

HySure was found to be the best performing fusion algorithm in terms of standard deviation and entropy (Appendix 3.8.4). It led to the visually most convincing results when inspecting the colour composite images (Fig. 3.3). HySure also showed significant correlations between spectral diversity and plant species richness (Appendix Fig. 3.7), together with one of the lowest RMSE between the number of spectral species and plant species.

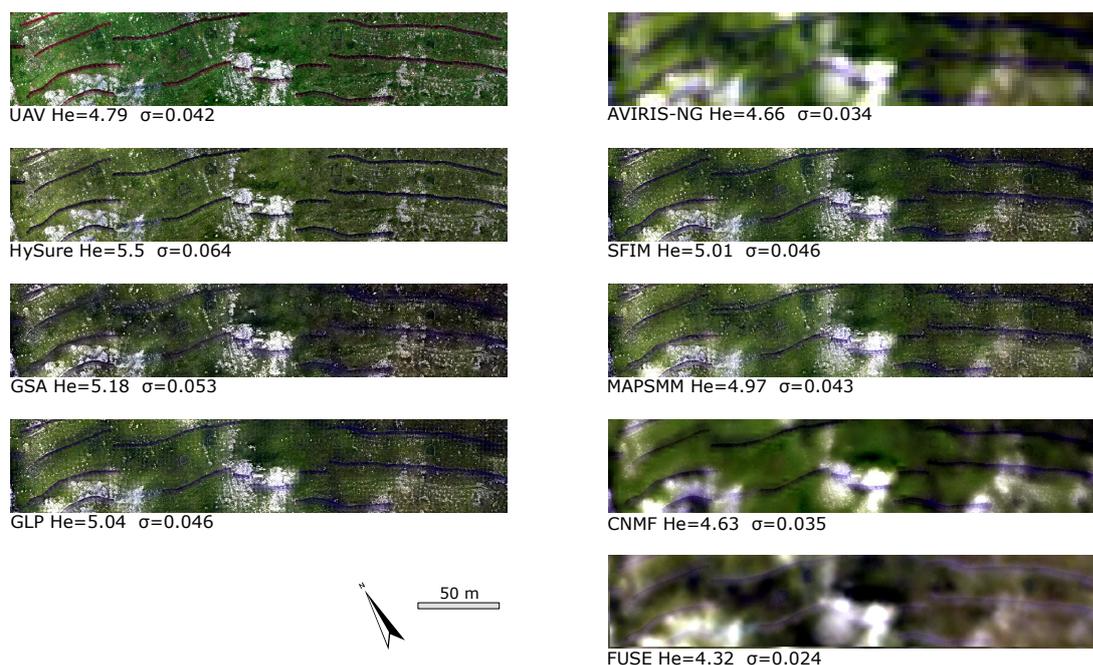


Figure 3.3: True colour composites of the study area acquired by the UAV camera, the AVIRIS-NG sensor, and processed from fused datasets with seven different fusion methods (HySure, GSA, GLP, SFIM, MAP-SSM, CNMF, Fuse). High entropy (He) values indicate rich information content in the image. High standard deviation (σ) indicates high image contrast.

3.4.1 Spectral diversity versus plant species richness

Comparing our three spectral diversity metrics calculated for the different datasets with plant species richness, we found a wide range of relationships. Overall, no correlations ($p > 0.05$) were found for the three metrics when using airborne AVIRIS-NG data, indicating an inappropriate spatial resolution for this dataset (Fig. 3.4). Both UAV and fused datasets did not allow the prediction of plant species richness based

on CHV either (Fig. 3.4a). However, for CV we found a significant negative relationship with plant species richness for both the UAV and fused datasets (Fig. 3.4b). The high values of spectral information content in plots with low species richness suggested that other factors like biomass or intraspecific spectral variability may affect spectral diversity. The spectral species richness derived from the UAV dataset and the fused data product (Appendix Fig. 3.8) showed, in contrast, significant positive relationships with plant species richness (Fig. 3.4c). Using the fused product instead of the UAV dataset, the relationship between spectral species richness and plant species richness improved in terms of ρ , and the number of spectral species was closer to the number of observed plant species (RMSE=8.47 against 12.37, Fig. 3.4c). The result of the ANCOVA, however, suggested that the slopes of the regressions between both CV or spectral species richness and plant species richness did not differ between the UAV and the fused dataset ($F_{1,52}=0.40/0.57$, $p=0.53/0.45$, CV/spectral species richness). Similarly, the intercepts did not statistically differ between the two approaches ($F_{1,53}=1.14/3.676$, $p=0.29/0.065$).

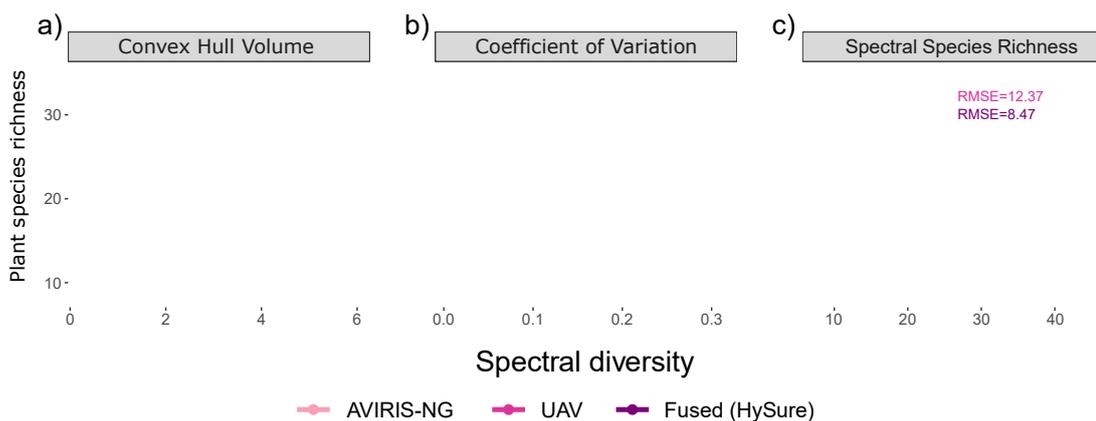


Figure 3.4: Spectral diversity metrics (a,b,c) derived from AVIRIS-NG, UAV and the HySure fused dataset versus *in-situ* plant species richness. ρ = Spearman correlation. Linear regression lines were plotted only for significant relationships ($p < 0.05$).

3.4.2 Confounding effects of the spectral-biodiversity relationship

To study confounding effects of the spectral-biodiversity relationship, we used linear models to examine the relationship between spectral diversity and i) total biomass, ii) the ratio of dead to total biomass, and iii) the ratio of life forms (i.e., graminoids, forbs and legumes) to live biomass. In these models, the explanatory variables, represented

by the different biomass metrics, were independent (i.e., no multicollinearity, variance inflation factor less than 3.5). As for the previous analysis, we found no significant relationship between the spectral diversity and biomass metrics when using airborne AVIRIS-NG data (Appendix Table 3.4). The relationships between spectral diversity and biomass metrics were, in contrast, significant and very similar for the UAV and the fused dataset (Appendix Table 3.4). We therefore show the results for the fused dataset only (Fig. 3.5): Total biomass was found to have a significant positive relationship with CV (slope = 0.001, CI(0, 0.002)) and seemed to be the most confounding factor of the spectral diversity-biodiversity relationship. This result may be explained by a significant negative correlation between total biomass and species richness in the study area ($\rho = -0.40$, $p=0.035$), where nutrient additions lead to more biomass but a decrease in species richness. Furthermore, plots with high total biomass displayed a high percentage of accumulated dead biomass ($\rho = 0.73$, $p<0.001$). However, we found a negative relationship between CV and dead:total biomass (slope = -1.42, CI(-2.56,-0.283)). These results suggest that dead biomass played a crucial role in shaping the spectral information content only in the presence of low to intermediate total biomass. Therefore, there must be other factors influencing the spectral information content in high biomass plots. Contrary to the findings obtained for CV, we found no significant relationship between CHV and any of our biomass metrics. The main reason might be that the CHV metric is highly susceptible to extreme values, which do not reflect the overall characteristics of a community. We found a negative relationship between spectral species richness and the ratio of graminoids to live biomass (slope = -1.04, CI(-1.68,-0.41)). Most plots with a high percentage of graminoids, mainly *Festuca rubra*, displayed low plant species richness due to the individual plants growing in clumps occupying a relatively large area. Similarly, the ratio of legumes to live biomass displayed a negative relationship with spectral species richness (slope=-3.62, CI(-5.90,-1.34)). In plots with high nutrient addition, legumes were suppressed, promoting the dominance of graminoids and a reduced plant species richness.

3.5 Discussion

The results obtained from UAV or fusing UAV data with airborne imaging spectroscopy data proved to be useful for quantifying plant species richness. In addition, we showed that a fused dataset can cope with the requirement of both high spatial and spectral resolution to remotely measure biodiversity (Wang et al., 2018a), a prerequisite, which is still challenging to obtain from a single sensor. Nevertheless, the results of

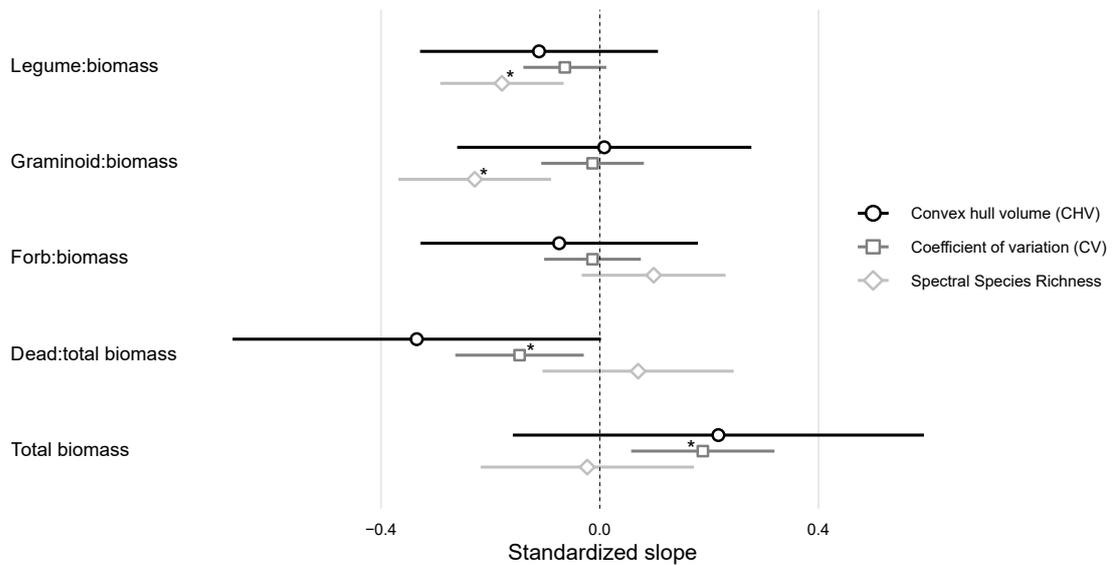


Figure 3.5: Standardised slope with 95% confidence intervals of the linear regression models between the three spectral metrics convex hull volume (CHV), coefficient of variation (CV) and spectral species richness and total biomass, the ratio of dead biomass to the total biomass and life forms (i.e., graminoids, forbs and legumes) to live biomass. Spectral metrics are calculated from the best fused product, i.e., obtained from UAV and airborne data applying the HySure fusion method. * Significant relationships.

this study confirm that remote sensing of plant species diversity remains challenging and that spatial resolution, choice of appropriate spectral metrics, and awareness of confounding factors – which might be ecosystem specific– are essential when leveraging the spectral diversity-biodiversity relationship in species-rich grassland ecosystems.

3.5.1 Trade-off between spectral and spatial resolution

Due to technical constraints, a trade-off between spatial and spectral resolution determines sensor design. Our results underpin the overwhelming importance of the spatial resolution in estimating plant species richness in grasslands. Grassland plants are relatively small compared to the grain size of remotely sensed data, decreasing our ability to quantify diversity. As previous studies in experimental settings demonstrated, a decreasing spatial resolution weakened the spectral diversity-biodiversity relationship (Gholizadeh et al., 2019; Wang et al., 2018a). At coarse spatial resolution, such as in our airborne data where the number of pixels per plot or community was

limited, it becomes difficult to establish any relationship between spectral and plant diversity. In addition, the difference in size and life forms between plant species in grasslands presents a challenge. The optimal spatial resolution may be very specific for a species and is often unknown *a priori*. Even with spatial resolutions of less than one centimetre, the detection of individual plants may only be possible under favourable conditions such as low structural complexity, low spatial overlap, and a low number of species (Lopatin et al., 2017). Very high spatial resolution may, on the other hand, enhance within-species variation and increase noise, i.e., mutual shading, making it difficult to establish a significant spectral diversity-biodiversity relationship. While the choice of spatial resolution is key to establishing a significant spectral diversity-biodiversity relationship, the same cannot be said for spectral resolution in our study. Although spectral resolution is known to affect the spectral diversity-biodiversity relationship (Rocchini, 2007; Wang et al., 2018b), it could not replace a high spatial resolution and was weaker than expected from other studies (Ollinger, 2011; Ustin and Gamon, 2010). We are aware that our fused product cannot replace an imaging spectrometer with high spatial resolution since it is synthetic. Nevertheless, our findings partly correspond with findings in other studies: Gholizadeh et al. (2019) showed, for example, that the standard deviation of NDVI performs well among other spectral diversity metrics. Wang et al. (2018b) found no additional benefit of using full-range spectrometer data in quantifying plant diversity. Spatial resolution was the limiting factor in both studies. We suggest two major reasons for the subordinate importance of high spectral resolution in comparison to high spatial resolution:

- 1) The combined effect of correlated bands and how spectral metrics condense the spectral information make the full information highly redundant and biased towards some spectral features (Rocchini, 2007). A bias is generated because the numbers of bands that capture different spectral features are not equal and some bands provide more information than others. For instance, if several bands capture the same spectral feature, i.e., if they are correlated, the contribution of this feature to the spectral diversity will be misleadingly high. In contrast, the contribution of single bands that capture a distinct spectral feature will contribute insufficiently to spectral diversity. Using principal component analysis (PCA) to reduce data dimensionality may not resolve this issue since the first PCA axes will reflect the set of the most correlated bands among those with a greater contribution. Some specific spectral bands capture the relevant species information that is necessary to successfully apply the spectral variation hypothesis. For example, Schweiger et al. (2018) showed that only the local maxima of the coefficient of variation that correspond to known absorption features of plant pigments, water content, and carbon-based leaf constituents were required to estim-

ate plant diversity. Nevertheless, the choice of spectral features to best represent plant species richness remains an issue of future research. In particular, different spectral regions display contrasting responses to plant species richness. Möckel et al. (2016), for example, reported positive correlations between reflectance and plant diversity for chlorophyll absorption bands, and a negative one for the NIR region of the electromagnetic spectrum.

2) The spectral diversity approach does not decouple leaf- from canopy- effects. The measured reflectance may include canopy structure as well as different leaf traits and their interactions. Canopy structure, rather than leaf traits, may thus drive the majority of the reflectance signal (Kattenborn et al., 2019b; Yao et al., 2015). Grassland canopy variables, such as total biomass, are highly related to the VIS and NIR region of the electromagnetic spectrum (Tucker, 1977). Thus, the reflectance of a few bands in the VIS and NIR region of the spectrum may capture most of the remotely sensed variance between plants. In general, the spectral diversity-biodiversity relationship studied at leaf level (Frye et al., 2021; Schweiger et al., 2018) cannot be easily upscaled to the plant or community level. Thus, it is crucial to understand the effect of canopy structure on spectral diversity and its impact on the relationship between spectral diversity and plant species richness. In this light, it is surprising that spectral metrics from UAV data are rarely used (Conti et al., 2021; Villoslada et al., 2020), despite increasing data availability, high spatial resolution and the potential of the on-board sensors to quantify the VIS and NIR part of the spectrum. Despite the relatively small areas covered, UAVs are very beneficial for studying the spectral diversity-biodiversity relationship and assessing the capabilities of other platforms. Moreover, the results of this study encourage the use of UAVs for operationally estimating plot-scale plant diversity. As such, our study can be considered a valuable contribution to monitoring and conservation/protection efforts at small to medium spatial scales. Taking into account that commercially available spaceborne data at 30 cm spatial resolution already exist today (e.g., WorldView-3) and an increasing amount of commercial companies have started to operate in the sector of readily available, very high spatial resolution multispectral datasets, it is likely that operational monitoring of biodiversity should also be possible at larger scales. However, it remains to be investigated what the impact of a reduction of spatial resolution from 10 cm (UAV data in this study) to e.g., 30 cm would be on the performance of our proposed method to monitor grassland biodiversity.

3.5.2 Selection of the spectral diversity metrics

Our results also suggest that selecting appropriate spectral metrics plays an important role in quantifying plant species richness and may not be compensated by using additional spectral information. A successful spectral metric reflects species richness rather than extreme values in the spectral data, that originate from different sources, which do not reflect the overall characteristics of the community. These extreme values may represent spectral noise, bare ground reflectance (Gholizadeh et al., 2018), illumination geometry (Weyermann et al., 2013) or dead biomass. Metrics that are heavily influenced by extreme values, i.e., CHV and CV should therefore be used with care (Gholizadeh et al., 2018). In our case, the presence of dead biomass and its spectral contrast to live biomass (Beerli et al., 2007; Numata et al., 2007; Schweiger et al., 2015a) was partially responsible for the high spectral diversity calculated by the CHV and CV metrics. Removing the spectral signal for dead biomass from the data would theoretically be possible by using spectral unmixing techniques. However, this requires an additional processing step. It might be easier to tackle this problem by instead using metrics such as spectral species richness which are less sensitive to extreme values (Rocchini et al., 2016). Such a classification-based approach can be less sensitive to pixels corresponding to dead biomass. In particular, dead biomass may be classified as a distinct spectral species, which minimises its effect upon spectral diversity. Yet, this metric is only suitable if the spectral differences between plant species are large enough to identify single species (Wang et al., 2018b) or at least different plant life forms (Polley et al., 2019; Schweiger et al., 2017). The good performance of the spectral species richness metric in our study is in line with similar plant life form or plant community type classifications used in previous studies with UAV data (Fraser et al., 2016; Kattenborn et al., 2019a; Lu and He, 2018; Villoslada et al., 2020). The better performance of the spectral species richness metric has also been found in large-scale satellite applications (Schmidtlein and Fassnacht, 2017). In addition to the selection of the spectral metric, also the way in which plant diversity was measured may affect the spectral-biodiversity relationship. We used the number of plant species (richness) as a measure of plant diversity. However, Wang et al. (2018b) found an improved relationship between spectral diversity and plant diversity in experimental grasslands when adding species evenness to species richness. In particular, species evenness combined with species traits may better represent the complexity of the canopy structure (Rossi et al., 2020), which can drive spectral diversity. Overall, to maximise the spectral diversity-biodiversity relationship, we suggest testing and comparing various plant diversity indices that incorporate both

the relative abundances of species and a measure of differences (e.g., in traits or phylogeny) between them.

3.5.3 Confounding effects of biomass in the spectral diversity-biodiversity relationship

In contrast to the studies of Gholizadeh et al. (2018, 2019), Schweiger et al. (2018) and, Wang et al. (2018a,b) spectral information (i.e., spectral complexity) was negatively correlated with plant diversity in our study, independent of the number of spectral bands considered. We hypothesise that plant biomass was the strongest confounding factor since increasing biomass is assumed to cause higher canopy structure complexity and consequently higher spectral complexity. Our hypothesis partly reflects the spectral diversity-biodiversity relationship found by Villoslada et al. (2020), which turned negative in communities with high plant biomass. In our grassland ecosystems, fertilised plots produced high amounts of plant biomass, which in turn led to a steep decrease in plant species richness (Borer et al., 2014b). In contrast, in the grasslands artificially composed of a limited species pool studied by Gholizadeh et al. (2018, 2019), Schweiger et al. (2018) and, Wang et al. (2018a,b), plant biomass was positively correlated with species richness (Wang et al., 2016). Overall, a positive relationship between biomass and plant species richness relationship from experimental grassland (Tilman et al., 1996), does not hold for naturally assembled or fertilised grasslands (Borer et al., 2014b; Fraser et al., 2015) with major consequences for deriving plant species richness from spectral diversity.

A first possible explanation for the positive spectral diversity-biomass relationship in high biomass communities is the presence of large amounts of dead biomass (Gavazov, 2010). However, the spectral response of dead biomass is relatively homogeneous. Therefore, in communities where dead biomass is more abundant than live biomass, the homogeneity of dead biomass could lead to a decrease in the spectral information content. High biomass can also lead to high canopy complexity and a diverse spectral response (Zhang et al., 2015), for example due to shadowing. Hence, in high biomass plots with only a few plant species, these few species may cause heterogeneous patterns of light extinction and scattering of radiant flux as described by canopy reflectance models (Verhoef, 1985), which can lead to high spectral information despite low plant species richness. Similarly, varying observation geometries between the sun, target pixel and sensor, the so-called bidirectional reflectance distribution func-

tion (BRDF), can heavily affect the measured spectral information (Müller et al., 1998; Schaepman-Strub et al., 2006), which can result in a few species causing high spectral diversity. We tried to reduce BRDF effects by using a high amount of image overlap, which produces near-nadir view geometries (Assmann et al., 2018), but did not further minimise BRDF effects (Li et al., 2012; Vöggtli et al., 2020; Wierzbicki et al., 2018). Yet, we think that it may be valuable to address these issues in future studies. For example, the local illumination and observation geometry for each pixel could be calculated based on the characteristics of the sensor, the solar angle and the local orientation of the canopy (Jia et al., 2020). In particular, canopy orientation information could be obtained from a digital surface model generated through photogrammetry from the UAV imagery. Sensor view zenith and azimuth angles may be calculated using the projection vectors from the camera to each pixel (Tu et al., 2018). Alternatively, a recent study (Arroyo-Mora et al., 2021) showed that BRDF effects of vegetation could be mitigated under diffuse light conditions (i.e., clouds). Obtaining spectral data under different light conditions is possible with UAVs and should therefore be used to further investigate the impact of diffuse light conditions on spectral diversity measurements.

Confounding effects on the spectral diversity-biodiversity relationship not considered in this study are the temporal variability of spectral diversity due to phenology, management and weather conditions (Gholizadeh et al., 2020; Rossi et al., 2021; Schmidtlein and Fassnacht, 2017). Furthermore, bare soil removed from our analysis could also be a good proxy for species richness, either because it indicates sparsely vegetated areas with many unique species or areas with generally low species numbers. Therefore, investigating the spectral diversity-biodiversity relationship at multiple temporal stages and in different ecosystems exhibits a valid direction for future research suitable for UAV applications.

3.6 Conclusions

Spectral diversity-biodiversity relationships depend on the grassland ecosystems studied. The correlation between plant biomass and plant species richness, which can be positive or negative, can confound this relationship. We found that spectral metrics that rely on spectral complexity are much more strongly influenced by the correlation between species richness and plant biomass than classification-based spectral metrics. Classification-based spectral metrics, such as spectral species richness, can mitigate confounding effects and lead to satisfactory results in species-rich grasslands, i.e., a positive correlation between plant species richness and spectral diversity. In addition,

we were able to show that fusion techniques that combine the high spatial resolution of UAV mounted cameras with the high spectral resolution of airborne imaging spectroscopy improved the small-scale estimation of plant species richness in grasslands. Hence, data fusion represents a powerful way to achieve adequate spatial and spectral resolution for quantifying biodiversity using remote sensing techniques. Nevertheless, a high spatial resolution from UAV data proved to be more important than high spectral resolution from airborne imaging spectroscopy. Our results suggest that spatial resolution should be prioritised in future satellite missions aiming to quantify species richness in grasslands. We are aware that obtaining spatial resolutions in which an individual plant corresponds to a pixel will not be feasible. Therefore, investigations to compensate spatial resolution by spectral or even temporal resolution should be a future goal. To our knowledge, no study has simultaneously analysed the trade-offs between the spatial, spectral and temporal dimensions of remote sensing data for quantifying biodiversity to date.

3.7 Acknowledgements

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3.8 Appendix

3.8.1 Appendix S1: Radiometric calibration of UAV data

We employed basic camera radiometric corrections based on image's exposure time, focal ratio, and ISO speed using Pix4D. To obtain reflectance data, the sensor band spectral sensitivity must be known and the images need to be radiometrically calibrated. The sensor band spectral sensitivities used in this study (Appendix Table 3.3) were measured by Holman et al. (2019) for an equivalent camera (i.e., same 24 MP APS-C sensors) by using a double monochromator fitted with an integrating sphere. Pix4D uses the empirical line correction method for radiometric calibration (Holman

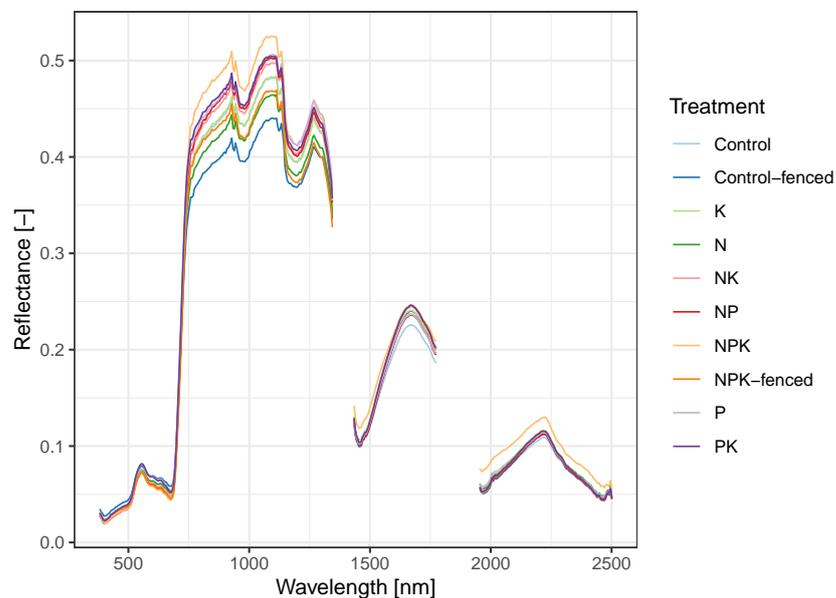
et al., 2019; Iqbal et al., 2018). At-surface reflectance of white calibration targets, visible from the UAV, were recorded after the flight using a spectroradiometer (XHR-1024i, Spectra Vista Corporation) that measures both upwelling and downwelling radiation with a spectral resolution of 1.5 nm covering the 350–2500 nm wavelength range. The measured reflectances were resampled using the full width at half maximum (FWHM) values and spectral sensitivity of the UAV bands assuming a Gaussian distribution (R package `prospectr v.0.1.3` function `resample2`). The UAV datasets and the *in-situ* measured reflectance data from the calibration targets were then used to convert the UAV data to reflectance data using the empirical relationship found between the two datasets.

Table 3.3: UAV camera band sensitivities. Sensitivities were measured by Holman et al. (2019) using a double monochromator fitted with an integrating sphere.

Model	Channel	Wavelength Range (nm)
RGB camera	Red	580-660
	Green	420-610
	Blue	410-540
NIR Camera (modified)	NIR (blue channel)	800-900

3.8.2 Appendix S2: Average AVIRIS-NG spectra

Figure 3.6: Average AVIRIS-NG spectra per treatment. The treatments consist of nutrient addition (Nitrogen N, Phosphate P and Potassium K) applied separately as well as in all possible combinations, fencing, and a control without any experimental treatment.



3.8.3 Appendix S3: Results of linear regression models

Table 3.4: Results of the linear regression models (observations = 28) testing the relationships between three spectral diversity metrics derived from the airborne AVIRIS-NG, UAV and fused dataset versus biomass metrics. CI = 95% confidence interval, R^2 = coefficient of determination representing the proportion of variance explained by the explanatory variables, significant relations in bold.

Explanatory variables	Convex hull volume (CHV)			Coefficient of variation (CV)			Spectral Species Richness		
	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
Airborne (AVIRIS-NG)									
(Intercept)	1.143	-0.614 – 2.900	0.191	-2.629	-3.762 – -1.495	<0.001			
Biomass legumes	-2.85	-9.653 – 3.954	0.394	0.076	-4.314 – 4.466	0.972			
Biomass graminoid	-0.101	-1.993 – 1.790	0.913	-0.563	-1.783 – 0.658	0.349			
Biomass forbs	-1.404	-4.570 – 1.762	0.368	-1.566	-3.609 – 0.477	0.126			
Biomass dead	2.718	-2.328 – 7.764	0.276	2.068	-1.188 – 5.324	0.201			
Total Biomass	-0.002	-0.005 – 0.001	0.213	-0.001	-0.003 – 0.001	0.458			
R^2	0.14			0.21					
UAV									
Explanatory variables	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.322	-0.780 – 1.425	0.55	-1.677	-2.107 – -1.247	<0.001	3.808	3.273 – 4.342	<0.001
Biomass legumes	0.155	-4.113 – 4.423	0.941	-1.335	-3.000 – 0.331	0.111	-1.877	-3.946 – 0.192	0.073
Biomass graminoid	0.654	-0.532 – 1.841	0.265	-0.048	-0.511 – 0.415	0.83	-0.75	-1.325 – -0.175	0.013
Biomass forbs	-0.913	-2.899 – 1.073	0.351	-0.283	-1.058 – 0.492	0.457	0.523	-0.440 – 1.486	0.272
Biomass dead	-3.536	-6.702 – -0.370	0.03	-1.457	-2.693 – -0.222	0.023	0.389	-1.145 – 1.924	0.604
Total Biomass	0.001	-0.001 – 0.003	0.347	0.001	0.000 – 0.001	0.036	0	-0.001 – 0.001	0.917
R^2	0.27			0.4			0.44		
Fused (HySure)									
Explanatory variables	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
(Intercept)	0.347	-0.790 – 1.483	0.533	-1.917	-2.313 – -1.521	<0.001	3.389	2.800 – 3.979	<0.001
Biomass legumes	2.248	-6.650 – 2.153	0.301	-1.293	-2.828 – 0.241	0.094	-3.62	-5.903 – -1.337	0.003
Biomass graminoid	0.037	-1.186 – 1.261	0.95	-0.06	-0.487 – 0.366	0.772	-1.04	-1.675 – -0.406	0.003
Biomass forbs	-0.6	-2.648 – 1.449	0.55	-0.108	-0.822 – 0.606	0.757	0.796	-0.266 – 1.858	0.134
Biomass dead	-3.244	-6.508 – 0.021	0.051	-1.421	-2.560 – -0.283	0.017	0.679	-1.014 – 2.373	0.414
Total Biomass	0.001	-0.001 – 0.003	0.244	0.001	0.000 – 0.002	0.007	0	-0.001 – 0.001	0.809
R^2	0.23			0.48			0.58		

3.8.4 Appendix S4: Data fusion

We tested different state-of-the-art fusion techniques to generate a dataset that reflects the UAV imagery's spatial resolution and the spectral resolution of the AVIRIS-NG imaging spectroscopy dataset. The respective techniques are usually classified into two groups: readapted pan-sharpening-based methods and subspace methods. In general, the pan-sharpening methods mainly comprise component substitution (Aiazzi et al., 2007; Chen et al., 2014) and multiresolution analysis (Aiazzi et al., 2006; Liu, 2000). Subspace methods exploit the spectral characteristics of the scene via a subspace, represented by a set of base vectors or spectral signatures (i.e., spectral endmembers; Eismann and Hardie, 2004; Simoes et al., 2015; Wei et al., 2016; Yokoya et al., 2011). The fused product is reconstructed by combining endmembers of imaging spectroscopy data with corresponding abundances in the multispectral data set. To identify

a well-performing fusion algorithm with our data sets, we compared seven different state-of-the-art fusion techniques. The first group of fusion techniques employed, i.e., Generalized Laplacian Pyramid (GLP), Smoothing filter-based intensity modulation (SFIM), and Gram Schmidt adaptive algorithm (GSA), belongs to the category of pan-sharpening methods (Meng et al., 2019). They employ component substitution or multiresolution analysis to solve the data fusion task. Here, instead of using the geometrical details of one panchromatic band, the methods are adapted to use the details from multiple bands (i.e., from four bands; Selva et al., 2015). For the GLP and the SFIM methods, each AVIRIS-NG band was reconstructed using least square linear regression with the UAV bands. GSA solves multiple pan-sharpening problems at a time after grouping the AVIRIS-NG bands with respect to one UAV band based on correlation analysis. The fusion techniques of the second group belong to the subspace methods. These methods solve the fusion problem by estimating spectral information of a subspace (e.g., principal components or spectral endmembers) and formulating a cost function that optimises the estimated high spectral and spatial data relative to the input images. They include Bayesian methods like maximum-a-posteriori estimation with a stochastic mixing model (MAP-SMM) and fast fusion based on solving a Sylvester equation (FUSE), which use a-priori reflectance distribution information in the scene to solve the fusion task (Wei et al., 2016). Subspace methods that use a set of inherent spectral characteristics, (i.e., endmembers) of a scene, like the coupled nonnegative matrix factorization (CNMF), can be regarded as unmixing-based fusion approaches. A method that combines both spectral unmixing and a Bayesian method is the Hyperspectral Super-resolution (HySure) algorithm (Simoes et al., 2015). In brief, HySure belongs to the subspace methods and combines a convex optimisation problem under a Bayesian framework with spectral unmixing techniques to extract spectral endmembers of a scene for the fusion of two datasets. In linear unmixing approaches, it is assumed that the spectral response of each pixel is a linear combination of the pure spectral signatures of the underlying endmembers (Clevers and Zurita-Milla, 2008). The goal of the optimisation task in HySure consists in estimating the abundance fractions of the endmembers for every high-resolution pixel. Endmembers are extracted from the AVIRIS-NG dataset and the respective abundances from the UAV imagery. We set the number of endmembers to 30 and used the Vertex Component Analysis algorithm to spectrally unmix our imaging spectroscopy data (Dias and Nascimento, 2006).

Data Fusion results

HySure was found to be the best performing algorithm in terms of standard deviation and entropy for the fusion of UAV 10 cm imagery with the AVIRIS-NG dataset. The HySure fused product led to the visually most convincing results when inspecting colour composite images. The algorithm reproduced all the features visible in the UAV data. In contrary, the SFIM and MAP-SMM datasets displayed block patterns of the size of the AVIRIS-NG spatial resolution. Both methods use information directly obtained from the low-resolution imaging spectroscopy dataset, causing these patterns. The FUSE and CNMF algorithms resulted in blurred images, appearing closer to the original AVIRIS-NG dataset. Some methods seem to suffer from the limited spectral overlap between sensors, which is particularly true for Bayesian methods like the FUSE algorithm. This result is confirmed by the analysis of the information content and contrast of the scene, revealing a degradation of the FUSE resulting imagery compared to the original datasets. In contrary, the majority of the fusion products increased the information content and contrast in the scene compared to the sole UAV and AVIRIS-NG datasets. In particular, HySure and pan-sharpening-based methods adapted for multispectral bands (i.e. GSA, GLP, SFIM) showed competitive results. Furthermore, the fusion methods were compared by their ability to quantify plant species richness through spectral diversity. Spectral species richness derived from the HySure fused product showed the highest positive correlation with plant species richness (Appendix Fig. 3.7). Although there was a clear difference between fusion methods in terms of information content and contrast, there was less difference in quantifying spectral diversity. Despite a significant correlation ($p < 0.05$) between spectral species richness derived from the FUSE and CNMF products and plant species richness (Appendix Fig. 3.7), the low number of detected spectral species (mean over all plots of 4.84 and 5.72, respectively) deviated strongly from the existing number of plant species (RMSE = 18.54 and 17.9). The GSA, GLP, SFIM, MAP-SMM and Hysure methods showed a RMSE between 7.41 and 9.89. Poor results in estimating plant species richness in terms of correlation using the spectral species richness approach were only derived from the GSA product. One reason could be noise in the fused dataset, as it was not adequately denoised during post-processing with the residual principal component transformation (Roger, 1996) used for GSA and GLP, SFIM, MAP-SSM. These four methods do not include implicit denoising in their algorithms. Besides, GSA strongly suffers from a limited spectral overlap of the sensors, as the algorithm takes advantage of the correlation between the multispectral and imaging spectroscopy bands, possibly subject to low or no correlation, to solve the data fusion task. Concerning the other two spec-

tral diversity metrics, i.e., CHV and CV, derived from our investigated fusion methods, none of them showed significant positive correlations with plant species richness. Surprisingly, we found a low to an intermediate negative correlation between spectral diversity calculated with CHV or CV and plant species richness for most fused products.

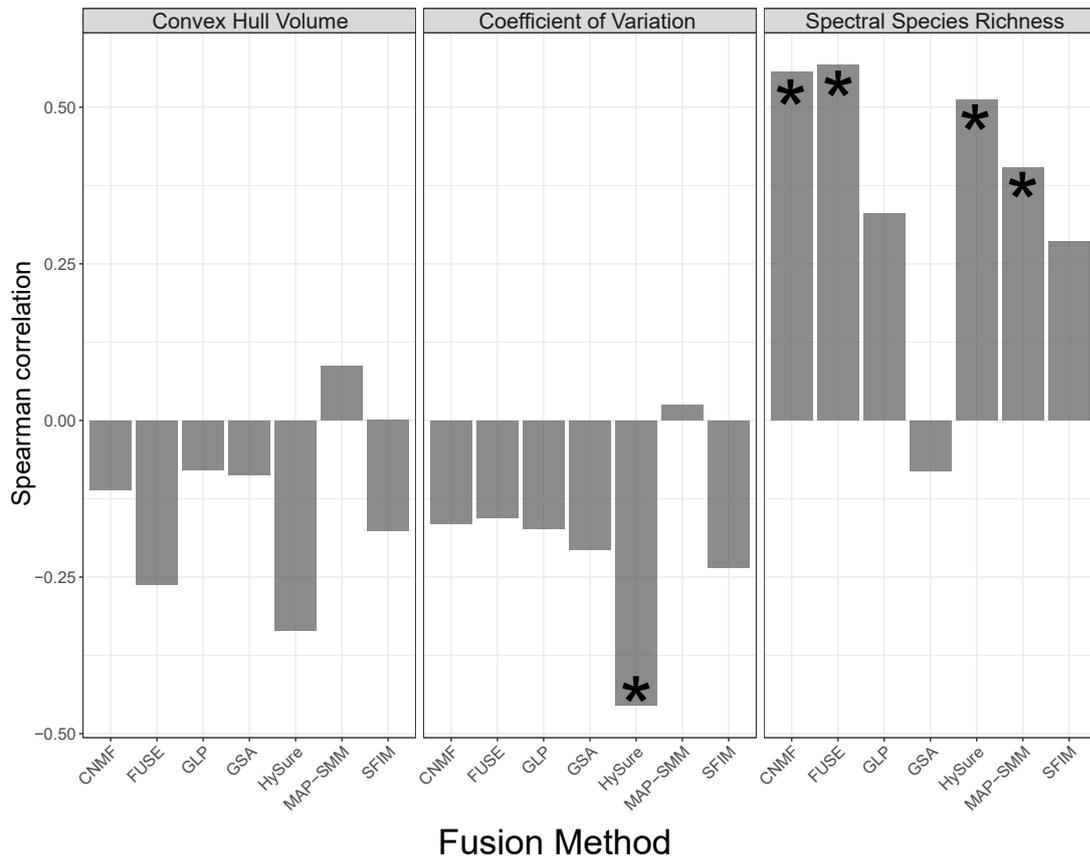


Figure 3.7: Spearman correlation between plant species richness and spectral diversity metrics (coefficient of variation, convex hull volume and spectral species richness) derived from fused data with different fusion techniques. * significant correlation $p < 0.01$

Data fusion discussion

As found in the comparative analysis of data fusion algorithms by Yokoya et al. (2017), our analysis confirmed that HySure was the best performing algorithm. Yokoya et al. (2017) found the method to be the most accurate and consistent in all tests including visual, statistical and classification-based assessments. The outstanding perform-

ances of HySure could be explained by its implicit denoising capacity. The algorithm uses a total variation regularisation process to denoise effectively by preserving edges and smoothing noise in homogenous regions (Simoes et al., 2015). In particular, the regularisation process is used in a vector form, promoting solutions in which edges and other details are aligned among the different bands. This is not the case for non-vector regularisation processes. Therefore, compared to other methods, HySure was able to preserve the spatial features visible in the UAV data. Furthermore, unmixing-based approaches seemed to have a clear advantage in tackling the low spectral overlap between the UAV and AVIRIS-NG datasets. This advantage could arise from the fact that spectral endmembers used in the unmixing-based approaches contain highly correlated spectral bands facilitating the data fusion (Iordache et al., 2011). Our fusion methods comparison was based on visual inspection and spectral information and contrast quantification in the scene. Given the unavailability of a high spatial and spectral resolution reference scene, the quality of the fused dataset was further validated by its performance of quantifying plant species richness through spectral diversity. Validation via quantification of plant species richness is not considered to reflect the overall quality of the data fusion results but was one of the goals of this study. Species richness quantification reflected our results from the visual and spectral information content inspection and was in line with the land cover classification results of Yokoya et al. (2017). Data fusion methods have been employed to improve classification accuracies for a long time (Pohl and Van Genderen, 1998). Methods selection is crucial, as different methods have been developed for specific classification tasks or scenarios. For instance, MAP-SMM fused data resulted in visual block patterns of the pixel size of the airborne AVIRIS-NG data. This method maximises the preservation of spectral information, however, at the expense of spatial features, highlighting the necessity of a less pronounced spatial resolution between fused datasets to avoid such effects.

3.8.5 Appendix S5: Spectral species map

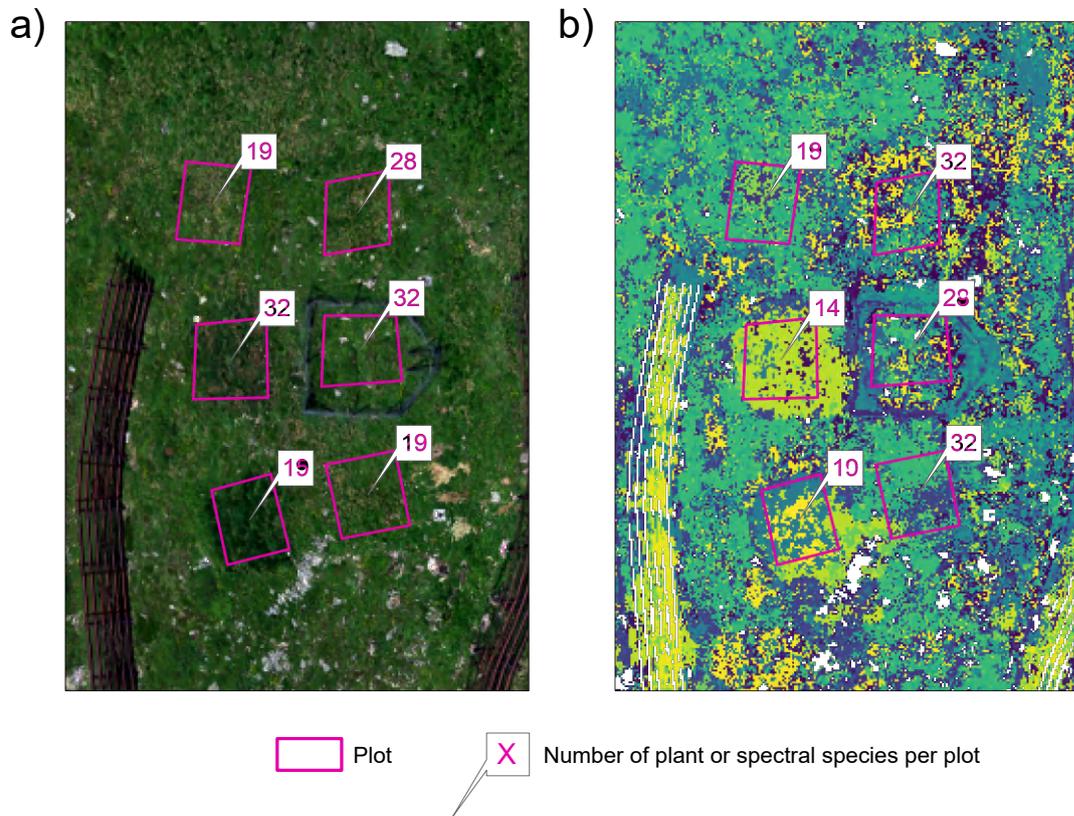


Figure 3.8: a) UAV RGB image displaying six plots in block 3 with the number of plant species per plot. b) Classified spectral species in the same area from the best fused product, i.e., obtained from UAV and airborne data applying the HySure fusion method, and the number of spectral species per plot.

4

Remote sensing of spectral diversity: A new methodological approach to account for spatio-temporal dissimilarities between plant communities

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in the Bibliography chapter.*

Description of author's responsibilities

CR: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Project administration. Mk: Conceptualization, Validation, Writing - review & editing. MS: Conceptualization, Writing - review & editing. MES: Conceptualization, Writing - review & editing, Supervision. RMH: Conceptualization, Funding acquisition. ACR: Conceptualization, Validation, Writing - review & editing, Supervision.

4.1 Abstract

The increasing availability of remote sensing data allows the quantification of biodiversity in space and time. In particular, spectral diversity, defined as the variability of electromagnetic radiation reflected from plants, can be assessed with remote sensing. Plant traits vary diurnally and seasonally due to plant phenology and land management. This results in strong temporal variation of spectral diversity, which cannot be accurately represented by remotely sensed data collected at a single point in time. However, knowledge of how datasets sampled at multiple points in time should best be used to quantify spectral diversity is scarce. To address this issue, we first introduced a new approach using spatio-temporal spectral diversity based on the dissimilarity measure Rao's quadratic entropy index (RaoQ). Thereby, we demonstrated how RaoQ can be used to partition the total spectral diversity of a region (γ SD) into additive alpha (α SD, within communities) and spatio-temporal beta (β SD; between communities) components, allowing the calculation of β SD from community mean spectral features, independent from α SD. Second, we illustrated our methodological approach with a case study in which β SD is calculated from Sentinel-2 satellite data at high temporal resolution for managed grasslands which differ across a large gradient of environmental properties. We were able to show differences in β SD and separate its components into phenological and management effects. Furthermore, the contribution of different plant communities to β SD was assessed, and the results were validated against a dataset of *in-situ* measured β diversity from plant surveys. Compared to spatial dissimilarities from distinct stages of the growing season, using spatio-temporal dissimilarities between communities produced a more accurate estimation of the uniqueness of a community. This study shows how to account for temporal variations in the spectral diversity of plant communities and demonstrates that this improves the estimation of plant biodiversity through remote sensing. Spectral diversity in space and time makes it possible to assess mechanisms that drive biodiversity and identify plant communities relevant for conservation purposes.

4.2 Introduction

The worldwide loss of biodiversity (Barnosky et al., 2011; Ceballos et al., 2017) and the associated decline of ecosystem services call for a comprehensive monitoring of biodiversity (Gossner et al., 2016; Hautier et al., 2009; Newbold et al., 2016). In particular, plant biodiversity affects productivity and stability of an ecosystem, and plays a critical

role in maintaining ecosystem functions (Díaz et al., 2006; Hautier et al., 2014; Tilman et al., 1996, 2006). Yet, measuring plant diversity across large scales in the field requires a high investment of human and financial resources and suffers from biases due to environmental conditions and the person in charge (Jetz et al., 2016; Löhmus et al., 2018). Seasonality of plants, observer experience and perceptions, as well as physical exhaustion in challenging working environments, are possible reasons for biases in botanical surveys (Burg et al., 2015; Rich and Woodruff, 1992).

New methods of assessing plant diversity via spectral diversity obtained from remote sensing (Wang and Gamon, 2019) can provide a straightforward large-scale continuous estimation of biodiversity at relatively high spatial and temporal resolution (Cawse-Nicholson et al., 2021; Pettorelli et al., 2018). The variability in spectral reflectance from plant communities found in spectral data, known as the spectral diversity, is an expression of plant taxonomic, phylogenetic and functional diversity (Cavender-Bares et al., 2017; Gholizadeh et al., 2019; Ma et al., 2019; Oldeland et al., 2010; Rocchini et al., 2010, 2018a; Schweiger et al., 2018; Ustin and Gamon, 2010; Wang et al., 2018b). Spectral diversity can be calculated from different spectral features such as the spectral reflectance at a certain wavelength, a combination of several wavelengths (Gholizadeh et al., 2019; Ma et al., 2019; Rocchini et al., 2004), vegetation indices (Rocchini et al., 2018b) or optical traits (Homolová et al., 2013; Ollinger, 2011; Rossi et al., 2020; Ustin et al., 2009). Thereby, the spatial resolution of the reflectance data (i.e., the pixel size) is a critical factor influencing the level of ecological organization (i.e., species, communities, ecosystems) that can be captured. Whittaker (1960) defined that the total diversity, gamma (γ) diversity, of a region includes two components: alpha (α) diversity (within community diversity), and beta (β) diversity (between community diversity). Partitioning plant diversity into α and β diversity provides deeper insights into plant community assembly processes that generate and maintain plant biodiversity in ecosystems (Münkemüller et al., 2012). To quantify α diversity based on remote sensing data, the spatial resolution (pixel size) of these data needs to be equal to or smaller than the average size of a plant growing in that community (Hakkenberg et al., 2018). As a coarse pixel represents the spectral signal of multiple plant species, β diversity between plant communities can be quantified (Rocchini et al., 2018b; Rossi et al., 2020). However, spatial diversity and its partitioning into α and β describe only one part of the overall spectral variability of plants. Capturing the temporal variation of spectral data may be more important to distinguish between different plant development stages, functional groups or management types (Huang et al., 2019), which are important for species distribution patterns and their function (Schwinning and Kelly, 2013). For example, spectral data collected over a time-period covering multiple flowering phases

may allow co-occurring plant species to be better differentiated (Nagendra, 2001). Similarly, spectral data with high temporal resolution may capture inter-annual differences in leaf properties (e.g., water content) that result from differences in soil microclimatic properties, phenology or nutrient availability over the course of the growing season (Anderegg, 2015; Chavana-Bryant et al., 2017; Gamon et al., 2019; Gholizadeh et al., 2020; McKown et al., 2013; Meireles et al., 2020; Wong and Gamon, 2015; Yang et al., 2016). The same holds for capturing different ecosystem management states (anthropogenic stressors), such as grazing, mowing or fertilizing (Giménez et al., 2017; Homolová et al., 2014). Therefore, to fully capture spectral diversity and to understand which processes contribute to biodiversity dynamics, both spatial and temporal spectral variation need to be accounted for.

So far, indices to quantify spectral diversity have been used exclusively to capture spatial variation in reflectance data (Dahlin, 2016; Rocchini et al., 2010, 2017; Wang et al., 2018b) and have mostly not considered the level of ecological organization (i.e., species, communities, ecosystems). Only recently, Laliberté et al. (2020) proposed an index that allows the partitioning of the total spectral variation of a region into independent within (α) and between (β) community diversity, and Rocchini et al. (2019) proposed a method to quantify the change of spectral diversity in space over time. Lopes et al. (2017) tried unsuccessfully to use spatio-temporal spectral diversity to quantify α diversity based on coarse spatial resolution data. To our knowledge, no study so far has assessed taxonomic diversity through spatio-temporal dissimilarities in spectral features between communities and quantified the importance of spectral variation over both space and time. In addition, none of the commonly used spectral diversity indices have been implemented in a way that allows spectral diversity to be partitioned into temporal and spatial components.

In order to fill this gap, we developed a new methodological approach and included the spatio-temporal spectral dissimilarity of plant communities when calculating Rao's quadratic entropy index (RaoQ) to obtain total γ spectral diversity of an area (γ SD). Similar to the partitioning proposed by Laliberté et al. (2020), RaoQ was partitioned into space and time. Consequently, it was not only possible to quantify α spectral diversity (α SD) and β spectral diversity (β SD) separately, but also the contributions of space and time, as well as their interaction, to β SD.

We first introduce an implementation of RaoQ that allows spatio-temporal variations to be accounted for when quantifying spectral diversity (i.e., α SD, β SD and γ SD). We then tested our new methodological approach specifically for β SD, based on a case study using Sentinel-2 multispectral and multi-temporal satellite data in grasslands. We (i) calculated β SD for differently managed grasslands and partitioned it into the

contribution of space, time and their interaction, ii) compared how the contribution of a community to β SD over space and the entire growing season differs from the contribution of a community to β SD in space at different stages of the growing season (spatio-temporal versus mono-temporal spectral datasets) and (iii) validated the results using *in-situ* measured β diversity from plant surveys. We used our case-study to highlight the importance of assessing temporal in addition to spatial variations in spectral features when quantifying plant biodiversity.

4.3 Spectral diversity over space and time

Prior to introducing our new methodological approach, the definition of the term “plant community” as used in this study is explained. Here, a plant community is a group of interacting plant individuals representing multiple species occurring together in a spatially constrained unit (Stroud et al., 2015). The unit equals either; a pixel, an aggregation of pixels of remotely sensed data, or plots in field surveys. This definition is not free of debate and implies artificially bounded units with an overwhelming emphasis on localness (Ricklefs, 2008). However, instead of relying on a few individual pixels/plots covering the region of interest, remote sensing makes it possible to have the full region covered continuously by equally sized pixels/plots. Hence, the geographical area of interest can be divided into communities of a specific size and shape (e.g., pixel or an aggregation of pixels) depending on the spatial resolution of the remote sensing data and the ecosystem considered (Fig. 4.1). The extent of a community remains an artificial unit, but our approach allows us to vary the size of communities, which provides insights into scale dependencies of within and between community diversity (Gering and Crist, 2002; Laliberté et al., 2020). We assume the region of interest contains S plants spread over P communities recorded at D dates, and that each community includes the same number of plant individuals S_p ($S_p = S/P$).

4.3.1 Using Rao’s quadratic entropy to calculate spectral diversity in space

Our new methodological approach is based on RaoQ, which is an index frequently used to estimate spectral diversity as it is sensitive to the number of pixels and their pairwise spectral differences (Khare et al., 2019; Rocchini et al., 2017, 2018a,b; Torresani et al., 2019). Here, we use RaoQ to calculate γ SD (Rao, 1982; Ricotta and Marignani,

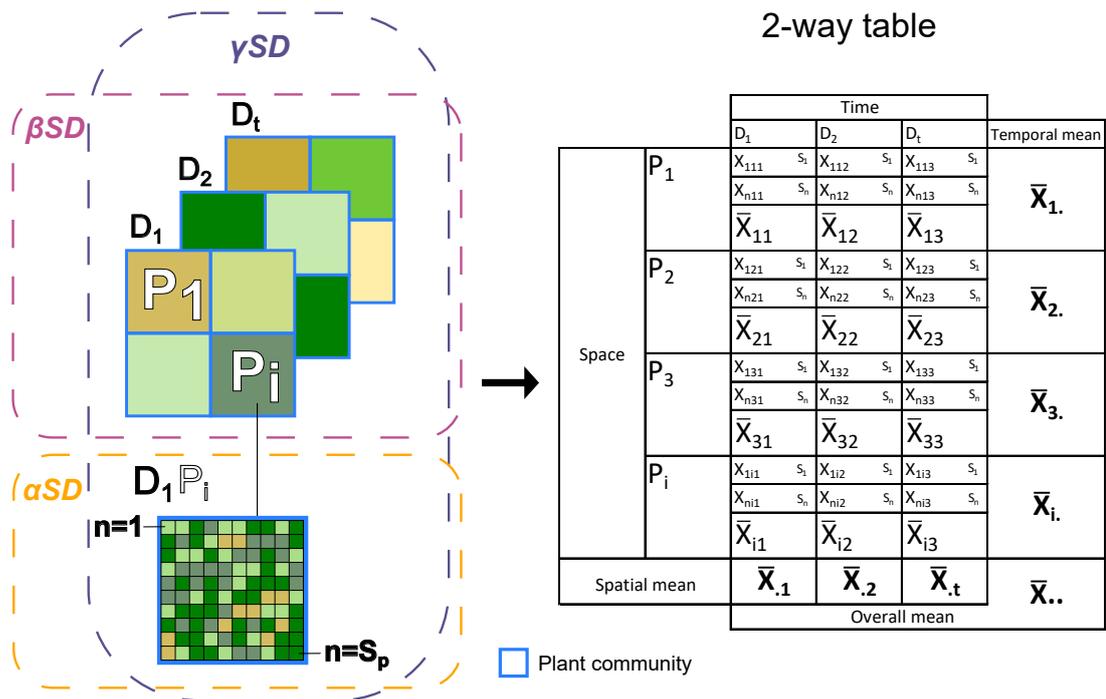


Figure 4.1: Each pixel or aggregation of pixels represents a plant community P_i with a community mean (\bar{X}_{it}) of a variable X (e.g., vegetation index, the reflectance at a certain wavelength or trait). In an ecosystem where an individual plant n matches or is larger than the pixel size (e.g., forests with a data resolution of a couple of meters), communities consist of an aggregation of S_p plant individuals and the community mean of X is calculated from the individual values (X_{nit}). Otherwise, when the pixel size matches the community size (e.g., grasslands with a data resolution of several meters), \bar{X}_{it} is directly derived from remotely sensed values. In this case, only βSD can be derived. Adding temporal information from multiple datasets D in time results in a 2-way design with two explanatory variables (i.e., space and time), each consisting of different categories (i.e., communities and datasets, respectively), that can be studied with a two-way ANOVA, in conjunction with the response variable X .

2007), which equals the total spectral dissimilarity between all plants in the region of interest. We can then calculate γSD at a specific time t (γSD_t) in the region of interest. Thereby we i) assume that the dissimilarity between plants is calculated from the mean dissimilarity of spectral features (e.g., reflectance of specific band or standardized vegetation indices, Botta-Dukát, 2005), ii) use Euclidean distance between spectral features to calculate dissimilarity, and iii) assume that all communities and/or plants are equally important. These assumptions and the fact that the average of the squared pairwise differences of a random variable equals twice the variance of that variable

(Champely and Chessel, 2002) reduces RaoQ to a spectral variance calculation between plant individuals (equation 4.1, Appendix 4.9.1 for a proof):

$$\gamma SD_t = \frac{1}{NS} \sum_{k=1}^N \sum_{n=1}^S (X_{ntk} - \bar{X}_{.tk})^2 \quad (4.1)$$

where S is the number of plants in the area of interest, X_{ntk} is the spectral feature value k of the n th individual at time t , N is the number of spectral features and $\bar{X}_{.tk}$ is the mean value of spectral feature k across all individuals in the area of interest at time t . Apart from division by the number of observations (i.e., number of plants), the proposed index is equal to the spectral variance proposed by Laliberté et al. (2020).

4.3.2 Implementation of spectral diversity in time

So far, only γ spectral diversity in space at a specific time t (i.e., γSD_t) have been considered. Thus, in a next step we calculated γSD by adding the temporal variance of spectral features to equation 4.1, similar to what Chalmandrier et al. (2015) did with a multiplicative framework using Chao's index applied to functional and phylogenetic data. γSD represents the total dissimilarity in spectral information between individuals regardless of their space and time allocation (equation 4.2).

$$\gamma SD = \frac{1}{N D S} \sum_{k=1}^N \sum_{t=1}^D \sum_{n=1}^S (X_{ntk} - \bar{X}_{..k})^2 \quad (4.2)$$

where D is the number of images in time, X_{ntk} is the value of spectral feature k of the n th individual at time t and $\bar{X}_{..k}$ is the mean value of spectral feature k across all individuals and images in time in the region of interest. Furthermore, γSD can be calculated if each single γSD_t is known; the total variance (i.e., γSD) is the pooled variance from mono-temporal datasets (i.e., γSD_t , Rudmin, 2010).

4.3.3 Spatio-temporal components of γSD

Previous studies partitioned γSD , calculated as the sum of squares (SS), into different spatial components, i.e., αSD and βSD , analogous to an ANOVA (Laliberté et al., 2020). We propose calculating γSD as the spectral variance (equation 4.2), which equals the average of the total sum of square (SS_{TOT} divided by the number of observa-

tions). ANOVA partitions SS_{TOT} into one component (β SD) capturing the variability between group means (e.g., communities), and the variability within a group (e.g., a community) into another component (α SD, Pavoine et al., 2005). In general, partitioning the SS_{TOT} allows the allocation of the overall variance of a dataset to different sources of variability in an additive manner (de Bello et al., 2011). Here, for the first time an extension of the SS partition to spectral data with a two-way ANOVA was applied, examining the influence of two different categorical independent variables (factors) on a continuous dependent variable. The factors consist of different categories. The combination of two categories belonging to different factors represents a group (e.g., community i at time t). The SS_{TOT} (equation 4.3) is partitioned into the SS of the two factors SS_T and SS_S , and their interaction (SS_{TS}), as well as the within-group component (SS_W ; Nayak, 1986; Pavoine, 2012). The sum of SS_T , SS_S and SS_{TS} equals the between-group SS (SS_B).

$$SS_{TOT} = SS_W + \overbrace{SS_S + SS_T + SS_{TS}}^{SS_B} \quad (4.3)$$

Here, the two factors of the two-way ANOVA are space and time with different categories, i.e., different plant communities and dates (Fig. 4.1). The SS_{TOT} divided by the number of observations (NDS) equals γ SD, and the categories of the two factors are composed of P communities and D repeated measurements in time (equation 4.4). A group consists of a community with S_p plants at a certain point in time t (equation 4.4):

$$\begin{aligned} \gamma SD &= \frac{1}{NDS} \overbrace{\sum_{k=1}^N \sum_{t=1}^D \sum_{n=1}^S (X_{ntk} - \bar{X}_{..k})^2}^{SS_{TOT}} \\ &= \frac{1}{NDS} \overbrace{\sum_{k=1}^N \sum_{t=1}^D \sum_{i=1}^P \sum_{n=1}^{S_p} (X_{nitk} - \bar{X}_{itk})^2}^{SS_W} \\ &\quad + \frac{1}{NDS} \overbrace{S_p \sum_{k=1}^N \sum_{t=1}^D \sum_{i=1}^P (\bar{X}_{itk} - \bar{X}_{..k})^2}^{SS_B} \end{aligned} \quad (4.4)$$

where X_{nitk} is the value of spectral feature k of the n th individual of the i th community at time t and \bar{X}_{itk} is the mean value of spectral feature k of the i th community

and time t . The within-group component SS_W divided by the number of observations corresponds to the average α SD (equation 4.4), i.e., the mean spectral variance over all communities and timesteps. α SD may be quantified for datasets with high spatial resolution, where a pixel may represent an individual plant. In contrast to a mono-temporal approach, α SD is calculated as an average over multiple temporal datasets, yielding a more robust representation of the community diversity. The between-group component SS_B divided by the number of observations represents β SD (equation 4.4, 4.5). β SD is the variance of between-community mean spectral features over space and time and can be partitioned into the components for space (βSD_S), time (βSD_T) and their interaction (βSD_{TS} ; Fig. 4.2, equation 4.5).

$$\begin{aligned}
\beta SD &= \frac{1}{N D P} \sum_{k=1}^N \sum_{t=1}^D \sum_{i=1}^P (\bar{X}_{itk} - \bar{X}_{..k})^2 \\
&= \underbrace{\frac{1}{NP} \sum_{k=1}^N \sum_{i=1}^P (\bar{X}_{i.k} - \bar{X}_{..k})^2}_{\beta SD_S = SS_S / (NDS)} + \underbrace{\frac{1}{ND} \sum_{k=1}^N \sum_{t=1}^D (\bar{X}_{.tk} - \bar{X}_{..k})^2}_{\beta SD_T = SS_T / (NDS)} \\
&\quad + \underbrace{\frac{1}{NDP} \sum_{k=1}^N \sum_{t=1}^D \sum_{i=1}^P (\bar{X}_{itk} - \bar{X}_{i.k} - \bar{X}_{.tk} + \bar{X}_{..k})^2}_{\beta SD_{TS} = SS_{TS} / (NDS)}
\end{aligned} \tag{4.5}$$

where $\bar{X}_{i.k}$ is the mean value in time of spectral feature k of the i th community and $\bar{X}_{.tk}$ is the mean value in space of spectral feature k of the t th dataset and $S_p/S = 1/P$.

βSD_S quantifies the diversity between communities after averaging their temporal variability. When using a mono-temporal dataset, βSD_S is the only term that is not zero ($\beta SD = \beta SD_S$ for $D = 1$). When using a multi-temporal dataset βSD_T quantifies the change in diversity between mono-temporal datasets, irrespective of the spatial patterns of diversity (i.e., averaging over communities). βSD_{TS} can be used to quantify differences in spectral features between communities, which are not quantified by βSD_S and βSD_T (Fig. 4.3). βSD_{TS} delivers additional information, because βSD_S and βSD_T are averaged out at larger spatial or temporal scales.

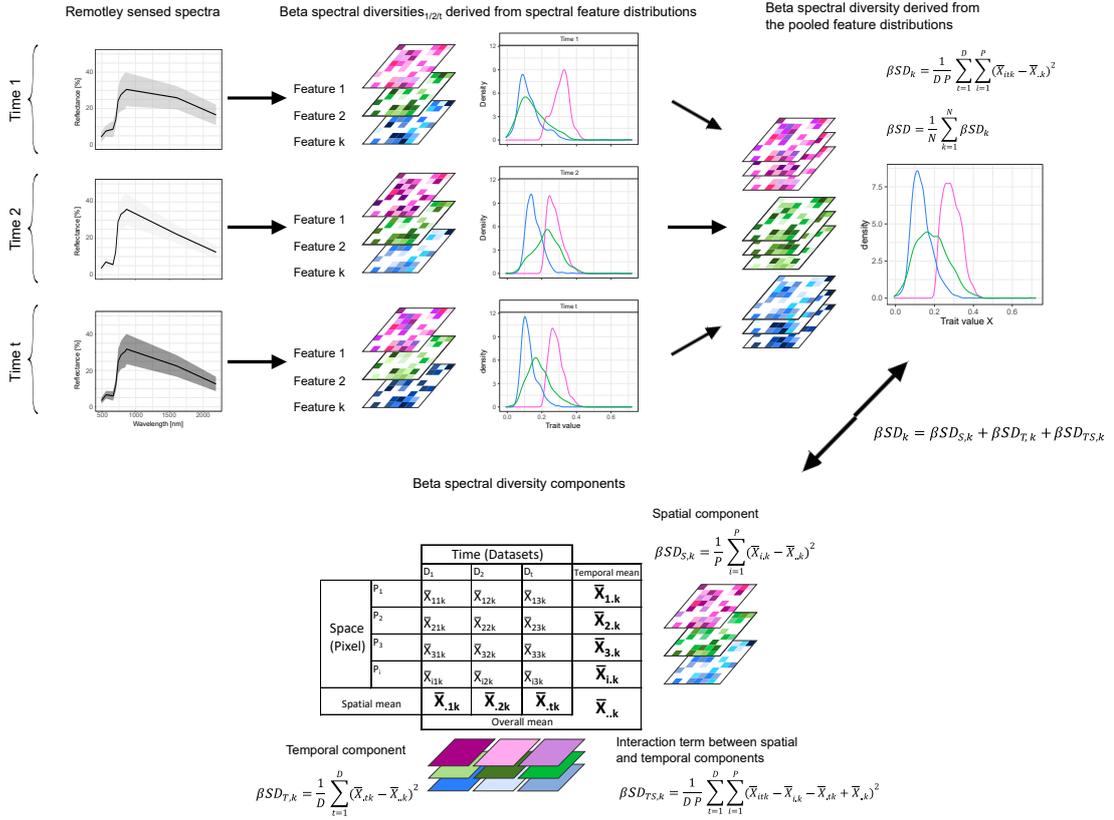


Figure 4.2: Proposed approach for calculating β spectral diversity (βSD) of a region of interest, where a pixel or aggregation of pixels corresponds to a plant community P_i . Community mean spectral features for each dataset in time \bar{X}_{itk} are derived from the measured reflectance spectra. βSD equals the variance of the community spectral features over space and time, which corresponds to the pooled spectral feature variance from the single datasets in time. From the partitioning similar to a two-way ANOVA of γSD (equations 4.4 and 4.5) three components of βSD emerge: βSD_S (spatial), βSD_T (temporal), and βSD_{TS} (interaction term).

To summarize, γSD equals the average of αSD in space and time plus the three components of βSD (equation 4.6).

$$\gamma SD = \overline{\alpha SD} + \overbrace{\beta SD_S + \beta SD_T + \beta SD_{TS}}^{\beta SD} \quad (4.6)$$

To calculate αSD a spectral feature per individual plant (X_{ntk}) is required, while for βSD only the community mean spectral features for each dataset in time \bar{X}_{itk} is needed.

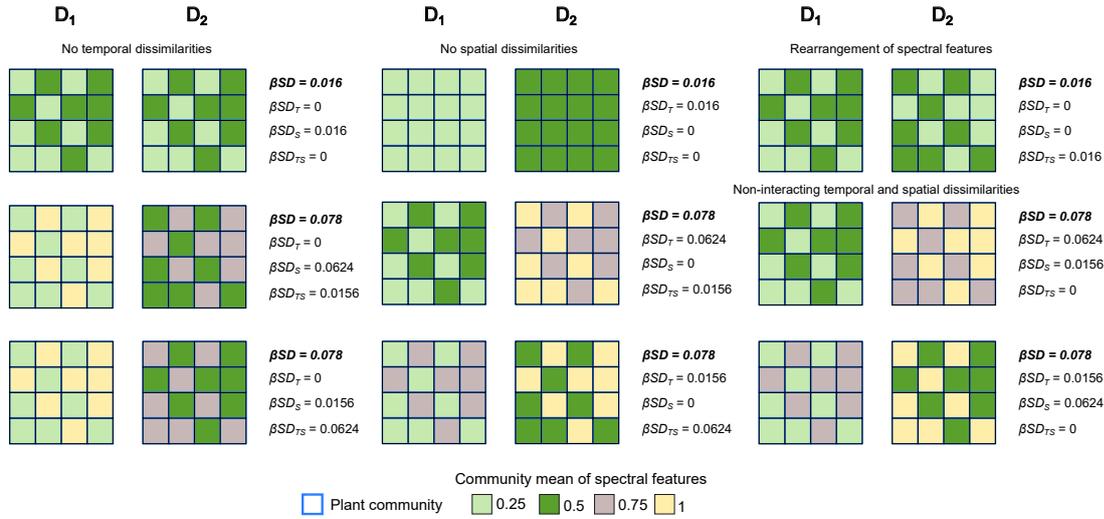


Figure 4.3: Beta spectral diversity (βSD) and its components, i.e., βSD_T (temporal), βSD_S (spatial), and βSD_{TS} (interaction term), calculated for simulated and simplified landscapes, consisting of 16 communities. Each community can display four possible community mean spectral features (0.25, 0.5, 0.75, 1) over two time periods D_1 and D_2 . βSD_{TS} equals zero when no spatial or/and temporal dissimilarities between communities or no-interacting spatial and temporal spectral feature dissimilarities exist. The case where βSD_{TS} equals zero indicates that there is an identical dissimilarity of spectral features across space and time between communities. βSD_{TS} equals βSD (i.e., $\beta SD_S = \beta SD_T = 0$) when there is a rearrangement of spectral features between communities in time. It is possible to have a situation where βSD_S or βSD_T is zero, while βSD_{TS} is not zero. This is the case when there is a spatial or temporal dissimilarity between communities; however, if averaged respectively over time or space, the spectral feature dissimilarities are zero.

4.4 Calculating βSD from spatio-temporal Sentinel-2 satellite data: a case study

To demonstrate how our new methodological approach works and to highlight the advantage of calculating spatio-temporal spectral diversity we conducted a case study using Sentinel-2 satellite data. Sentinel-2 data for an approximately 1300 km² area of south-eastern Switzerland (latitude 46°34' to 46°54'N, longitude 9°58' to 10°25'E, Appendix Fig. 4.6a) were obtained. This area contains several grassland ecosystems under different management regimes (Appendix 4.9.2 and Rossi et al. (2020) for a detailed description of the study area). Detailed data processing procedures for the Sentinel-2 data are provided in Appendix 4.9.3.

A pixel size of 10 x 10 m was used. Hence, based on our earlier definition, a pixel represents a grassland community, and spectral features of a pixel are representative

of the community mean (\bar{X}_{itk}). The coarse spatial resolution of the Sentinel-2 data does not allow a direct quantification of α SD and γ SD in grasslands (see explanation above), thus, we specifically calculated β SD and its components. The two-way ANOVA partitioning requires a balanced design, i.e., the same number of individuals per community. We therefore assumed that each grassland community (i.e., a pixel) contained the same number of individual plants. β SD based on pixel values (\bar{X}_{itk}) was calculated of three spectral features, i.e., three vegetation indices (TGI, MTCI, CAI, Appendix 4.9.3), obtained from ten temporal Sentinel-2 datasets that covered the entire growing season (Table 4.1).

Table 4.1: List of Sentinel-2 datasets used in this study, sorted by growing degree days (GDD). All images or composite products show low cloud cover for the study area (<20%). DOY=day of year (Appendix 4.9.3 for details).

Acquisition date	Sensor	DOY	GDD [°C-days]	Acquisition year
27 May	Sentinel-2A	147	53	2017
16 June	Sentinel-2B	167	195	2018
26 June	Sentinel-2A	177	287	2017
06 July and 03 July	Sentinel-2A	187	343	2017
16 July	Sentinel-2A	197	419	2017
31 July and 26 July	Sentinel-2A and 2B	212	516	2018
15 August	Sentinel-2A	227	646	2017
27 and 20 August	Sentinel-2A	239	736	2018
09 September	Sentinel-2A	252	797	2018
14 October	Sentinel-2A	287	811	2017

4.4.1 β SD and its components for different grassland management types

We calculated β SD and its components, i.e., time, space and their interaction (equation 4.5) for four grassland management types separately; namely, grassland that was 1) mown and fertilized multiple times a year with organic or mineral fertilizer (henceforth referred to as “intensive meadows”), 2) mown with either no fertilization or slightly fertilized (once per year or every two years with organic fertilizer; “extensive meadows”), 3) protected and not managed (Swiss National Park SNP, “protected grassland”), and 4) summer grazing by cattle and/or sheep (“summer pasture”; Appendix Fig. 4.6b). Mowing takes place between mid-June and mid-September in all meadows, but the exact timing depends on the location and type of meadow. Wild

ungulates follow high-quality forage at the upper edge of spring green-up in the protected areas and stay within the SNP borders until the end of the hunting season (beginning of October; Rempfler, 2017). Livestock graze on alpine pastures for roughly three months, from mid-June to mid-September, with spatial constraints established by shepherds moving the animals from one grazing paddock to another. All available grassland pixels (i.e., communities) over the entire study area belonging to one of the four management types and the magnitude, as well as the contribution (in %) of the different spatial and temporal components to β SD of each management type were reported. We assumed that management events (e.g., mowing and grazing) and phenology alter the spectral response of a community (Wellmann et al., 2018). Thus, a particular community composition of plants, which for its part is stable in time, is characterized by multiple spectral responses in time. The differences between spectral responses in space and time are responsible for β SD and most likely reflect the diversity between communities in terms of species composition.

We found that the spatio-temporal β SD, calculated following our proposed approach, varied between management types across the study area (Fig. 4.4). Substantial differences were found in the magnitude and contribution of the different components (in %) to β SD between the management types (Fig. 4.4). Protected grasslands had the highest (59%) spatial component β SD_S, being responsible for an overall high β SD (Fig. 4.4). In contrast, when averaged over time, both extensive and intensive meadows had low spatial variances in spectral features, i.e., lowest β SD_S values. The temporal component β SD_T was highest for extensive meadows and summer pastures (Fig. 4.4). In particular the datasets obtained late (GDD=811) and early (GDD=53) in the growing season differed strongly from the other datasets (Appendix Fig. 4.7) and contributed most to β SD (Appendix 4.9.6). Phenological differences in spectral features increase β SD_T and therefore β SD. In contrary, management events (e.g., mowing) that occur heterogeneously in space and time keep the average spectral features in space almost even over time, reducing β SD_T. In the case of heterogeneous management in space and time, a rearrangement of spectral features occurs (example in Fig. 4.3), increasing β SD_TS. Therefore, it is not a surprise that β SD_T was highest in both meadow types experiencing mowing (Fig. 4.4). In intensive meadows, β SD_T contributed most (63%) to the high β SD value, indicating that communities changed more in spectral features than expected from the averaged temporal trend over the entire study area (β SD_T). This indicates potential for including β SD_T as a spatio-temporal component in the differentiation between communities. Although β SD_T is sensitive to the diversification of management practices, spatio-temporal variations could potentially lead to an overestimation of taxonomic or functional β diversity through β SD in managed

grasslands. The extent to which heterogeneity of management in space and time increases biodiversity is debatable (Socolar et al., 2016). Nevertheless, compared to the highest mono-temporal $\beta SD_{t|D=1}$ ($D=1$ equation 4.1; Appendix 4.9.5), spatio-temporal βSD mitigates the effect of high spectral variance occurring just once per growing season due to an even spatial distribution of mown and unmown meadows. The unmown areas could be mown just a couple of days later. The spectral variance captured at an individual date is therefore most likely not representative of differences between plant communities, since mowing date differences of a few days will not result in a diversified plant community composition. Although spatio-temporal βSD seems to offer a more consistent representation of biodiversity compared to mono-temporal spectral variance ($\beta SD_{t|D=1}$), quantifying the overall value of βSD could be of marginal interest for an ecological application. Quantifying the contribution of individual communities to βSD is, however, of much greater interest. Plant communities can contribute to βSD to varying degrees. Being able to correctly identify unique communities in an ecosystem is of great value for nature conservation. Using our new methodological approach, spatial-temporal dissimilarities between communities can increase (e.g., unique spectral values in time and space) or decrease (e.g., similar spectral values in time and space) the contribution of a community to βSD . The following considerations seek to demonstrate that our proposed spatio-temporal approach to calculate βSD improved the estimation of the community contributions to taxonomic β diversity.

4.4.2 Community contributions to βSD : Comparing mono-temporal to the proposed spatio-temporal approach

A main advantage of the proposed methodological approach is its ability to assign the overall βSD to different sources of variability, e.g., the three components space, time and their interaction. Furthermore, βSD may be partitioned into the contributions of specific communities as done by Laliberté et al. (2020) for a single dataset in time, which we here refer to as the community contribution to βSD of the i th community at time t ($CC\beta SD_{i,t|D=1}$). We compared community contribution to βSD calculated with our spatio-temporal approach, i.e., the contribution in space and time of the i th community ($CC\beta D_i$, equation 4.7), to a reference contribution to β diversity measured from *in-situ* plant surveys. Similarly, community contribution to βSD at a specific and thus different stage of the growing season (i.e., from a mono-temporal dataset, equation 4.7

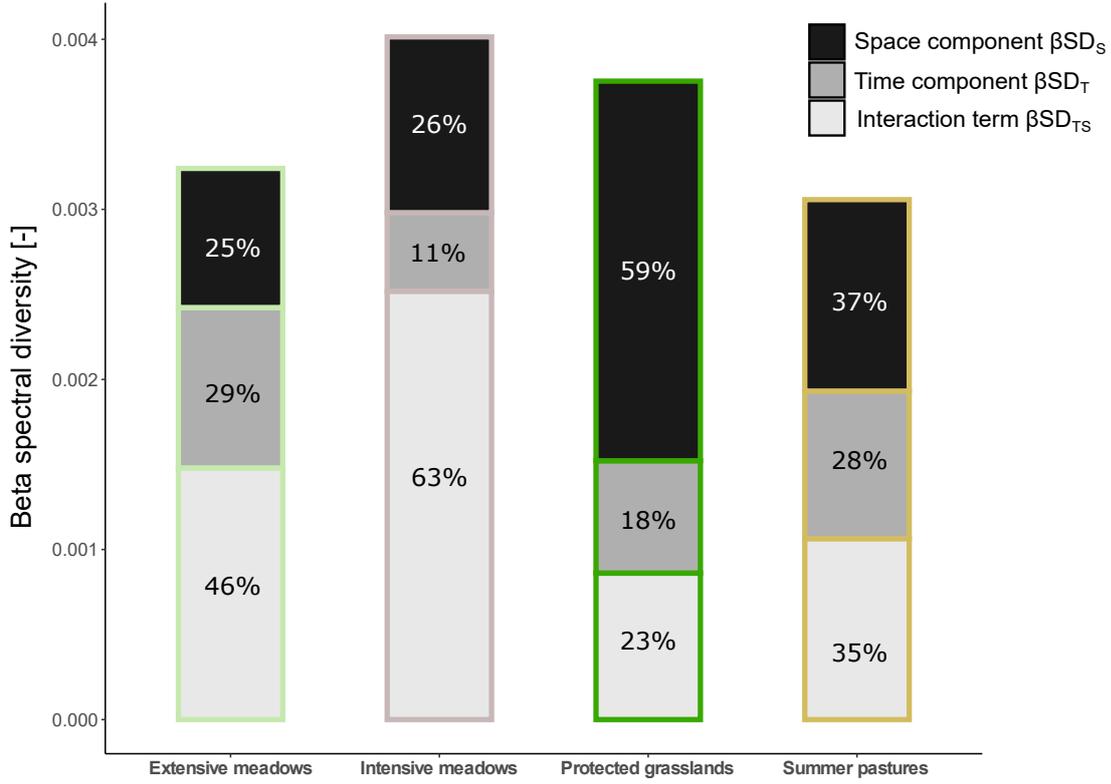


Figure 4.4: Barplots representing β spectral diversity (βSD) divided by components (equation 4.5) in different grassland management types (i.e., extensively used meadows, intensively used meadows, protected grasslands, summer pastures). The contributions percentage of space, time and their interaction to βSD spectral diversity are reported.

with $D=1$ and $\beta SD = \beta SD_{t|D=1}$) was compared with the *in-situ* reference. In doing so, only spatial dissimilarities between communities were considered.

$$CC\beta SD_i = \frac{1}{\beta SD N D P} \sum_{k=1}^N \sum_{t=1}^D (\bar{X}_{itk} - \bar{X}_{..k})^2 \quad (4.7)$$

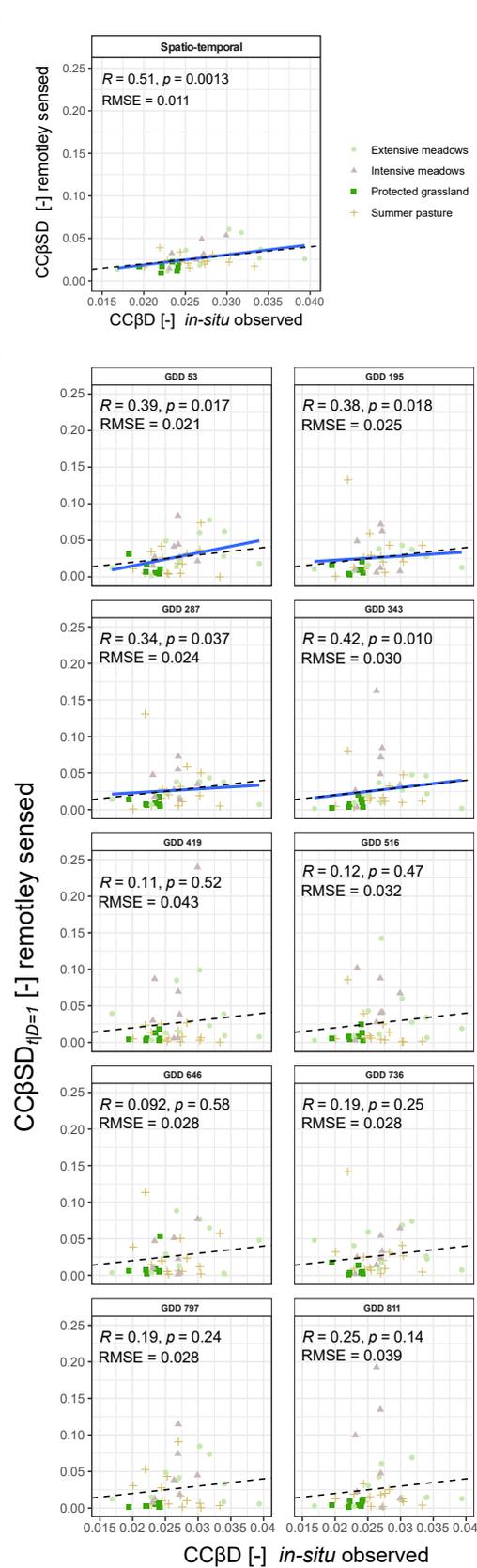
We calculated βSD on 38 locations (i.e., pixels) distributed across the study area (Appendix Fig. 4.6), independently of the management type ($\beta SD_{N=38}$). Each of these 38 pixels corresponds to the location of an *in-situ* reference plot and was 10 x 10 m in size. The plots were chosen to be located in a homogeneous area (i.e., same management type, high fractional vegetation cover) of at least 1 ha to avoid edge effects in the remotely sensed data. For each pixel, we calculated the community contribution to $\beta SD_{N=38}$ for the spatio-temporal dataset ($CC\beta SD_i$, equation 4.7) and for each of the

mono-temporal datasets ($CC\beta SD_{i,t|D=1}$).

The *in-situ* plant surveys were conducted during summer 2016 and 2017 along 10 m-long transects in each of the 38 reference plots. We calculated the community contribution of each plot to taxonomic β diversity ($CC\beta D_i$; Legendre and De Cáceres, 2013). In this case, β diversity was estimated by the Bray–Curtis dissimilarity (function `beta.div`, package `adespatial v0.3-10` in R) using species abundance data, as the Euclidean distance is not appropriate for the analysis of community composition data (Legendre and De Cáceres, 2013). To quantify the degree of correlation between the *in-situ* measured $CC\beta D_i$ and the remotely sensed $CC\beta SD_i$ and $CC\beta SD_{i,t|D=1}$, the Spearman correlation coefficient (ρ) and the root mean square error (RMSE) were used.

We found that the proposed spatio-temporal approach was very effective in estimating the measured local taxonomic contribution to β diversity ($\rho = 0.51$, $p = 0.0013$, $RMSE = 0.011$, $n=38$, Fig. 4.5a). More precisely, we were able to reduce the RMSE by 48% (RMSE from 0.021 to 0.011) when accounting for spatio-temporal dissimilarities between communities over the entire growing season compared to the best mono-temporal dataset (Fig. 4.5). No significant correlation between remotely sensed $CC\beta SD_{i,t|D=1}$ and locally measured $CC\beta D_i$ was found for six of the 10 mono-temporal datasets (Fig. 4.5b, $p > 0.05$). These results together with the high variability observed between mono-temporal spectral variances (Appendix Fig. 4.8) suggest that spectral dissimilarities calculated over both space and time (in contrast to dissimilarities over space at a single point in time) offer a better representation of differences between communities experiencing management types and distributed over a large elevation gradient inducing high temporal phenological variation.

Figure 4.5: a) Relationship between remotely sensed community contributions to β spectral diversity for our newly proposed approach ($CC\beta SD_i$), accounting for spatio-temporal spectral dissimilarities, and the contribution of the 38 field plots to β diversity calculated from species abundance ($CC\beta D_i$). b) Relationship between the remotely sensed community (i.e., plot) contribution to β spectral diversity for each mono-temporal dataset ($CC\beta SD_{i,t|D=1}$), accounting only for spatial dissimilarities, and $CC\beta D_i$. ρ = Spearman correlation, RMSE = root mean square error, GDD=growing degree days; the dashed line represents the 1:1 line. Linear regression lines were plotted only for significant relations ($p < 0.05$).



4.5 Discussion

In this study we developed a new methodological approach which extended RaoQ to include both spatial and temporal spectral variations of remotely sensed data. RaoQ can be used to partition γ SD, the spectral diversity of a region, into α SD (within community) and β SD (between community) components via a two-way ANOVA when using multi-temporal data. Partitioning of γ SD in space and time can help to reveal the scale and extent of a spectral feature, trait convergence and divergence (de Bello et al., 2009) and allows β SD to be calculated independently as done in the study case. Thereby, we included an interaction term between temporal and spatial β SD, unique for a remote sensing application, which allowed the quantification of differences in plant communities between two individual remote sensing datasets obtained at different times. By adding this spatio-temporal perspective, our approach can be seen as an extension to the spectral diversity approach proposed by (Laliberté et al., 2020).

4.5.1 β SD and its components

It is assumed that variation in spectral reflectance is associated with differences in plant traits. Plant traits indicate how plants exploit resources and interact with one another (Díaz et al., 2016; Garnier and Navas, 2012; Wright et al., 2004). Spectral diversity may therefore originate from interactions among co-occurring plants, e.g., by resource partitioning (Schoener, 1974). The partitioning of resources may change in time as suggested by the theory of temporal variability of the niche (Loreau, 2000). The quantification of β SD_T and β SD_{T_S} is in line with this niche concept, which states that temporal niche separation can be estimated by the variance of plant variables in time (i.e., traits and phenology; Kearney et al., 2010; Terradas et al., 2009). Furthermore, β SD_T and β SD_{T_S} are compatible with a metric-based measurement of phenology (Yan et al., 2015), i.e., the differences in phenology as pairwise distances between species or communities (Sapijanskas et al., 2014). Capturing variation on spectral features across time may therefore highlight distinct plant strategies, which determine species distribution patterns and their function (Huang et al., 2019; Pesaresi et al., 2020; Schwinning and Kelly, 2013).

If spectral variation in time may highlight the temporal niche separation, spectral variation in space (β SD_S) reflects the environmental heterogeneity, i.e., the number of available niches (Rocchini et al., 2010). The calculation of β SD_S is consistent with the calculation of spectral variance proposed by Laliberté et al. (2020), or RaoQ with

spectral features by (Rocchini et al., 2018b). The difference is that βSD_S is calculated after averaging the spectral features over multiple datasets, yielding a more robust spatial diversity quantification. Our results suggest that the total βSD is likely related to divergence in spectral feature composition resulting from management type or environmental properties (e.g., elevation). Management, such as mowing, impacts βSD by altering plant traits (Bouchet et al., 2017; McIntyre, 2008; Pakeman, 2011), or in some systems by accelerating flowering (Ollerton and Lack, 1992). In particular, heterogeneous mowing or grazing in space and time strongly promotes different life-history traits (e.g., time of flowering) and plant structural properties, i.e., short- vs. tall-growing plants (Johansen et al., 2019; Klimešová et al., 2010; Schütz et al., 2006). In grasslands with low anthropogenic disturbance, traits and therefore spectral features reflect conservative resource allocation strategies of plants (Louault et al., 2005; Peco et al., 2005; Rossi et al., 2020). Like traits, species composition is strongly dependent on the management type (Moog et al., 2002). Essentially, communities with similar management or/and environmental properties usually contain similar species and trait compositions. Compositional differences will become larger with increasing differences in management. As a result, management differences drive β diversity (Socolar et al., 2016). As the proposed βSD metric is sensitive to management differences in space and time, it is suitable for taxonomic or functional β diversity estimations. In comparison to (Rossi et al., 2020), where a mono-temporal approach was used, differences between certain management types (i.e., protected grasslands versus summer pasture) were more pronounced when accounting for spatio-temporal dissimilarities between communities. These results reflect the enhanced classification of different ecosystems and management types using multi-temporal remote sensing as reported by previous studies (Alcantara et al., 2012; Immitzer et al., 2019; Mousivand et al., 2015; Vuolo et al., 2018). However, the degree to which temporal variation in spectral features due to management reflects taxonomic or functional β diversity needs further investigation. In particular, heavily managed systems display high spatio-temporal variations in spectral features, which could inflate biodiversity estimates (Gholizadeh et al., 2020). The method proposed here allows spatial and temporal variation in βSD to be disentangled, and the increasing availability of multi-temporal datasets, this provides an opportunity to conduct these studies.

4.5.2 Mono- versus multi-temporal approach to quantify community contributions to β SD

Our approach further allows the partitioning of β SD into the contributions of individual plant communities ($CC\beta SD$). We consider this as one of the major strengths of the presented approach. Such an approach could, for example, help conservationists identify areas of particular importance for biodiversity. The approach, which accounts for spatio-temporal dissimilarities, accurately predicted community contributions to taxonomic β diversity. In fact, we showed that the RMSE can be reduced by up to 74% (RMSE from 0.043 to 0.011, Fig. 4.5) when estimating *in-situ* measured community contributions to taxonomic β diversity ($CC\beta D$) from space by using multi-temporal datasets that cover the entire growing season compared to using mono-temporal datasets. Accounting for spatio-temporal dissimilarities between communities was crucial, since spatial dissimilarities between communities calculated by averaging the datasets over time only weakly predicted $CC\beta SD$ (Appendix 4.9.7). A spatio-temporal approach efficiently mitigates negative effects observed when using mono-temporal datasets, such as i) sub-optimal temporal windows not capturing key phenological indicators (i.e., flowering or end of season; Cole et al., 2014; Mannel and Price, 2012), or ii) the inability to compare the spectral signature of plants at the same phenological or management stage in large study areas. Finally, building on multiple datasets of differing angular sampling (i.e., solar zenith, azimuth angle) may offer a source of complementary reflectance information (Huber et al., 2010; Mousivand et al., 2015).

4.5.3 Methodological considerations

Spectral features

Our approach to calculating spectral diversity is compatible with a range of input data, e.g., original spectral bands, a set of vegetation indices, as well as spectral or trait features extracted via principal component analysis. The selected spectral features depend on the research question and available data. The determination of features that most effectively highlight differences between species and/or communities at a certain stage of the growing season is of importance for the estimation of biodiversity. Thereby, the composition of a community is a key factor. Species or communities displaying similar traits may not be distinguishable spectrally. The problem is magnified when only a low number of spectral features - or features that are not representative of species differences - are used (Rocchini, 2007). In contrast, species with highly

contrasting evolutionary histories, genetic backgrounds and/or environmental conditions, for example species belonging to different plant functional types (Schweiger et al., 2017), are distinguishable with a much higher success rate (Bahrami and Mobarashi, 2020). Depending on the feature type, a standardization (as proposed in the study case) should be applied to avoid the disproportionate contribution of certain features. Moreover, our method is not limited to remotely sensed data, but could also be applied to multi-temporal *in-situ* plant trait data (Kattge et al., 2020).

Number of datasets

Plant trait studies recommend that traits are sampled at least three times during the growing season (early, middle, late; Fajardo and Siefert, 2016; McKown et al., 2013), allowing sufficient trait variation to be captured in order to properly characterize species and communities. This recommendation is in line with our results in which spectral datasets from early, peak and late in the growing season captured a high percentage of variance. However, to better distinguish between communities with different species composition, spectral signatures in time covering phenological variations as well as management events are needed (Dudley et al., 2015; Pasquarella et al., 2018).

Spatial resolution

The availability of higher spatial resolution data than those used in our case study (e.g., drone data) would allow the calculation of α SD and thus γ SD in grasslands. For data with coarser spatial resolution than that provided by Sentinel-2, e.g., from the Landsat and MODIS missions, we see potential for using our approach to quantify β SD. However, for plant ecological applications, plant communities or individual species need to be represented by “homogeneous” pixels (i.e., spectral signal) in terms of vegetation cover and management types. Otherwise, spectral unmixing techniques may be needed to extract a pure spectral signal (Malenovsky et al., 2007). Spatial sampling units, such as those provided by MODIS, are often only partly covered by vegetation and therefore most likely violate the underlying assumption of equally distributed individual plants. An uneven spectral representation of individuals per community also occurs when shadows or soil fractions are masked out within a community. In such cases, SS_S and SS_T overlap (i.e., space and time are not independent of each other), and the proposed partitioning would not equate to γ SD ($SS_S + SS_T + SS_{TS} + SS_W \neq S_{TOT}$ in equation 4.3). Similarly, with an unbalanced design, the partitioning into α and β components, as proposed in our approach, may lead to average α SD exceeding γ SD,

as demonstrated by De Bello et al. (2010). To prevent this, the contribution of α SD within each community can be weighted by a factor that includes the contribution of individuals to γ SD (Villéger and Moullot, 2008). In order to partition β SD into its components, different types of adjusted SS exist for an unbalanced ANOVA (Hector et al., 2010). However, an implementation would not be straightforward. Alternatively, a workaround consisting of a rarefaction procedure to standardise the number of pixels per community could be used (Laliberté et al., 2020). Ultimately, if the number of individuals between communities does not differ much, partitioning as proposed in in this study (i.e., without using a workaround or adjusting SS) remains a good approximation (Hector et al., 2010).

Community size

When quantifying spectral diversity, important methodological considerations should include not only the number of individuals per community and the community composition, but also the community size. The size of a community influences how much of γ SD can be explained by α SD and β SD. Small communities with a low number of individuals will have a high contribution of β SD and a low contribution of α SD to γ SD. Laliberté et al. (2020) found that there is a specific community size above which the relative importance of β versus α components stabilizes. However, this size is most likely dependent on the ecosystem and the available spatial resolution of the remotely sensed datasets. Using an adjusted SS would allow the application of our proposed method to communities with different shapes and sizes, e.g., those derived from image segmentation (sets of pixels, also known as super-pixels, Ren and Malik, 2003) or by clustering the region of interest into communities based on environmental variables. In addition, the concepts of α and β diversity were developed for ecological studies with discrete plot data and may be less obvious and discernible on continuous scales as provided by remote sensing data. Finally, as pointed out by other studies, temporal components as well as spatial components of biodiversity can vary with community size (Korhonen et al., 2010; Soininen, 2010). Further research is therefore necessary to investigate the relationship between α and β diversity on the continuous scales provided by remote sensing in space and time.

4.6 Conclusions

The era of openly available satellite data at a high revisit time and high spectral resolution offers new opportunities for measuring biodiversity from space. In particular, temporal variation in remotely sensed spectral features can cast light on ecological processes, including species coexistence, environmental filtering and ecosystem functioning. Here, a new spatio-temporal approach based on RaoQ that accounts for the dissimilarity in spectral features between plants or communities over space and time was presented. Our approach allows the quantification of β SD in space and time by including differences in phenology and management practices, which is crucial when assessing biodiversity, especially in light of on-going global change. As such, it has the potential to identify communities of unique species composition and therefore high conservation value which could support ecosystem conservation and restoration decision-making processes. The approach is not limited to satellite data, but can be used with multi-temporal datasets collected from platforms carrying flexible spectral imaging devices for small-scale applications, i.e., drones. Although more work is required in understanding the effect of temporal variation of β SD, we believe that the properties of our methodology open up promising avenues for evaluating and testing ecosystem diversity changes across space and time. In addition, increased knowledge about temporal variation of spectral diversity helps to contextualise and compare a wider range of ecological large-scale studies.

4.7 Data availability

An R package was built to calculate the proposed β spectral diversity metrics and the contributions of their components from a stack of raster files (R package `stdiversity v0.1`; <https://github.com/RossiBz/stdiversity>). The `lcd` function of the package allows to map the contribution of each pixel in a dataset to β spectral diversity.

4.8 Acknowledgements

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4.9 Appendix

4.9.1 Appendix S1: Rao's quadratic entropy equals the spectral variance

To calculate γ SD at a specific phenological stage t in the region of interest we used Rao's quadratic entropy index ($\gamma SD_{RaoQ,t}$, equation 4.8).

$$\gamma SD_{RaoQ,t} = \frac{1}{2} \sum_{n=1}^S \sum_{m=1}^S d_{nmt} p_n p_m \quad (4.8)$$

where d_{nmt} is the difference between plant species n and m , and p is the proportion of how much area a species covers. By i) assuming that the dissimilarity between plants is calculated from the mean dissimilarity of spectral features (e.g., reflectance of a specific band or standardized vegetation indices, Botta-Dukát, 2005), ii) using the Euclidean distance between spectral features as dissimilarity measurement (equation 4.9), iii) assuming all communities and plants to be equally important (equation 4.10), and iv) the fact that the average over the squared pairwise difference of a random variable equals twice the variance of that variable (equation 4.11, Champely and Chessel, 2002), equation 4.8 can be rewritten as follows (equation 4.12, de Bello et al., 2011):

$$d_{nmt} = \frac{1}{N} \sum_{k=1}^N (X_{ntk} - X_{mtk})^2 \quad (4.9)$$

$$p_n = p_m = \frac{1}{S} \quad (4.10)$$

$$\frac{1}{S^2} \sum_{n=1}^S \sum_{m=1}^S (X_{ntk} - X_{mtk})^2 = 2 \frac{1}{S} \sum_{n=1}^S (X_{ntk} - \bar{X}_{.tk})^2 \quad (4.11)$$

$$\begin{aligned}
\gamma SD_{RaoQ,t} &= \frac{1}{2} \sum_{n=1}^S \sum_{m=1}^S d_{nmt} p_n p_m \\
&= \frac{1}{2NS^2} \sum_{n=1}^S \sum_{m=1}^S \sum_{k=1}^N (X_{ntk} - X_{mtk})^2 \\
&= \frac{1}{NS} \sum_{k=1}^N \sum_{n=1}^S (X_{ntk} - \bar{X}_{.tk})^2
\end{aligned} \tag{4.12}$$

where S is the number of plants in the area of interest, $X_{ntk,mtk}$ is the spectral feature value k of the n, m th individual at time t , N is the number of spectral features and $\bar{X}_{.tk}$ is the mean value of spectral feature k across all individuals in the area of interest at time t .

4.9.2 Appendix S2: Description of the study area

We included differently managed grasslands in south-eastern Switzerland in our case study (latitude 46°34' to 46°54'N, longitude 9°58' to 10°25'E; Appendix Fig. 4.6a). The study area contains two main valleys (Val Müstair, part of the Lower Engadine) and the Swiss National Park (SNP; Appendix Fig. 4.6b). The area includes four management categories based on different agricultural practices derived from landscape quality data and NHG (Federal act on the protection of nature and cultural heritage) contract surfaces from the canton of Grisons https://geodienste.ch/services/lwb_nutzungsflaechen and the Swiss Federal Office for Agriculture; namely, 1) mowed and fertilized multiple times a year with organic or mineral fertilizer (further referred to as “intensive meadows”), 2) mowed and none to slightly fertilized (once per year or every two years with organic fertilizer, “extensive meadows”), 3) protected and not managed (SNP, “protected grassland”), and 4) summer grazed by cattle, sheep or both (“summer pasture”; Appendix Fig. 4.6b). The study area features a dry inner-alpine climate with a mean annual temperature of 1°C at 1968 m a.s.l., and 6°C on the valley floor (1303 m a.s.l.). Mean annual precipitation is approximately 800 mm (weather stations Scuol and Buffalora; MeteoSwiss, 2018).

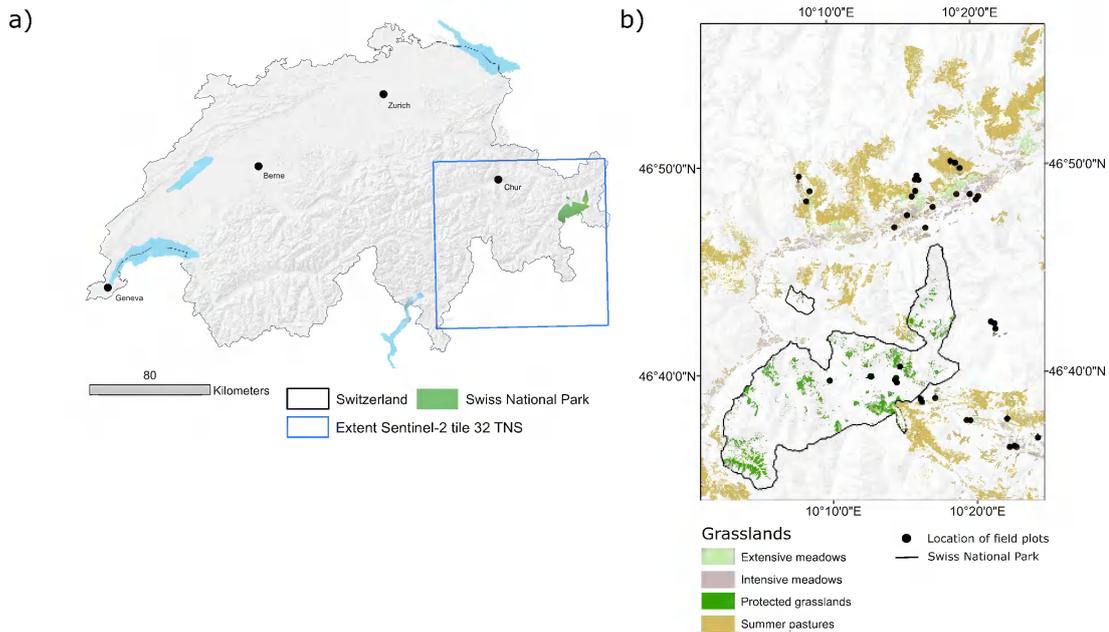


Figure 4.6: a) Location of the study area in the most eastern part of Switzerland. b) Distribution of different management types within the study area and location of field plots (black dots).

4.9.3 Appendix S3: Remote sensing data

We used open access Copernicus Sentinel-2 data (part of tile 32 TNS) L2A data (Berger et al., 2012; Drusch et al., 2012). These data were atmospherically corrected by the European Space Agency using the `sen2cor` procedure, which converts top-of-atmosphere reflectance to top-of-canopy reflectance and is available at the Sentinel-Hub. The Multi-Spectral Instrument (MSI) of the Sentinel-2 mission records a set of 13 spectral bands spanning from the visible (VIS) and near infrared (NIR) to the shortwave infrared (SWIR), with four bands at 10 m, six bands at 20 m and three bands at 60 m spatial resolution. The 60 m bands are used for atmospheric correction and cloud detection and were not considered in this study. We used a resolution enhancement method, which separates reflectance from geometrical information to resample the 20 m spectral bands to 10 m resolution (Brodu, 2017). These high-resolution data are used to fit a linear mixing model, where the reflectance of each pixel is considered to be a linear mixture of its components, e.g., a combination of vegetation and soil reflectance. Hence, the low-resolution bands are successively unmixed preserving their reflectance, while propagating the geometrical information to maintain sub-pixel details. We used the `Sen2Res` plugin to ESA's SNAP application for this procedure (SNAP plugin `Sen2Res v1.0`, <http://step.esa.int/main/third-party-plugins-2/sen2res/>). The perform-

ance of this approach was previously tested by Brodu (2017). The two satellites in the Sentinel-2 constellation provide a revisit time of 5 days in cloud-free conditions at the equator. To account for various plant phenological stages during the growing season, we used 13 datasets obtained between May 2017 and September 2018 (Table 4.1). From the datasets, we had to generate composite products for three time periods, resulting in ten-time steps. To decouple the inter-annual variability of land management (e.g., mowing) and the effect of temperature on plant phenology, the datasets were sorted based on accumulated growing degree days (GDD, [°C-days]). A GDD was defined to have a daily mean temperature above 4°C. We summed up all GDD from the beginning of the year to the date on which the spectral data were obtained. We used mean daily temperature data measured at the weather station Buffalora (46°39'N, 10°16.2'E; MeteoSwiss, 2018), located in the centre of our study area. The management types included in our study are highly stable over the years and management follows the phenological cycle. From the datasets, we had to generate composite products for three time periods, due to a high cloud cover (>10%). To do so, we started with the most recent dataset and generated an output image by replacing all cloud-covered pixels with the data taken from the preceding image in time. Remaining cloudy pixels were masked out using the sen2cor scene classification map. The use of composite products may artificially increase β SD. Therefore, we investigated the fraction of the overall variance (i.e., β SD) attributable to differences among spectral features of composite images and non-composite images. This is equivalent to conducting an ANOVA and calculating the coefficient of determination (R^2). Around 2% of variance was explained by the variability among means of composite images and non-composite images ($R^2=0.018$, $n=23'238'820$). Hence, in our case no artificial increase of β SD over the entire area due to composite images can be assumed. To mask out non-vegetated pixels in all our datasets, a grassland layer available for the region from the cantonal data (https://geodienste.ch/services/lwb_nutzungsflaechen) was used. All pixels not being grassland were excluded from the analysis. Furthermore, if a pixel appeared in less than 70% of all Sentinel-2 datasets used in our study due to clouds or snow, it was removed due to high temporal gaps.

4.9.4 Appendix S4: Vegetation indices

We took advantage of the full spectral range provided by Sentinel-2, i.e., VIS, NIR and SWIR spectral regions, to estimate β SD and calculated three vegetation indices (VI) from spectral data.

We used VI since they are easily and commonly derived from remotely sensed data (Bannari et al., 1995; Turner, 2014; Xue and Su, 2017), and are representative of plant functional traits. It is assumed that the variation in spectral reflectance is associated with differences in plant traits and canopy structure (Homolová et al., 2013; Ollinger, 2011; Ustin et al., 2009), which in turn represent structural (e.g., plant height, leaf area, leaf orientation) and chemical properties (e.g., pigments, leaf water content, dry matter content) that indicate how plants exploit their resources and interact with one another (Díaz et al., 2016; Garnier and Navas, 2012; Wright et al., 2004).

An additional advantage of using VI is their possible standardization to a theoretical range, facilitating the application and comparison of multi-temporal datasets. In addition, VI derived from datasets of different sensors are known to be strongly correlated, thus bearing the potential to be converted from one device to another (Steven et al., 2003).

The following three VI were used to calculate β SD:

1. MERIS terrestrial chlorophyll index (MTCI, equation 4.13, Dash and Curran, 2004) is derived from the red edge and NIR range of the spectrum. MTCI is linearly correlated with vegetation canopy nitrogen content (Clevers and Gitelson, 2013).

$$MTCI = \frac{R_{740} - R_{705}}{R_{705} - R_{665}} \quad (4.13)$$

2. Triangular greenness index (TGI, equation 4.14, Hunt et al., 2011) describes the total pigment content of the vegetation (Kong et al., 2016) and is defined as the triangle area consisting of three vertices in the blue, green, and red (RGB) colour-space.

$$TGI = -0.5[168 (R_{665} - R_{560}) - 105(R_{665} - R_{497})] \quad (4.14)$$

3. Cellulose absorption index (CAI, equation 4.15, Hill, 2013) can be quantified from the ratio of the two SWIR bands provided by Sentinel-2. High CAI values are found in dry and non-photosynthetic vegetation (Guerschman et al., 2009; Nagler et al., 2003).

$$CAI = \frac{R_{2190}}{R_{1610}} \quad (4.15)$$

To compare communities based on multiple vegetation indices, the same normalization procedure has to be applied to all Sentinel-2 datasets. All three indices were normalized (i.e., divided) by their potential index range, i.e., MTCI with a range from -1 to 15, TGI with a range from 0 to 10, and CAI with a range from 0 to 2. Data gaps in the time series were filled using a linear interpolation between the Sentinel-2 datasets (package *rtsa v0.2* in R; Filipponi, 2019).

As suggested in literature (a few examples are Kolecka et al., 2018; Motohka et al., 2010; Pettorelli, 2013; Wardlow et al., 2007; Zhang et al., 2003) the vegetation indices varied depending on phenology or management events (Appendix Fig. 4.7).

4.9.5 Appendix S5: Mono-temporal quantification of βSD

According to the variation of vegetation indices in time (Appendix Fig. 4.7), the quantification of mono-temporal $\beta SD_{t|D=1}$ (equation 4.5, $D=1$) is supposed to vary based over the course of the growing season. Hartley's Fmax test was used to verify whether the mono-temporal $\beta SD_{t|D=1}$ (i.e., spectral variances) calculated for all grassland communities were statistically different from each other. The analysis of individual, mono-temporal datasets revealed significant differences in $\beta SD_{t|D=1}$ over the course of the growing season for all management types (Hartley's test, $F_{max} > 1$, $n \geq 160'864$, Appendix Fig. 4.8). Particularly in meadows, the highest diversity was attributable to the co-occurrence of mowed and unmowed meadows. The maxima were occurring around the start of mowing for intensive meadows (GDD=287) and for extensively used meadows (GDD=516), respectively (Appendix Fig. 4.8). The highest $\beta SD_{t|D=1}$ in summer pasture was found at the start of livestock grazing (GDD =195, Appendix Fig. 4.8). This corresponds with the spring green-up of vegetation at higher elevations. Towards the end of the growing season, both in summer pastures and protected grasslands (GDD=797, 811) $\beta SD_{t|D=1}$ was decreasing. As also suggested by the trend of average vegetation indices (Appendix Fig. 4.7), $\beta SD_{t|D=1}$ in pastures and protected grasslands were more related to the different stages of leaf development than to management practices. The differences in spectral diversity over the course of the growing season underpin the importance of assessing temporal variations in spectral diversity in combination with spatial variations.

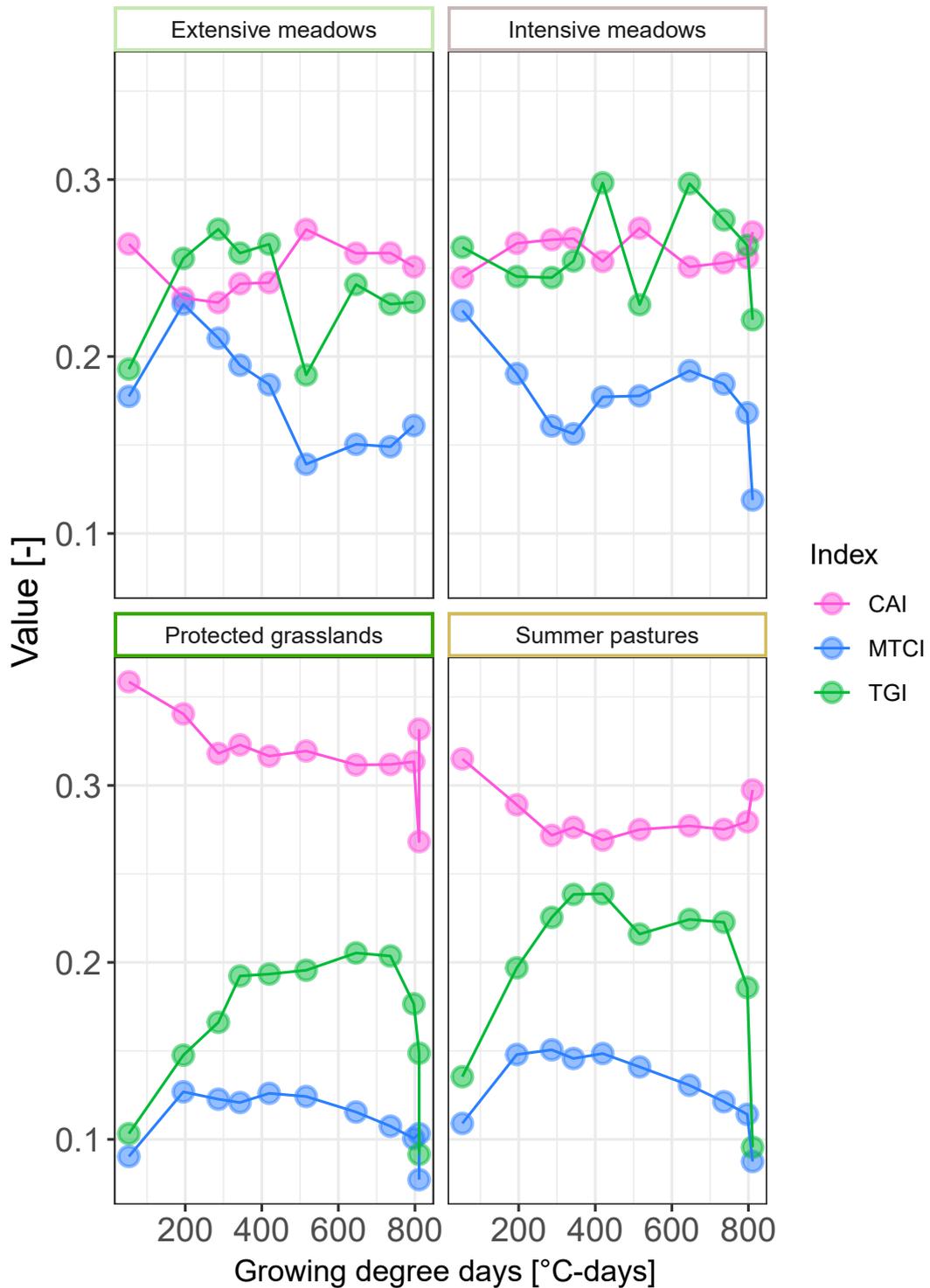


Figure 4.7: Average time series profiles for three vegetation indices (CAI, MTCI, TGI) calculated from Sentinel-2 datasets for different grassland management types. The three vegetation indices were used to calculate β spectral diversity (β SD).

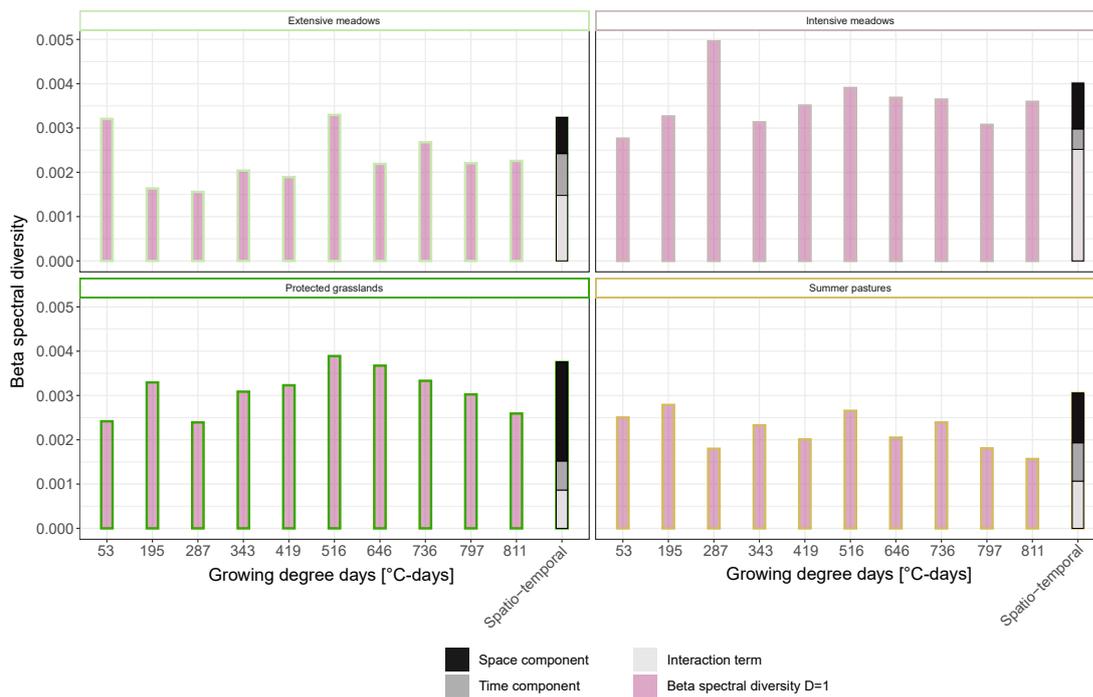


Figure 4.8: Single dataset β spectral diversity and the proposed spatio-temporal β spectral diversity and its components calculated from the mean of three vegetation indices for different stages of the growing season and different grassland management types.

4.9.6 Appendix S6: Contribution of distinct, mono-temporal datasets to β SD calculated by the spatio-temporal approach

We demonstrated that a major advantage of our proposed spatio-temporal approach is its ability to assign the resulting variance in β SD to different sources of variability (i.e., a temporal, a spatial and an interaction term). Below, an example is provided to calculate the contribution of the t th dataset to β SD ($DC\beta SD_t$, equation 4.16), which can be expressed as a percentage.

$$DC\beta SD_t = \frac{1}{\beta SD N D P} \sum_{k=1}^N \sum_{i=1}^P (\bar{X}_{itk} - \bar{X}_{..k})^2 \quad (4.16)$$

We calculated the contribution of each dataset to β SD ($DC\beta SD_t$, equation 4.16) for the different grassland types over the entire study area. Two temporal datasets (i.e., early and late in the growing season) contributed the most to the total variation in β SD in almost all management types (Appendix Fig. 4.9). Specifically, for meadows, datasets representing mowing events contributed highly to variation in β SD (GDD=287 and GDD=516, respectively, in intensive and extensive meadows). Our results suggest that at least three temporal datasets (early, peak and late in growing season) should be used to capture a high amount of the total spectral variation in time. To investigate the influence of the number of datasets used, β SD for all management types together was analysed by increasing the number of datasets starting from the dataset at the growing season peak (GDD = 419) and at the two extremes of a phenological cycle (i.e., start and end of the growing season, GDD = 53 and GDD 811). All other datasets were added subsequently in order of GDD. Adding more datasets, after the first three, resulted in stepwise modest variations of β SD (< 3.5%). We found a decrease of 8.7% from the maximum value of β SD with three datasets (early, peak and late in growing season), when using all datasets. These modest variations of β SD after its maximum suggested a convergence of β SD, which is in line with the convergence of the sample variance to the population variance for the normal distribution.

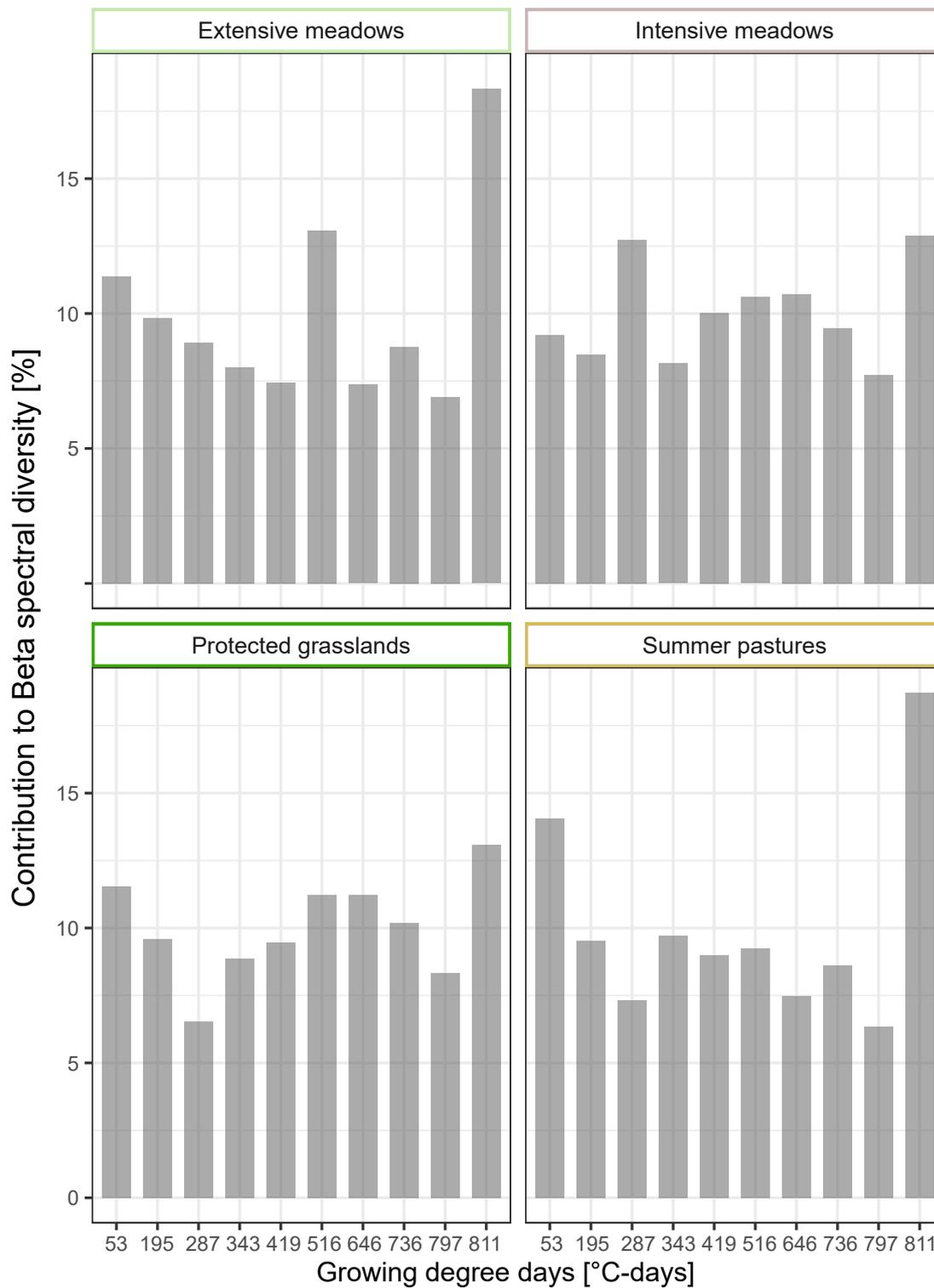


Figure 4.9: Barplots representing the contribution in percentage of each Sentinel-2 dataset ($DC\beta SD_t$) to βSD in different grassland management types.

4.9.7 Appendix S7: Community contributions to βSD_S and βSD_{TS}

Instead of calculating the entire spatio-temporal community contribution to βSD ($CC\beta SD_i$, equation 4.7), we report the contribution of each community to βSD_S ($CC\beta SD_{S,i}$, equation 4.17), i.e., the contribution based on the average spectral values over all ten datasets, and βSD_{TS} ($CC\beta SD_{TS,i}$, equation 4.18, Appendix Fig. 4.10). For βSD_T , no community contribution can be calculated since βSD_T is independent of space (i.e., has no spatial reference).

$$CC\beta SD_{S,i} = \frac{1}{\beta SD_S N P} \sum_{k=1}^N (\bar{X}_{i,k} - \bar{X}_{..k})^2 \quad (4.17)$$

$$CC\beta SD_{TS,i} = \frac{1}{\beta SD_{TS} N P} \sum_{k=1}^N \sum_{t=1}^D (\bar{X}_{itk} - \bar{X}_{i,k} - \bar{X}_{.tk} + \bar{X}_{..k})^2 \quad (4.18)$$

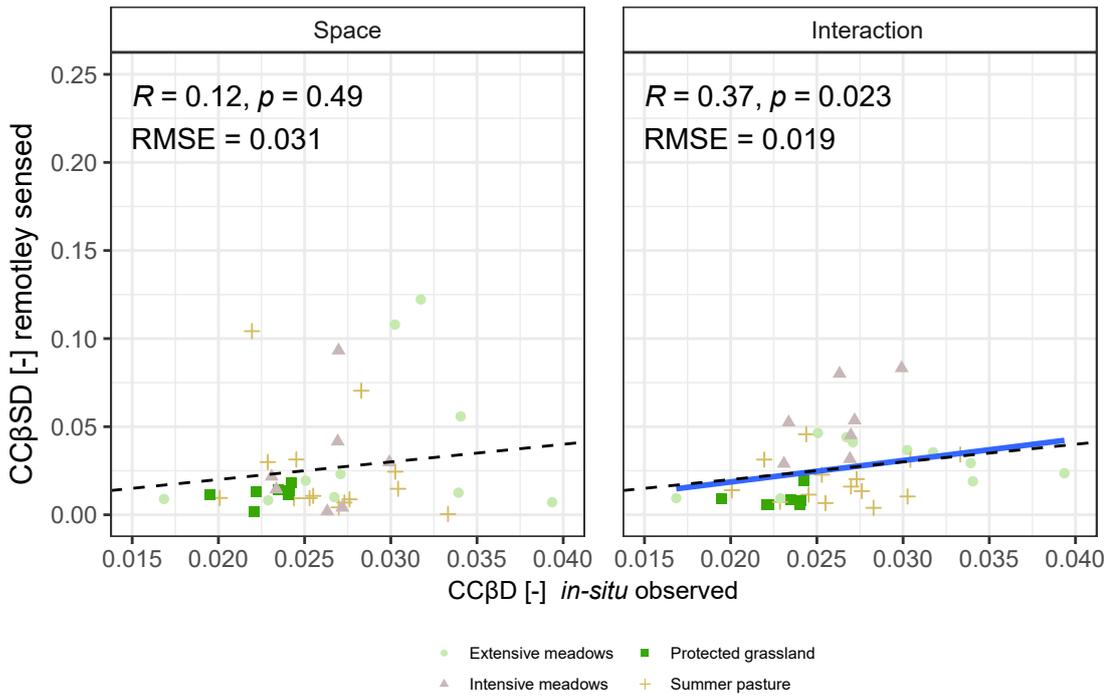


Figure 4.10: Relationship between (left) the remotely sensed community contribution to β spectral diversity in space βSD_S , (right) the interaction component βSD_{TS} , and the contribution of the 38 field plots to β diversity calculated from *in-situ* species abundance ($CC\beta D_i$). ρ = Spearman correlation, RMSE = root mean square error, GDD=growing degree days; the dashed line represents the 1:1 line. Linear regression lines were plotted only for significant relations ($p < 0.05$).

5

Synthesis

In this thesis opportunities were highlighted and challenges tackled in remote sensing of grassland biodiversity. Thereby, understanding the particularities of the grassland ecosystems under observation and the implication of spatial, spectral, and temporal resolutions of optical remote sensing on plant diversity estimations was essential to bridge the work of ecologists and remote sensing specialists. The findings of this thesis are also crucial to develop systematic measurements and operational missions to monitor biodiversity remotely.

This chapter summarises first the main conclusions of each chapter through the answers to the questions asked in Section 1.7. Second, general considerations focusing on plant biodiversity in the Swiss National Park and its surroundings are examined and discussed. Finally, additional research avenues are presented and conclude the thesis.

*"In order to more fully understand this reality,
we must take into account other dimensions of a broader reality."*

JOHN ARCHIBALD WHEELER

5.1 Main findings

The previous chapters addressed three major research questions formulated in Chapter 1. In the following sections these questions are discussed.

5.1.1 What component of functional diversity is captured with remote sensing as we move to coarser spatial resolutions?

The result in Chapter 2 suggests that at the spatial resolution of tens of meters, remote sensing captures characteristics at the community level of grasslands, where a community is defined as a group of organisms representing multiple species living in a specified place having the size of a pixel. The use of multispectral satellite data with the inversion of a 1-D columnar RTM allowed quantifying CWM of traits, i.e., community-level trait values weighted by species abundances, in alpine grasslands. In particular, CWM of SLA could be accurately assessed from Sentinel-2 data by optimising the RTM inversion process (i.e., constraining the input variables, testing different cost functions, multiple solutions and adding gaussian noise). Overall, the physical scaling of the optical signal from canopy to leaf level through an RTM was found to be well suited to link trait metrics at the community level with remote sensing data. Remotely sensed CWMs, in line with *in-situ* measured CWMs from previous studies (Garnier et al., 2007; McIntyre, 2008), were found to reflect different management practices and their importance is underpinned by their relationship to ecosystem processes and services (de Bello et al., 2010; Díaz et al., 2007b).

Pixel values being representative of CWMs indicate that satellite remote sensing derived diversity in grasslands translates into the ecological concept of β -diversity. As explored in Chapter 2, mapping CWM in a spatially continuous manner has allowed to calculate β -FD, i.e., the functional diversity between-communities, over the entire landscape. Furthermore, the results presented in Chapter 2 highlight the importance of quantifying β -FD from space as it delivers additional information on the impact of management types, differing from locally measured α -FD values. Additionally, changes in β -diversity provide the scaling factor that allows us to predict changes in the overall diversity (i.e., γ -diversity) from measured changes in α -diversity (Socolar et al., 2016). Furthermore, as shown by previous studies quantifying α - and β -FD separately can reveal the origins and maintenance of plant diversity across regions (De Bello et al., 2010; Spasojevic et al., 2014). For instance, high spectral β -FD could result from turnover in functional trait composition across environmental gradients (e.g., soil properties, elevation), whereas high α -FD might result from local biotic interactions among co-occurring plants (e.g., resource partitioning).

The conclusion that satellite remote sensing derived diversity represents β -diversity, was underpinned by the non-significant correlation between α -FD, i.e., within-community FD, and the remotely sensed FD. The surrogacy hypothesis suggests that a higher spectrally observable landscape heterogeneity reflects a higher local plant diversity

(Rocchini, 2007; Rocchini et al., 2016). However, the results of this thesis demonstrated that at the spatial resolutions of satellite data with pixels containing many individual plants and plant species, remotely sensed diversity does not serve as a proxy of trait difference between individual plants. Hence, only the diversity between plant communities can be quantified. This finding is supported by previous studies (Polley et al., 2019; Schmidtlein and Fassnacht, 2017) and corroborated by the example in Chapter 2 of heavily fertilised meadows: low within-community diversity due to fertilising (Carmona et al., 2015) can be coupled with high heterogeneity between communities on a landscape scale due to parcel size and subjective management decisions (Socolar et al., 2016). In addition, as shown in Chapter 3, a successful estimation of within-community diversity in a species-rich grassland requires high spatial resolution.

Nevertheless, a link between within community FD and satellite data was evident in the results. The diversity of the community influenced our ability to estimate CWM from satellite data with RTMs. Relatively simple RTMs, like the one used in Chapter 2, reduce the data and computational requirements through approximations that are often unrealistic such as the turbid medium approximation. For example, in Chapter 2 the assumption of homogeneity implied by the turbid medium was violated for high FD values of a community. Thus, one important consideration has to be made about using RTMs in combination with satellite data. The remote sensing estimation of β -FD is not entirely independent from α -FD, since the latter influences the success of β -FD quantification. Hence, the extent to which model approximations render RTMs ineffective for estimating CWMs depends on the management types and environmental conditions that shape α -FD.

5.1.2 What are the key ingredients for the successful estimation of plant species richness from remotely measured spectral diversity in species-rich grasslands?

The findings in Chapter 3 demonstrate that spatial resolution is key for the successful estimation of plant species richness - a result that is supported by previous studies (Gholizadeh et al., 2019; Wang et al., 2018a). The optimal pixel size for estimating α -diversity in grasslands appears to be in the range of a leaf of herbaceous plant species. Even though the hypothesis of spectral variation underlying the use of spectral diversity does not require the detection of individual plants, a pixel size comparable to the plant size, i.e., a few cm, is needed. In contrast, some previous studies have successfully used coarse satellite data (Rocchini, 2007; Rocchini et al., 2004) to map species

richness in grassland. Estimating species richness from satellite data may work only if the between community diversity β of a particular neighbourhood, that is derived from satellite data (Chapter 2), is representative of the within-community diversity α . Hence, at coarse spatial scales, it is possible to see something indirectly related to species richness rather than species richness per se. Similarly, the spatial resolution of airborne data can be already too coarse when the number of pixels per plot or community is restricted, as in the case of Chapter 3. On the contrary, sensing platforms providing high spatial resolution data, such as UAVs, enabled the quantification of plant species richness through spectral diversity. Alternatively, airborne or spaceborne remote sensing products can be used to predict plant diversity indirectly through empirical regression methods (Fauvel et al., 2020; John et al., 2008) or, as suggested in Chapter 2 by taking advantage of the correlation between model uncertainties and α -FD. However, those methods use an empirical approach that cannot be translated into other observation configurations without losing predictive power (Verrelst et al., 2015a).

In order to address the importance of spectral resolution, the sensor used in combination with the UAV platform demonstrated a very low spectral resolution. A trade-off between spatial and spectral resolution is a recurring issue in remote sensing due to the technical constraints of sensors. Therefore, a data fusion approach between airborne imaging spectroscopy data and the multispectral UAV data was used to create a high spectral and spatial resolution dataset. Thereby, different state-of-the-art fusion techniques were used and the HySure algorithm was found to be the best-performing algorithm (chapter 3). The outstanding performances of HySure could be explained by its implicit denoising capacity and the fact that unmixing-based approaches have a clear advantage in resolving the low spectral overlap between the UAV and airborne datasets (Yokoya et al., 2017). Compared to the spatial resolution, the spectral resolution showed marginal results in estimating plant species richness through spectral diversity. The high correlation between some spectral bands, the way spectral metrics condense the spectral information and the fact that the spectral diversity approach does not decouple leaf from canopy effects were made responsible for the subordinate role of high spectral resolution. As suggested in previous studies (Schweiger et al., 2018), most of the spectral variation corresponds to known absorption features of plant pigments, water content and carbon-based leaf constituents. Furthermore, even when the goal is to retrieve traits via RTMs (Chapter 2), a limited spectral range is sufficient and can enhance trait estimations (Féret et al., 2018). Hence, using the complete spectral information can be counterproductive and it is necessary to take an accurate choice of spectral features to calculate spectral diversity or estimate plant traits.

Besides the spatial resolution, the spectral metric was a key ingredient for a correct

estimation of plant species richness and may not be compensated by using additional spectral information. Spectral metrics based on the spectral information content (i.e., spectral complexity) are heavily influenced by extreme values and were found to reveal a negative correlation with plant species richness. In line with the study of Gholizadeh et al. (2018), where the soil was shown to confound the spectral diversity-biodiversity relationship, spectral diversity based on the spectral complexity was inferred to be sensitive to live and dead biomass. Increasing biomass was assumed to cause higher canopy structure complexity, resulting in increased spectral diversity through, for example, shadows in high spatial resolution images. Similarly, the presence of dead biomass with its homogeneous spectral response differing from live biomass (Beeri et al., 2007; Schweiger et al., 2015b) was deemed to be partially responsible for the high spectral diversity values calculated with metrics based on the spectral complexity. Not only spectral diversity is shaped by such confounding effects, but they also play a major role in our ability to estimate CWM of traits and therefore the between-community FD from remote sensing as observed in Chapter 2. To address confounding effects, a metric that is less sensitive to extreme values, such as spectral species richness, was found to be well suited. This method is based on the hypothesis that species or groups of species can be identified across the landscape based on their spectral signature (Féret and Asner, 2014), with each species or group of species showing lower within-group spectral variability than among-groups variability. Such a classification-based approach can be less sensitive to pixels corresponding to the soil, shadows or dead biomass by identifying them as distinct spectral species and thus minimising their effect on spectral diversity. Such an approach is not limited to the within-community diversity estimated in Chapter 3 but could be used for between-community diversity as well (Rocchini et al., 2021; Schmidtlein and Fassnacht, 2017). In contrast, metrics that are heavily influenced by extreme values should be used with care, considering the above-mentioned sources of error.

5.1.3 How important is the temporal resolution for remote sensing of plant biodiversity?

In Chapter 2 the discrimination ability between pasture categories through functional traits demonstrated a variance among the observed dates. In line with other studies (Gholizadeh et al., 2020; Schiefer et al., 2021), phenology, flowering and management events were found to affect plant trait retrieval from canopy reflectance and plant diversity estimations in mono-temporal approaches. However, those spectral variations

in time can be used to enhance the estimation of plant biodiversity. In Chapter 4, the RMSE could be reduced by up to 74% when estimating *in-situ* measured community contributions to taxonomic β -diversity from space by using multi-temporal datasets that cover the entire growing season compared to using mono-temporal datasets. Furthermore, in comparison to the findings in Chapter 2, differences between certain management types (i.e., protected grasslands versus summer pasture) were revealed to be more pronounced when accounting for spatio-temporal dissimilarities between communities as done in Chapter 4. Overall, grasslands are dynamic ecosystems and building on multiple datasets in time covering phenological variations as well as management events is necessary for a proper estimation of biodiversity.

In order to do so, a method to account for spatio-temporal spectral diversity based on the Rao's quadratic entropy dissimilarity measure was introduced. First, as highlighted in Chapters 2 and 3, the spatial resolution of the remote sensing data is a critical factor influencing the level of ecological organisation that can be captured. Therefore, the proposed method allows partitioning the spectral or functional diversity into α and β components. Second, the method considers the temporal variation of spectral data by calculating α -diversity as the average over multiple temporal datasets and β -diversity represented by three components, i.e., space, time, and space-time interaction. Starting from the total dissimilarity in spectral information between plant individuals, regardless of their space and time allocation, the study demonstrated how to allocate the overall variance of a dataset to different sources of variability, e.g., α , β -space, or β -time, with an approach similar to a two-way ANOVA. The proposed approach allows quantifying β -diversity in space and time and their respective importance, thereby highlighting differences in phenology and management practices over large areas that drive biodiversity. Key aspects to consider for successful use of the method reflect the findings of Chapter 2 and 3: i) the use of spectral features that most effectively highlight differences between species and/or communities, ii) the spatial resolution and the extent determine the ability to quantify α and/or β diversity and, iii) several datasets enough to cover phenological variations as well as management events.

5.2 General contributions and considerations

The loss of grassland biodiversity calls for global monitoring of plant biodiversity (Chapter 1) supported by remote sensing (Jetz et al., 2016; Skidmore et al., 2015). The often poor alignment of field-observed biodiversity metrics with remote sensing products, however, hinders us from fully embracing and adopting remote sensing for

biodiversity monitoring in grasslands (Skidmore et al., 2021). This thesis contributes to translating ecological concepts into remote sensing applications, shows that a full consideration of different aspects of remote sensing resolution (spatial, spectral and temporal) and grassland management practices is critical, and provides different solutions to propel to the forefront a global biodiversity monitoring system involving different remote sensing platforms. In particular, explaining spectral or trait patterns in light of ecological concepts is likely to lead to a better mechanistic understanding of how remote sensing derived diversity arises from the underlying ecology of landscapes and the biological attributes of constituent species or communities. The following sections discuss general contributions and considerations resulting from this thesis on remote sensing methodology and the investigation of a non-intervention policy in grasslands from a plant diversity point of view.

5.2.1 No platform stands above all

Given the limited access and cover of field-based studies on traits and species diversity in grasslands, the remote sensing methods investigated in this thesis present the opportunity to collect relevant biodiversity data required to address today's most pending environmental issues exhaustively and efficiently. As suggested by the findings in this thesis, the exhaustive monitoring of biodiversity is possible only with the integration of different remote sensing platforms. The larger extent captured by spaceborne sensors introduce higher-level diversity effects (e.g., β -diversity) and the spatial resolution provided by current and forthcoming satellite sensors (Cawse-Nicholson et al., 2021) might be deemed too coarse for capturing directly α -diversity in grasslands. In addition, notably, capturing only spectral or functional differences between communities over 60% of spectral or trait variation of a region is overlooked (Fig. 5.1 and 2.7). The forth-coming hyperspectral satellite missions, such as the Surface Biology and Geology mission (Cawse-Nicholson et al., 2021) or the Copernicus hyperspectral imaging mission (Rast et al., 2019), will substantially improve the estimation of traits and functional diversity globally. Nevertheless, such satellite missions would be limited to the community-level in grasslands. In contrast, satellite data, such as those of the private company Planet, with high spatial and temporal resolution could play a crucial role in assessing biodiversity, should they become more accessible for a broader user group. At the same time, rapid progress is being made with UAVs offering novel ways to use remote sensing to advance our understanding of the relationship between spectral diversity and multiple dimensions of biodiversity at finer spatial scales (Chapter

3). In this thesis, UAV data showed promising results for estimating α -diversity, but are only suitable for a limited area. Combining different platforms and sensors is therefore the need of the hour. To integrate data from different sensors to assess biodiversity, the partitioning of the total spectral diversity proposed in Chapter 4 provides a mathematical framework, which helps to compute the total estimation of plant biodiversity. For example, a possible biodiversity monitoring could leverage the α -diversity derived from a few representative communities with UAV data and quantify β -diversity in space and time from satellite images over the entire area. Similarly, multi-temporal satellite data could be used to identify unique communities on a regional scale that should be closely investigated on a local scale. Another way to successfully integrate data from different platforms to estimate biodiversity was shown in Chapter 3. Data fusion, based on spectral unmixing techniques, is a powerful way to achieve adequate spatial and spectral resolution by combining different sensors and platforms. Due to the increasing availability of different sensors, data fusion can emerge as a valuable option. In particular, data fusion is an important option in estimating plant diversity since: i) remote sensing devices are usually designed as a trade-off between spatial and spectral resolution, ii) spatial resolution clearly delineates the diversity level that can be derived remotely, and iii) certain spectral features capture most of the variance between plants.

5.2.2 From communities to pixels

In the framework of this thesis, it was fundamental to show how concepts applied to discrete plot data used in ecological studies fit the pixel-based data provided by remote sensing. In particular, the thesis highlights the feasibility of remote sensing to measure some Essential Biodiversity Variables (Pereira et al., 2013) used to monitor changes in biodiversity. For example, CWM traits from pixels values were derived and by analysing their variation over the entire region, as done in Chapter 2, offers promising avenues to understand biodiversity response to environmental, land-use change, and policy. The CWM trait information acquired on large scale can be further used to estimate ecosystem service and enhance species distribution models over large spatial extents. Critical in translating CWM, α - and β -diversity concept into remote sensing applications remains the definition of a community. The estimation of biodiversity is affected by the community size and the spatial extent of the area covered (Anderson, 2018). In the framework of this thesis, an ecological community was assumed to match a pixel or aggregation of pixels of remote sensing data. The definition of community

given is a purely spatial one: plant community is a group of interacting plant individuals representing multiple species occurring together in a spatially constrained unit (Stroud et al., 2015). Different in the ecological domain, communities are often defined as areas of uniform vegetation. This framing of a community is however the subject of considerable debate revolving around the question of what exactly constitutes an ecological community and limiting ecology to a discrete and local concept (Ricklefs, 2008). A community is frequently so heterogeneous with poorly marked boundaries that it cannot be located with any degree of accuracy. Furthermore, the behaviour of plants offers in itself no reason at all for the division into communities (Gleason, 1926). Although the coarseness of spaceborne remote sensing observations does not solve the arbitrariness of the community concept, the continuous data provided over space could mitigate the weaknesses of the discrete and local community approach. Furthermore, combining data from different sensors with the proposed approaches would allow us to further understand the relationship between α - and β -diversity with varying community size or digressing from the community concept to a continuum of spatial and temporal scales within entire regions. This thesis's regional and continuous perspective can produce new insights and promote new ecology theories and research. For example, populations dynamics that link interactions among species over large regions could be quantified.

5.2.3 Many roads lead to biodiversity estimation

In addition to the size of the community or pixel, the value representing it needs some consideration. In this thesis, two approaches to derive biodiversity from measured spectra were explored. First, traits were derived from reflectance spectra with a radiative transfer model and consequently used to quantify functional diversity (Chapter 2). This approach showed several advantages such as: i) the provision of uncertainties to each trait retrieval, ii) providing a common ground between trait-based ecology and remote sensing, iii) minimising the dependency on field observations. Overall, the consistency of the approach across different datasets provides a solid base for evaluating management practices on CWM of SLA and makes a PROSAIL application attractive for biodiversity monitoring. Second, spectral diversity to quantify biodiversity was used (Chapter 3). Using the variation in space of the full spectral information as a direct proxy for plant diversity depends on fewer user decisions as compared to other approaches (e.g., selecting the plant traits and modelling approach to predict traits

from spectra). The approach was already introduced 20 years ago (Palmer et al., 2002), but has only recently gained popularity (Cavender-Bares et al., 2017; Gholizadeh et al., 2018; Schweiger et al., 2018). The spectral diversity-biodiversity relationship is still not extensively researched and necessitates further investigations. The first problematic issues, such as confounding factors and the decoupling of leaves from canopy effects, already emerged in Chapter 3. Furthermore, using the full spectral information to calculate spectral diversity was overrated. The spectral information needs to be reduced to a few bands reflecting absorption or reflectance features relevant for biodiversity quantification. As observed in Chapter 4 and by Schneider et al. (2017), the use of specific vegetation indices could be used to calculate spectral diversity. The use of vegetation indices would be close to a trait-based approach such as that of Chapter 2, since spectral diversity primarily reflects functional diversity (Schweiger et al., 2018). Thus the difference between both explored approaches seems to be more a matter of terminology. Critical is how traits or spectral properties are derived and the accounting of temporal variation of the remotely sensed reflectance. Accounting for spatio-temporal spectral variability as done in Chapter 4 is the first step towards an integration of multi-temporal data. It highlights the issues of mono-temporal approaches in remote sensing of plant biodiversity. Since temporal fluctuations of the spectral signal are not limited to grassland, estimating biodiversity in forests should also rely on multi-temporal datasets.

5.2.4 Non-intervention policy is a valuable management option

In this thesis remote sensing was used to quantify the effect of different management types on plant diversity. The findings offer new insights into the debate on whether a non-intervention policy, i.e., long-term protection endeavour, that allows natural processes to take their course, is a valuable management strategy to increase biodiversity. CWM trait values reflecting plant ecological strategy directly relevant to growth, survival and reproduction (Díaz et al., 2016; Wright et al., 2004) showed hardly any differences between SNP and pastures in the surrounding area (Fig. 2.5). Despite the abandonment of pasture activities for over a century, plants continue to display conservative and acquisitive use of resources. The agricultural legacies and the partly intensive grazing by wild ungulates characterise today's landscape in the park. The population of ungulates in the SNP is comparable to an extensively managed pasture, ensuring the preservation of open grazing areas. Furthermore, tall plants that invest in rapid growth can still be found on nitrogen-enriched soils around former stables.

To represent an overall situation of plant diversity, in particular trait diversity, the result of locally measured α -diversity based on two traits (i.e., LDMC and SLA, Chapter 2) were combined with multi-temporal diversity β -diversity of Chapter 4 (Fig. 5.1). The diversity of traits found in a plant community demonstrates the effective use of diversely available resources. At the local level (i.e., α -diversity), moderate grazing, as occurring in the park, shows a very high diversity of traits (Fig. 5.1). A diverse pattern of traits and/or spectra is favoured by selective grazing pressure from wild ungulates (Schütz et al., 2003). Thus, in a confined space, grazed plants are next to those left undisturbed. In contrast, meadows fertilised several times a year in the Engadine and the Val Müstair show a lower functional diversity. These fertilised meadows are strongly characterised by an uneven ratio in favour of competitive plants with fast growth. Such inefficient use of resources can lead to reduced ecosystem functioning. As shown by previous research in Chapter 3, eutrophication decreases plant diversity and weakens the grassland ecosystem, thereby lowering survival rates in the face of abiotic and biotic hazards (Hautier et al., 2014).

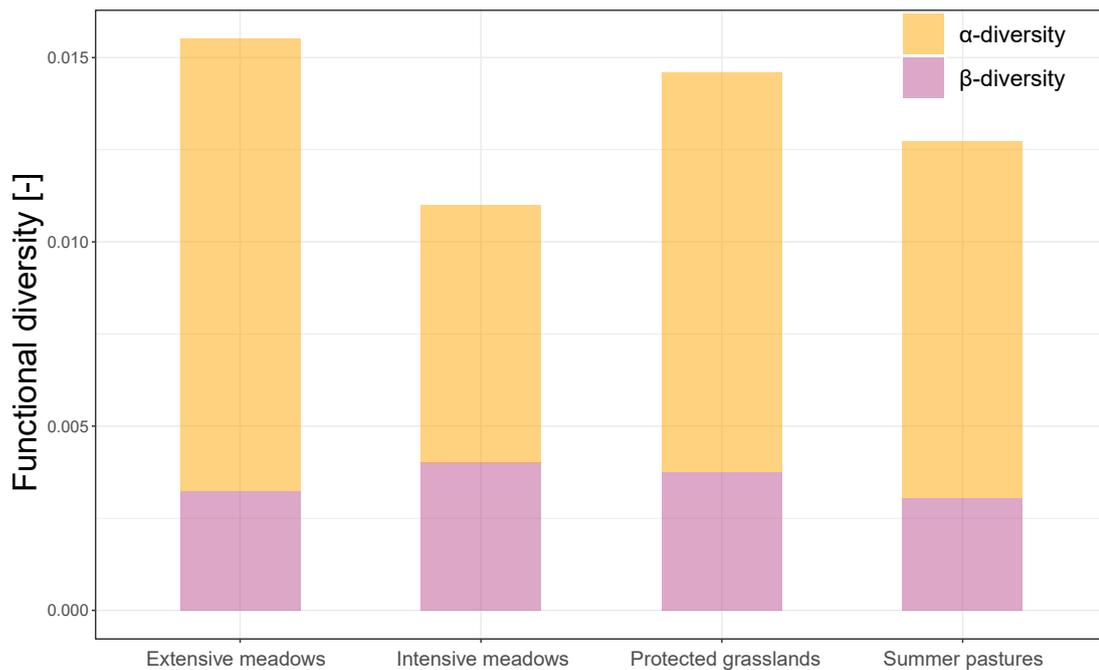


Figure 5.1: Functional diversity with partitioning into α (within-community) and β over time (among-communities) for different management types.

On a broader scale (i.e., β -diversity) the park displayed the highest spatial diversity averaged over the entire growing season (Chapter 4). This result is somehow in con-

trast with the result of Chapter 2 where just one trait and data from the peak of the growing season were used. Again, the importance of multi-temporal approaches and the choice of spectral features is underpinned in remote sensing of biodiversity. In addition, β -diversity values must be interpreted with care. For example, when intensively managed grassland reduces the total abundance of the many species across the region, β -diversity can increase as species become rarer (Socolar et al., 2016). Nevertheless, a protected area that encompasses a high variation of spectral or traits can only be seen as positive, as it ensures higher ecosystem resilience.

Overall, the sum of small-scale and large-scale functional diversity (Fig. 5.1) gives a landscape picture that is alarming due to the widespread presence of intensively managed meadows with low plant diversity. More extensive forms of management and protection from human intervention should be introduced to ensure biodiversity and the resilience and functionality of the whole ecosystem in the region. As shown in this thesis non-intervention policy consisting of agricultural land abandonment and establishment of strict protection is a valuable management practice to enhance plant diversity. Different from agricultural abandonment alone (Kahmen et al., 2002), protection has favoured all sorts of herbivores that increase plant biodiversity and functionality (Olf and Ritchie, 1998; Risch et al., 2018). Furthermore, the operating costs of the SNP are in line with agricultural subsidies. The ecosystem service provision of protected areas is however not just limited to biodiversity, but also provides a whole range of cultural and intellectual services (Backhaus et al., 2013; Smit et al., 2017; Stritih et al., 2021).

5.3 Future directions

The methods outlined in this thesis open up new opportunities for quantifying various aspects of plant biodiversity and bring forward some open questions. These open questions highlight various research opportunities for the future. In the following sections, some potential future directions are discussed.

5.3.1 Trade-offs between remote sensing dimensions

There is still uncertainty around the role of the newly emerging spaceborne imaging spectrometers with high temporal and spectral, and limited spatial resolution in estimating local plant diversity in grasslands. These include PRISMA (Lopinto and Ana-

nasso, 2020); DESIS (Müller et al., 2016); SBG (Cawse-Nicholson et al., 2021). The results of this thesis suggest that when it comes to quantifying plant diversity, spatial resolution should be prioritised. In general, future studies should refrain from using coarser spatial resolution data as the one used in this thesis (e.g., MODIS data; Schmidtlein and Fassnacht, 2017). Instead, conducting spectral diversity investigation from aerial photographs or SkySat satellites with a ground resolution of 10-50 cm could be promising for a grassland biodiversity quantification (Dalmayne et al., 2013). However, achieving resolutions in which one individual plant corresponds to one pixel on a global scale seems unlikely for grassland. Furthermore, in this thesis, the spatial, spectral, and temporal dimensions of remote sensing for plant biodiversity estimation were analysed only two at a time. Therefore, testing the degree to which spectral and temporal resolution combined can compensate for spatial one should be a priority for future research. To the best of my knowledge, there is no such study that simultaneously analysed trade-offs between the three dimensions of remote sensing when quantifying biodiversity. Such a study could take advantage of a UAV platform equipped with an imaging spectrometer, that repeatedly flies over different ecosystems throughout the growing season. Possible findings should shed light on the capabilities of spaceborne imaging spectrometers for biodiversity estimations. Most likely new creative ways of estimating local diversity from coarse satellite data need to be developed. In that sense, a possible approach could be based on the spectral species concept (Chapter 3; Féret and Asner, 2014) and spectral unmixing techniques. The idea is that the number or abundance of endmembers per pixel, each representing a spectral species, are used respectively to proxy species richness or evenness.

5.3.2 Spectral diversity is only one piece of the puzzle

The diversity of spectral reflectance across sets of pixels has been proposed to relate to conventional metrics of plant biodiversity. However, as highlighted in this thesis as well as in recently published studies (Conti et al., 2021; Imran et al., 2021) different limitations need to be addressed in the future to ensure the success of the spectral diversity approach for large scale biodiversity estimations. In contrast, spectral diversity demonstrated consistency in estimating the productivity of an ecosystem (Chapter 3, Schweiger et al., 2018; Villoslada et al., 2020). Spectral diversity may therefore help to detect the form and drivers of biodiversity-ecosystem function relationships across space and time (Williams et al., 2021; Yan et al., 2021). In particular, stabilising effects on productivity found on local scales (Hautier et al., 2014) could be investigated on

large spatial scales.

In recent years a multitude of methods have been developed for spectral diversity. Nevertheless, a comparison between methods is missing and is urgently needed to guide a successful application. In particular, a comparative study testing the spectral-biodiversity relationship with varying spectral metrics and plant diversity indices should be welcomed.

Other indicators like geomorphology, topography, geology, and hydrology may better explain plant diversity at broader spatial scales. Heterogeneity of the physical environment, alongside climatic variables, has been studied to significantly affect the distribution of vegetation and biodiversity (Burnett et al., 1998; Hjort et al., 2015). Nevertheless, only recently, the impact of the so-called geodiversity on biodiversity has gained attention and the capabilities of remote sensing were recognised (Zarnetske et al., 2019). Spectral diversity can be seen as an integrating part of geodiversity (Lausch et al., 2019). Nevertheless, other remotely sensed products could potentially enhance biodiversity estimations. For example, active sensors such as Light Detection and Ranging (LiDAR) or Synthetic Aperture Radar (SAR) play an increasingly important role in remote sensing of vegetation structure and abiotic components and their diversity in space and time. In short-stature vegetation, such as grassland, the level of structural detail picked up by LiDAR may however not be high enough to capture fine-scale differences in vegetation structure, but this remains to be tested. Another critical aspect of geodiversity is thermal heterogeneity. Differences in temperature within landscapes influence the organisms, affecting processes such as respiration as well as heat and energy exchange which, in turn, set thermodynamic constraints on species behaviour, growth, reproduction, and survival (Huey et al., 2012; Jones, 1985). Once again, remote sensing sensors like the thermal infrared sensors on the Landsats, the ECOSTRESS sensor on the International Space Station or FLIR cameras used on UAVs allow measuring land surface temperatures directly. Furthermore, since thermal heterogeneity is a result of fine-scale differences in vegetation structure, it could be estimated from remote sensing products such as LiDAR (Zellweger et al., 2019). Finally, remotely sensed thermal diversity would not only be critical for plant diversity but could additionally be used to estimate animal diversity (Elsen et al., 2020). Overall, using just spectral diversity to estimate biodiversity seems to be reductive given the potential of remote sensing. Therefore, exploring the integration and comparison of different remotely sensed diversities (e.g., spectral, thermal, structural and topographic) on different scales from UAV and satellite data should be a future goal.

5.3.3 A wider use of radiative transfer models

The research conducted in this thesis has pointed out the potential of mapping SLA on a global scale in grasslands with a physical-based model. Specific leaf area is a critical trait in capturing leaf economics, reflecting the plant form and function (Díaz et al., 2016). However, to map SLA globally, the inversion of the PROSAIL model used in this thesis is computationally intensive. In recent years, machine learning-based RTM emulation has shown to decrease the computational demands of radiative transfer models by approximating their output utilising statistical machine learning and active learning (e.g., Berger et al., 2021; Gómez-Dans et al., 2016; Hauser et al., 2021; Pérez-Suay et al., 2017). In addition, emulated RTM can be implemented into cloud-based computing such as Google Earth Engine (Campos-Taberner et al., 2018). Such cloud-based services allow for large-scale and fast processing of remote sensing data and provide access to complete archives of various sensors without the need for downloading the data (Gorelick et al., 2017). Thus, new opportunities arise for estimating traits on global and multi-temporal scales. At the same time, the further development of PROSPECT (Féret et al., 2021) increases the number of traits that can be derived remotely with a physical-based approach (Verrelst et al., 2021). Uncertainties and inversion strategies need to be investigated to facilitate the confident use of these new models for global applications. Emerging traits maps would allow greatly benefit the quantification of ecosystem services (Lavorel et al., 2011) and could be integrated as products in the Copernicus Land Monitoring Service. Compared to Corine Land Cover they would provide a more sophisticated product on land-use changes on a global scale, e.g., eutrophication of natural grasslands or abandonment of grasslands could be monitored. Similar, species distribution models or animal movement research still relies on quite simple vegetation indices. Incorporating PROSAIL outputs that resemble better forage quality and quantity in such models and analysis should be investigated and could improve our understanding of species distribution in space and time.

5.3.4 Remote sensing of trophic interactions

This thesis provided a baseline against which to assess future changes regarding plant functional diversity in the SNP and surroundings. This baseline is all the more important as wolves are repopulating the region. Wolves have been shown to change the relative abundance and behaviour of herbivores (Ripple and Beschta, 2012a,b), which in turn affect plant composition and diversity. Therefore, in the near future datasets from the same constellation used in this thesis, the Sentinel-2 mission, which is planned to

provide data at least until 2032, could be used to provide a picture of the interactions between the wolf and plant diversity in an alpine ecosystem over large geographical extents. At a local scale a monitoring baseline for the biodiversity of grassland communities in the park and surroundings is currently established with the method evaluated in Chapter 3.

In Section 5.2 the issue of community arbitrariness was raised. Depending on the spatial scale and size of a community chosen, the plant diversity estimation and related ecosystem functions could lead to misleading results (Messier et al., 2017). In addition to studying plant diversity and its components with varying community sizes, communities could also be defined based on image segmentation. The resulting communities would not resemble regular-shaped plots but would be closer to the oldest irregular plots established by Josias Braun-Blanquet in the SNP in 1917. Sometimes taking a step back could be the best way forward.

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Curriculum Vitae

CHRISTIAN ROSSI

Education

- 2016-2021** PhD candidate, University of Zurich Remote Sensing Laboratories, Swiss Federal Institute for Forest, Snow and Landscape Research WSL and Swiss National Park. PhD Thesis: *Remote sensing of grassland biodiversity*. Focus: Satellite, UAV and airborne optical data, biodiversity of alpine meadows and pastures, plant traits
- 2013-2015** MSc in Environmental Engineering, University of Trento (Italy). Master thesis investigating the dynamics of active channels in gravel bed rivers with optical data taken in the laboratory. Focus: river engineering, river morphology, hydrological modelling, natural hazards and ecology. Erasmus period of six months at the Luleå University of Technology (Sweden).
- 2009-2013** BSc in Environmental Engineering, University of Trento (Italy). Focus: mathematics, physics, chemistry and GIS.

Professional Experience

- 2016-2021** Research assistant, Research and Geoinformation Department, Swiss National Park. Focus: research coordination, database management, interactive web apps, data and GIS analysis, temperature monitoring, supervision of interns, student excursions
- 2018-2019** Teaching assistant for GEO113 Fernerkundung und Geographische Informationswissenschaft I - Earth Perspective courses within the Department of Geography, University of Zurich.

Graduate courses and training

- Promotionsseminar I
- Promotionsseminar II
- Principles and Theory in geography
- Graduate school retreat I & II
- Scientific writing course
- Voice training and presentation skills
- Making science videos for the web
- Storytelling skills
- Proposal Writing & Funding
- Vegetation Ecology Lab
- Ecosystem Services Workshop
- Creating the job hunting package
- R course
- Landscape ecology
- SQL and database design
- Summer School Close-range Sensing in Alpine Terrain

Publications and Conferences

Publications **Rossi, C.**, Kneubühler, M., Schütz, M., Schaepman, M.E., Haller, R.M., and Risch, A.C.: From local to regional: Functional diversity in differently managed alpine grasslands, *Remote Sensing of Environment*, 236, 111415, <https://doi.org/10.1016/j.rse.2019.111415>, 2020.

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Conference proceedings **Rossi, C.**, Risch, A.C., Schütz, M., Kneubühler, M., Schaepman, M.E., and Haller, R.M.: A regional assessment of functional diversity in heterogenous grassland with different agricultural management, <http://www.parks.ch/snp/pdf>, 6th Symposium for Research in Protected Areas, November 2017, Salzburg.

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Conferences **Rossi, C.**: Assessing plant traits from Sentinel-2 images: a physical based approach in differently managed alpine grasslands, EO4Alps, 27-29 June 2018, Innsbruck.

Rossi, C.: Assessing plant traits from Sentinel-2 images: a physical based approach in differently managed alpine grasslands, *Graubünden forscht* 2018, 19-20 September 2018, Davos.

Rossi, C.: Assessing plant traits and diversity from local to regional scales in differently managed alpine grasslands, 16th Swiss Geoscience Meeting, December 2018, Bern.

Rossi, C.: Sentinel-2: A frequent detector of functional diversity on broad spatial scales, Living Planet Symposium, 13-17 May 2019, Milan.

Rossi, C.: Contemplating Spatial and Temporal Components of Functional Diversity: Full Exploitation of Satellite Data for Biodiversity Monitoring, World Biodiversity Forum, 23-28 February 2020, Davos.

Other
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lications Anderwald, P., **Rossi, C.**, and Schütz, M.: Nahrungsangebot in Raum und Zeit. in: Nahrungsnetze im Schweizerischen Nationalpark. Nat.park-Forsch.Schweiz 109/1 (eds. Schütz, M., Anderwald, P., and Risch, A.C.), Haupt Verlag, Bern, 11-22, 2020.

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Reviewer for journals

- Remote Sensing of Environment
- Remote Sensing
- Journal of Environmental Management