Satellite remote sensing of plant functional diversity

Hauser, L.T.

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Chapter 1.: General introduction

1.1. On the importance of monitoring biodiversity

There is widespread consensus that biodiversity is crucial for the resilience of Earth's ecosystems. Yet, the current and projected rates of biodiversity loss are largely exceeding historic rates of biodiversity decline (IPBES, 2019; Rockström et al., 2009), and are currently mostly driven by the impacts of human activities on the planet (Chapin et al., 2000; Rands et al., 2010). Sustaining biodiversity has been a central focal point within nature conservation and environmental management efforts (Blab et al., 1999) but its importance is increasingly acknowledged across fields, sectors and stakeholders (IPBES, 2019).

To enable a deep understanding of the pace, drivers and consequences of changes in biodiversity, we need reliable and well-understood methods to monitor biodiversity dynamics across large areas and over prolonged periods of time (Rands et al., 2010). The need and importance of a global, harmonized biodiversity observation system that can deliver frequent and relevant data is increasingly recognized by scientists and decision-makers as crucial for biodiversity conservation (Jetz et al., 2016; O'Connor et al., 2015; Rocchini et al., 2015; Skidmore, 2015). Sole reliance on traditional field sampling methods to meet this challenge is widely considered unfeasible given the spatial and temporal scales involved (O'Connor et al., 2015; Scholes et al., 2012). This has inspired a growing body of research on alternative monitoring tools including the application of remote sensing for large-scale monitoring of plant biodiversity (Wang and Gamon, 2019).

As of 1st January 2021, there are 94 operational dedicated earth observation satellites orbiting our planet, collecting tremendous amounts of data about earth's atmosphere and surface (Spacebook, 2021). Can we use this wealth of observational data to better monitor the complex biological diversity embedded in our planet's ecosystems? This dissertation thesis examines the capabilities of multispectral satellite remote sensing to map plant biodiversity, with focus on the European Space Agency (ESA)'s flagship Sentinel-2 satellite, by considering different approaches, conditions, scales, and means for validation. This introductory chapter provides a brief overview of the most pressing current knowledge gaps that persist and have challenged the use of operational multispectral satellite earth observations in biodiversity research thus far, and introduces the four research chapters of this thesis.

1.2. What is biodiversity?

In its broadest definition, biodiversity encompasses the totality of variation in life on Earth (DeLong Jr, 1996; Gaston, 2010). This definition transpires that biodiversity is a multi-layered concept embodying a great variety of phenomena at different (nested) conceptual levels and spatial scales following the central organizing principles of modern biology (Anderson, 2018; Gaston, 2010). This is mirrored by the different dimensions of biodiversity that have emerged in the scientific literature, offering a variety of perspectives in grasping variation of life, including taxonomic diversity, phylogenetic diversity and functional diversity (Meatyard, 2005). Combining these dimensions, the term biodiversity includes the diversity of all species originated through evolutionary history across the tree of life, the genetic variation within them, and the vast variety of functions that each organism, species and ecosystem possess to access and allocate resources for life to persist. Inherent to its multidimensionality, biodiversity is complex to measure and not graspable by a single indicator (Hamilton, 2005; Kaennel, 1998). Holistic efforts to monitor, quantify and study biodiversity will require integrative approaches that go beyond solely taxonomic identities and aim to incorporate intra- and interspecific traits in an attempt to comprehensively quantify diversity in ecological communities (Mason et al., 2005; Violle et al., 2014).

Ecosystem functioning is strongly tied to biodiversity (Tilman et al., 2014). A large body of research underpins that the combined functional traits (i.e. functional diversity) rather than the taxonomic identity of organisms (as represented by species diversity) play a crucial role in shaping the relationship between biodiversity and ecosystem functioning (Díaz et al., 2007; Duncan et al., 2015; Funk et al., 2016). These traits represent measurable features of an organism that influence performance, fitness, or resource strategies (Cadotte et al., 2011; Musavi et al., 2015). Combinations of traits and the diversity thereof within a community relate to the variety of strategies, responses, and coping mechanisms prevailing in an ecosystem - affecting its productivity, adaptability, vulnerability to disturbances as well as ecosystem functioning more generally (Cadotte et al., 2011; Cardinale et al., 2011; Grime, 1998; Hooper, 2002; Isbell et al., 2011; Mori et al., 2013; Ruiz-jaen and Potvin, 2010). As such, the assessment of functional diversity patterns is highly relevant to monitoring the health (productivity, stability) and biodiversity of our ecosystems (Schneider et al., 2017). At present, however, taxonomic diversity (species) tends to be the most common measure in biodiversity research and conservation practice (Gaston, 2010), with functional diversity mostly applied to relatively small spatial scales (Karadimou et al., 2016; Smith et al., 2013). In response, throughout this thesis, I have emphasized work towards the large-scale monitoring of plant functional diversity through satellite remote sensing, with complementary consideration of taxonomic diversity (species).

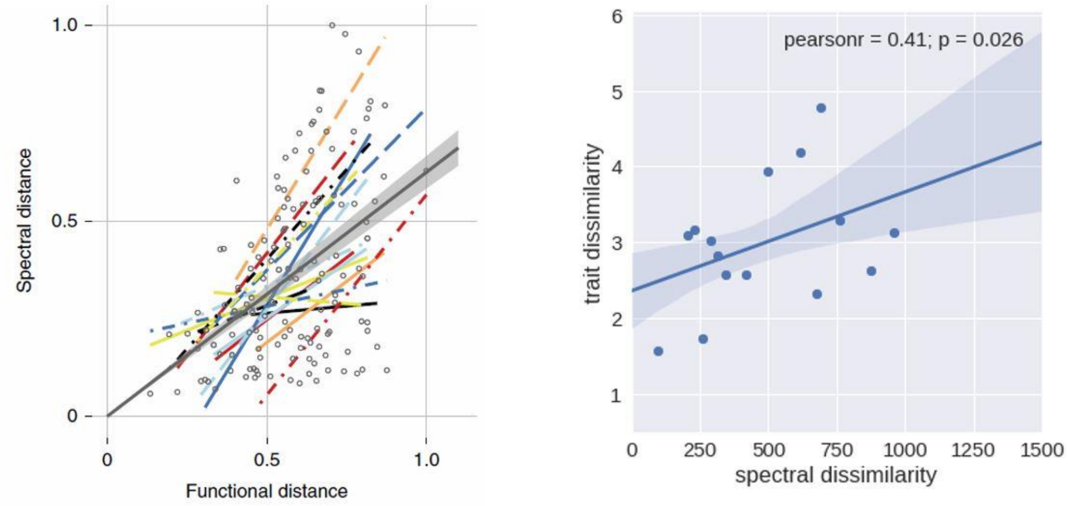
1.3. The promise of remote sensing

1.3.1. Need for quantitative monitoring of large-scale biodiversity dynamics

Improved monitoring of biodiversity dynamics at large scales can equip us to better understand and act upon its changes in order to successfully address biodiversity losses and halt further exacerbation of the ongoing crisis (O’Connor et al., 2015; Skidmore, 2015). Traditional field measurements for assessment of plant diversity in terrestrial ecosystems are laborious and therefore have generally been small-scale, discrete, and limited in spatial extent (Asner et al., 2015; Chiarucci et al., 2011; Götzenberger et al., 2012). Combined field efforts, and inclusion of airborne/drone local campaigns, in networks and global traits databases still tend to be inconsistent, and temporally and geographically constrained (Jetz et al., 2016) or bound by the limitations of interpolation (Granger et al., 2015). While these field studies and networks thereof are extremely valuable, they will likely not suffice to address the data gaps in biodiversity research especially when it comes to large-scale, spatially continuous, repeated assessments of inter-, and intra- specific variation. The deployment of satellite earth observation measurements, on the other hand, offers currently attainable and repeatable global coverage. Unsurprisingly, a growing body of research has acknowledged the potential of satellite remotely sensed spectral information to derive or serve as proxies of biological diversity on the ground as a timely and important opportunity to detect changes in the Earth's biodiversity over large regional scales across our planet (Rocchini, 2007; Schmidtlein and Fassnacht, 2017; Torresani et al., 2019).

1.3.2. The potential of optical remote sensing of vegetation

Remotely sensed radiative properties provide critical information on the features of the Earth's surface (Anderson, 2018; Butler, 2014). Since its earliest explorations, the scientific community has established a strong tradition of studying vegetation spectral characteristics in the terrestrial sphere (Jensen, 2013). Optical remote sensing benefits from the evolution of plants in interaction with solar radiation. Many of the aboveground plant properties (physiology, biochemistry, and structure) can be captured through spectral responses from solar reflection (Homolová et al., 2013). The way plants interact with sunlight and harvest solar energy through photosynthesis provides a window into plant strategies for resource allocation and, combined together, to the functioning of entire ecosystems (Ollinger, 2011). Consequently, distinctive features of vegetation and related resource strategies are conjointly imprinted in the reflectance spectra as light interacts with the chemical bonds and structural composition of plants. As such, plant spectra integrate functional and phylogenetic components that are relevant in quantifying biodiversity. Several empirical studies, such as those performed at the Cedar Creek biodiversity experiment site (Schweiger et al., 2018) and those performed for mangrove ecosystems (Hauser et al., in prep), provide evidence to support the idea that plant functional dissimilarity (of aboveground traits) translates into spectral dissimilarity. Thus, spectral reflectance can serve as an important informant of ecological functioning and the diversity of vegetation found in-situ. Fig. 1.1 presents the relationship between spectral dissimilarity and functional dissimilarity found in both datasets.



Schweiger et al. (2018):
Leaf traits vs spectra of
19 perennial grassland-prairie species

Hauser et al. (in prep):
Spectral versus trait dissimilarity
Six common mangrove species (Ca Mau, Vietnam)

Fig. 1.1: The relationship between spectral dissimilarity and functional dissimilarity found in leaf trait spectra across 19 perennial grassland-prairie species (left) and six common mangrove species found in Ca Mau, Vietnam (right).

The trait - spectral dissimilarity relationships are based on radiative interactions of the incoming light with the biochemical, biophysical, and structural characteristics of individual plants and the propagation of light back through the canopy to the observer. Different plant properties interact differently with the light of different wavelengths (spectral regions). For instance, at the leaf level, reflectance in the visible part of the spectrum is dominated most strongly by leaf pigments, such as chlorophyll and senescent material, and in the infrared region, spectral responses are dictated heavily by cellular molecules (including water) as well as structural components, such as cell-wall thickness, waxiness of the cuticle and trichomes (Feret et al., 2008). While, at the canopy level, spectral reflectance is shaped more by canopy structure, such as branching structure, leaf size, leaf clumping, leaf angle distribution, and canopy water storage, especially in the infrared regions (Asner, 1998; Ollinger, 2011).

The analysis and understanding of the trait-spectra relationships can help us decipher the sources of variation that contribute to spectral variation in vegetation. Specifically, spectral responses are guided by the universal principles of physics which can describe the interaction of light with vegetation elements (Verhoef, 1998). To model and simulate these principles, the development of radiative transfer models (RTMs) has sought to describe the relationships between incident radiation to vegetation based on the physical relationships to angular, structural, biochemical, and biophysical characteristics (Jacquemoud and Ustin, 2019; Jacquemoud et al., 2009; Verhoef, 1998). At present, RTMs encapsulate our best mechanistic understanding of the coordination among leaf properties, canopy structure, and resulting spectral signatures at the leaf and canopy scales, but abstracted to operate with different degrees of complexity and assumptions (Jacquemoud and Ustin, 2019). When used in inversion, different RTMs can be applied either at the leaf and canopy scales to retrieve leaf traits from spectral reflectance or in hybrid approaches where statistical algorithms are trained on RTM simulations (Verrelst et al., 2019a).

Even so, spectral profiles do not capture all critical aspects of plants. A clear example is the range of important functional traits that do not interact with light, such as seed mass or root length for instance. In particular, optical satellite remote sensing is constraint by the relatively superficial penetration depth of visible and near-infrared radiations, and as such mostly focuses on the overstorey (top of the) canopy. This limits insight into lower layers of the canopy. Nevertheless, overstorey and understory ecological processes are strongly related and in constant interaction (Chamagne et al., 2016; Li et al., 2018; Poorter and Bongers, 2006; Wu et al., 2017).

1.3.3. Translating spectra to plant diversity concepts

The interaction of vegetation with light creates spectral signatures of the terrestrial environment of our planet that can help to elucidate biodiversity patterns and the identification of functional traits and diversity thereof. Not much consensus exists yet on how to link these optical features to determine biodiversity metrics at multiple scales and to develop robust measures for a more complete understanding of species and functional mixtures as biodiversity components (Skidmore, 2015; Wang and Gamon, 2019). Wang and Gamon (2019) categorized remote sensing approaches to biodiversity assessments into four types of remote sensing approaches intended to yield plant diversity estimates (Fig. 1.2). These include: i) the characterization of habitat, ii) mapping the dominant vegetation through species identification, iii) information entropy through optical/spectral diversity metrics, and iv) quantifying functional diversity through spectrally derived plant functional traits. This information is then used to link to the standard traditional biological metrics of species or functional diversity.

Comparative research on the performance of different approaches and metrics from multi-spectral satellite platforms in estimating plant diversity remains limited. These four approaches involve:

- Habitat-based approaches utilize indirect methods of assessing biodiversity. Habitat heterogeneity has been regarded as a key factor governing species richness and as a covariate of biodiversity (Stein et al., 2014). In general, habitat mapping approaches tend to focus on classification systems based on environmental conditions rather than assessing biodiversity through functional or taxonomic composition.
- The use of satellite-derived spectral profiles for species mapping has been widely considered, yet thus far has seen only a few applications to complex ecosystems (Shoko and Mutanga, 2017; Wang et al., 2018). Spectral discrimination of species stands has generally been shown to be challenged in multi-spectral settings due to spectral and functional similarities among species and relatively large intra-specific variation in both spectral and functional characteristics (Cochrane, 2000; Hennessy et al., 2020; Price, 1994; Vaglio Laurin et al., 2016). Furthermore, heterogeneous ecosystems will require large, yet hard-to-acquire, libraries of species spectral endmembers to facilitate species discrimination (Vaglio Laurin et al., 2016). As such, species discrimination based on spectra alone is extremely challenging in complex ecosystems. This is further complicated by the limited spatial resolution of satellite remote sensing which implies that spectral signals are aggregates of multiple canopies and their background.

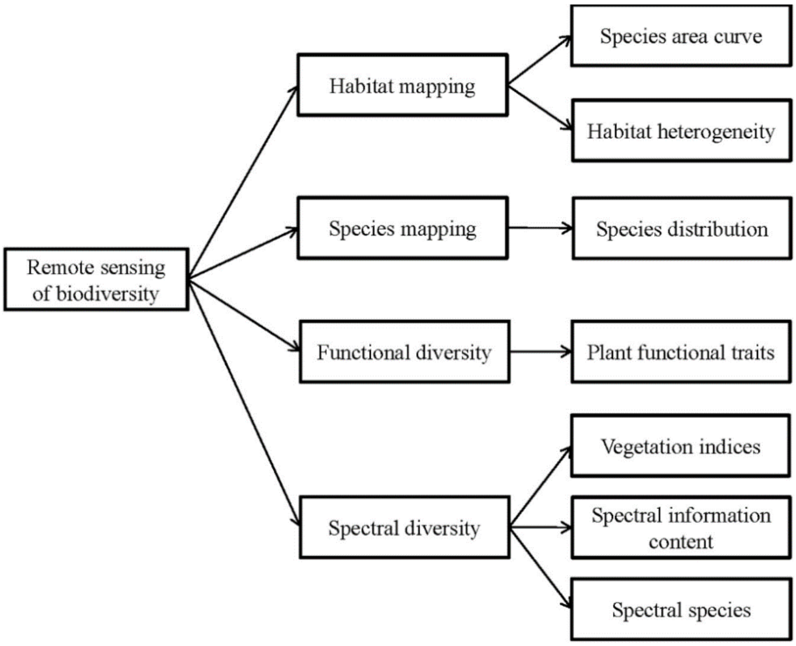


Fig. 1.2: Classification of different approaches to remote sensing of plant biodiversity developed by Wang and Gamon (2019) which illustrates four broad methodological categories, along with examples of specific sub-methods. In this thesis, the focus lies on the bottom two approaches implemented for multispectral satellite-based observations.

- Spectral measurements have been exploited directly in relation to biodiversity. Entropy in spectral information has been proposed to predict taxonomic diversity in the ‘Spectral Variability Hypothesis’ (Palmer et al., 2002). This hypothesis suggests that the diversity in spectral reflectance of an area is representative of in-situ plant diversity (Rocchini et al., 2010). Based on this, spectral diversity metrics dealing with the variability in spectral information have been deployed as a proxy of plant diversity in several (mostly airborne-based) studies (e.g. review by Wang and Gamon, 2019). Two theoretical concepts are central in the link between spectral diversity and in-situ plant diversity, namely 1) the physical relationship between optical properties and plant characteristics which is fundamental to radiative transfer theory (see section *1.3.2.*), and 2) the surrogacy hypothesis. The first emphasizes that spectral diversity directly captures plant variability through spectral differences caused by morphological, biochemical, physiological, and structural characteristics (Jacquemoud et al., 2009, 2006; Ollinger, 2011; Verhoef, 1998). The second suggests that spectral diversity can capture plant diversity indirectly through spectrally observable landscape heterogeneity or ‘environmental surrogacy’, as environmental heterogeneity drives plant diversity (Ewers et al., 2005; Palmer et al., 2002; Rocchini, 2007; Wang and Gamon, 2019). In addition to using spectra directly, vegetation spectral diversity may be based on direct derivates of spectra, such as vegetation indices (Rocchini et al., 2018), principal components (Gholizadeh et al., 2018; Rocchini et al., 2004), or the clustering and classification of reflectance spectra in ‘spectral species’ (Féret and Asner, 2014).

- Spectral signatures of vegetation can also be used to derive functional properties and from there calculate functional plant diversity. This can be relevant as not all spectral information captured might relate equally to plant diversity or covariates thereof (Asner, 1998). Methods for reflectance-based retrieval of plant trait estimates can be divided into two broad approaches; 1) purely statistical data-driven methods relying on empirical observations, or 2) physics-based inversion of an RTM either through look-up tables or hybrid approaches that use machine learning trained on RTM simulations (Verrelst et al., 2015). The use of optical traits that are physically related to spectra is particularly appealing given its universal applicability and relative independence of scarce in-situ measurements. The latter holds considerable advantages in terms of transferability as opposed to the former statistical approaches which heavily depend on comprehensive field measurements for training and that have been found to be site- and time-specific (Verrelst et al., 2015; Clevers, 2014; Ali et al., 2020a). Through physics-based simulation, we can generate large sets of training data for models to retrieve plant trait estimates and overcome the difficulty and scarcity of acquiring high-quality and harmonized in-situ measurements. These optically-derived trait estimates from spectral reflectance hold potential to be used in quantitative metrics of functional diversity (Botta-Dukat, 2005; Cornwell et al., 2006; Villéger et al., 2008). These metrics are traditionally developed for ecological data, however, recent adaptations for geometric pixel-based remote sensing data have been implemented with success in studies using airborne imaging spectroscopy (Durán et al., 2019; Gholizadeh et al., 2018; Schneider et al., 2017). Implementations of physics-based approaches to derive large-scale multivariate functional diversity from satellite remote sensing are at the time of writing still unstudied.

1.4. Challenges in linking ecological and remote sensing concepts of biodiversity

1.4.1. The next frontier: satellite remote sensing of plant biodiversity

The majority of the literature on remote sensing of plant biodiversity relies on the use of high-resolution or hyperspectral airborne remote sensing (Asner and Martin, 2009; Durán et al., 2019; Féret and Asner, 2014; Schneider et al., 2017) or emphasizes the need and potential of forthcoming high-resolution hyperspectral satellite remote sensing to conduct biodiversity assessments (Hill et al., 2019; Jetz et al., 2016). The focus on airborne and anticipated space-borne hyperspectral imagers can be understood as higher spatial and spectral resolutions present more opportunities to assess plant canopies in detail. However, airborne remote sensing campaigns remain relatively small-scale and cost-inefficient to overcome the biodiversity data gaps present at large (regional and global) scales and repeated over time. Therefore, the use of satellite remotely sensed earth observation is regarded as a crucial operational strategy to tackle current shortcomings for biodiversity and conservation, providing reliable technical solutions at global and timely scales.

Although the launch of high-resolution hyperspectral satellites is anticipated for the near future, research on the viability of currently operational satellite remote sensing for mapping plant diversity is much needed given the urgency of current crisis-level biodiversity losses. In addition, current empirical research on operational satellite missions will support a steep learning curve for the development of future satellite remote sensing sensors and methodologies. Therefore, a driving force behind the research done in this thesis lies in the discrepancy between the scientific acknowledgment of the role of satellite remote sensing for mapping plant biodiversity, and yet the lack of validation of currently operational satellite remote sensing to retrieve plant functional and taxonomic diversity estimates.

While remote sensing is increasingly advertised as a potential contributor to a global biodiversity monitoring system, a key question that remains is how to manage expectations on what can realistically be done with currently operational satellite earth observation platforms? From an engineering perspective, the capability of what can be achieved for biodiversity monitoring using satellite earth observation platforms depends on the specifications of the onboard instruments. Particularly relevant are the specifications that determine a sensor's capabilities and the value of their environmental observations which broadly include; spatial resolution (pixel size), temporal resolution (revisit time), and spectral resolution (wavelength range, number of bands, bandwidth), and signal-to-noise ratios.

At orbital altitudes, adequate signal-to-noise ratios can be attained by reducing the spectral resolution (combining narrow bands into broadbands, e.g., via spectral binning), or by reducing spatial resolution (e.g., pixel binning), but these choices limit the ability to distinguish individuals, species, and functional traits due to the degradation of spectral and spatial information (Gamon et al., 2020). In consideration of these trade-offs, the current fleet of earth observation satellites relies on sensors that operate at spatial and spectral resolutions that are generally inferior to airborne hyperspectral instruments. These constraints challenge a fine-grained local-scale interpretation, pose difficulties for validation of biodiversity estimates, and exhibit ill-posedness when retrieving multiple plant diversity indicators from limited spectral broadbands (Baret and Buis, 2008; Wang and Gamon, 2019). In acknowledgment of these challenges, the exact capabilities of satellite remote sensing for mapping biodiversity – remains understudied.

To assess what realistically can be achieved using currently operational satellite remote sensing, this thesis focuses on the application of Sentinel-2 observations for estimating plant diversity. Sentinel-2A was launched in 2015 and Sentinel-2B in 2017 which implies that by now they offer a significant and interesting catalog that consists of multiple years of observation. The pairing of Sentinel-2A and 2B form a constellation of polar-orbiting wide-swath multispectral imaging systems for land monitoring of vegetation, soil, water, and cover with 5–10 days revisiting time. Sentinel-2 provides improved spatial and spectral resolutions compared to most of its predecessors and peers including the Landsat satellites. Sentinel-2's spectral configuration includes four bands with 10m pixels (blue, green, red, and NIR) with similar placements to Landsat-8. Six bands are ingested at 20m pixels (in the red edge, NIR and SWIR). Three bands are measured at 60m spatial resolution for calibration. The placing of the 10-20m bands is of particular interest for monitoring of vegetation and includes - besides strong coverage of the visible and NIR ranges - four unique red-edge narrowbands that are of high relevance for plant/ ecosystem stress detection (Ustin and Middleton, 2021).

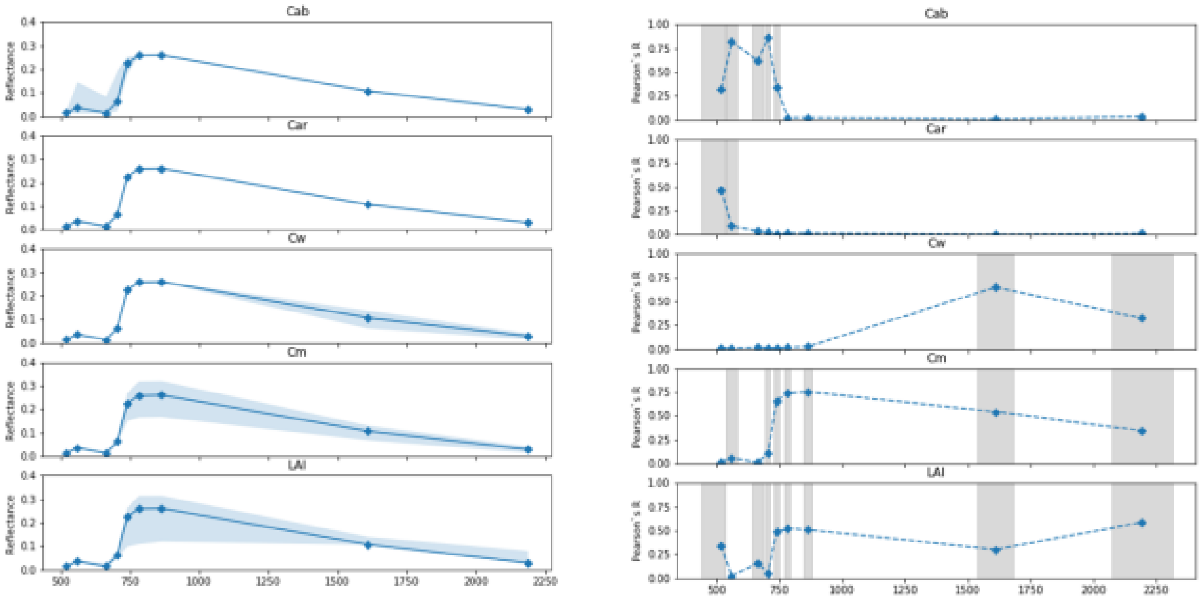


Fig. 1.3: Sensitivity analysis of PROSAIL's vegetation parameters (Chlorophyll content: (Cab), Carotenoids Content (Car), Leaf water Content (Cw), Leaf Mass per Area (Cm), and Leaf Area Index) to the spectral lay-out of Sentinel-2 MSI 10-20m bands. The left pane illustrates the range of variability in spectral response to changes in the parameters while all other parameters are kept constant at modes defined in Weiss and Baret (2016). The right pane depicts the correlation (Pearson's R) of different bands to changes the parameters using a range of simulations defined in Weiss & Baret (2016).

Prior to the studies presented in this thesis, a sensitivity analysis has been conducted to assess the potential of Sentinel-2's spectral layout for retrieval of physics-based vegetation parameters using the PROSAIL canopy RTM. The analysis is presented in Fig. 1.3. The results were later integrated in the work of de Sá et al. (2021). With the exception of carotenoids, Sentinel-2's bands show high responsiveness to PROSAIL's biophysical parameters. Based on this sensitivity analysis, Sentinel-2 observations therefore hold potential for the application to study plant diversity patterns. This thesis studies the performance and ecological relevance of

Sentinel-2 spectral observations for mapping in-situ plant diversity patterns dealing with the limitations of (coarser) spatial and spectral resolutions, and signal-to-noise ratios of these observations.

1.4.2. Disparities in the concept of scale in ecology and remote sensing

Our perception of biodiversity is affected by the spatial and conceptual scale of observation (Field et al., 2009; Jarzyna and Jetz, 2018). A general rule of thumb in ecology is to match the scale of observation with the phenomena of interest (Levin, 1992). However, this rule of thumb is severely challenged for remote sensing approaches to map plant diversity. In ecology, the concept of scale refers to the sampling scale shaped by the units of observation, i.e. grain size, and the extent of field sampling designs (Field et al., 2009). Importantly, biodiversity is defined through different levels of organization, i.e. conceptual scales or dimensions (see section 1.2 What is biodiversity?). Biological diversity can be assessed at within and between ecological communities scaling concepts (Whittaker, 1972; Jurasinski et al., 2009; Whittaker, 1972). Yet, the concept of communities is rather abstract. Vellend (2010) defines an ecological community as *"a group of organisms representing multiple species living in a specified place and time"* from which it can be derived that it is larger than the size of an individual organism, but how much larger is object dependent. In reality, the concept of community proves to be hard to define and is subject of considerable debate (Ricklefs, 2008).

In contrast, in remote sensing, scale has different dimensions, including; spatial, spectral and temporal dimensions (Anderson, 2018). The *spatial* dimension typically refers to the pixel size (grain size) and spatial extent of a remotely sensed image, but does not account for concepts of ecological communities. Diversity within or between communities therefore requires the challenging translation of the community concept through clusters of pixels requiring (arbitrary) scaling decisions or delineation. The *spectral* dimension includes band position, bandwidth, band interval, and spectral range dictated by the sensor instrument and further processing of data. The *temporal* dimension can refer to the time of sampling, revisit frequency, or temporal extent of observations.

While the number of fine-grain earth observation sensors in orbit is quickly increasing, allowing for smaller-scale, landscape, and even species- and community-scale patterns (Butler, 2014), the mismatch between ecology's sampling units and the homogenous relatively coarse raster offered by satellite remote sensing remains to exist (Wang and Gamon, 2019). This mismatch is further exemplified by the continuous nature of remotely sensed observations captured in geometric pixels versus the discrete spatial irregularities of ecological concepts (Laliberté et al., 2019). Mapping plant diversity from satellite observation requires a transfer of community diversity concepts from ecology to pixel-based remote sensing. This includes the initial translation of the community concept into clusters of pixels or, eventually, it may even be questioned whether the strong ecological focus of within vs. between communities may be maintained given that the spatially explicit continuity in remote sensing allows for multi-scale analyses of diversity patterns across community of different sizes. All in all, these differences point to the need for reconciliating traditional 'fluid' discrete ecological units of diversity as opposed to the spatially continuous yet fixed geometric pixels of remote sensing instruments.

1.4.3. Training and validation

Large-scale spatially explicit assessments on plant diversity represent a data and knowledge gap that can potentially be addressed by the deployment of satellite remote sensing (Jetz et al., 2016). Yet, exactly here lies a paradox: the difficulties in acquiring temporally and spatially consistent ground-data over large areas present a clear added value for the application of satellite remote sensing to achieve such. At the same time, the scarcity and mismatch of present data challenges the means to train data models to retrieve plant diversity estimates and validate these outcomes from satellite earth observation.

Scaling and relating field measurements to satellite remote sensing pixels requires upscaling taxonomic observations or leaf measurements to canopy-level or aggregate canopy community level that relate to the pixel raster of satellite observations (Abelleira Martínez et al., 2016). Notably, plant traits measured at the leaf level are not necessarily indicative of functional differentiation at the canopy level. The latter is influenced by plant height, canopy architecture and morphology, average leaf angle and leaf area per square meter and the spatial plant community composition. Likewise, from a remote sensing perspective, the strength of the relationship between spectra and the in-situ plant community changes the further we move away from leaf spectra or clearly delineated organismal canopy crowns towards aggregate image pixels at coarser scales common to most wide-swath remote sensing platforms (Cavender-Bares et al., 2020). As a result of this changing scale, vegetation spectra become increasingly aggregated. Depending on the size of canopy, different species will be merged but also with the understory and the abiotic environment (soil, dead biomass, water). Furthermore, in many cases, the overpass of the satellite observations and the in-situ individual species level trait measurements do not match exactly spatially and/or temporally (Schrodt et al., 2020). This requires interpolation which is challenging given the temporal dynamics of ecosystems and the need to account for intraspecific variation and plasticity of traits and species (Hulshof and Swenson, 2010).

Spectral retrieval of plant identities and traits will require prior principles and calibration to establish relationships between remote sensing derived spectra and in-situ ecological phenomena. To overcome the lack of available in-situ training data and the challenges of acquiring such data, the use of physics-based principles of light-vegetation interactions can be applied. It would allow us to model and simulate relevant spectral reflectance versus plant trait relationships in a generic way, even if very limited relevant field data is available (Clevers, 2014). Recently, a number of studies have shown success in applying physics-based RTM inversion on satellite earth observations (Sentinel-2) to estimate key plant traits in (semi-)natural ecosystems (e.g. Ali et al., 2020a, Ali et al., 2020b; Rossi et al., 2020; Vinué et al., 2018). Yet, to our knowledge, none of the existing satellite-based approaches so far has used or assessed the capability of RTM inversion to be applied to derive multiple traits simultaneously to obtain functional diversity estimates in heterogeneous (semi-)natural landscapes.

There are still many unknowns on how to implement scalable physics-based approaches for assessing functional diversity, especially in relation to multispectral satellite remote sensing. Different leaf and canopy scale RTMs exist with more or less subtle differences in parameterization (Bacour et al., 2002; Schlerf and Atzberger, 2006; Weiss and Baret, 2016). RTMs are strongly bound by assumptions which are generally violated to different degrees in (semi-)natural heterogenous landscapes. Diversity patterns are influenced by the number and selection of (RTM-based) traits (Legras et al., 2020). Moreover, there are numerous ways to conduct the inversion of RTMs, e.g. Look-up table based approach with different implementable cost functions, hybrid approaches using neural networks, support vectors machines, gaussian processes et cetera (Verrelst et al., 2019a, 2015). As such, the applicability of these models to large regional scales and across heterogenous landscapes using satellite earth observation will require thorough examination and validation.

In terms of validation, the scale and extent of satellite remote sensing in comparison to common field observations seriously challenges validation efforts for plant diversity assessments. Consequently, thorough groundtruthing of plant diversity estimates from remote sensing is still perceived immature (Kuenzer et al., 2014). So far, most validation studies focused on remotely sensed estimates of single trait mean values in relatively homogeneous (semi-)natural environments (Ali et al., 2020a; Brede et al., 2020; Brown et al., 2019; Darvishzadeh et al., 2019a, 2019b; Padalia et al., 2020; Rossi et al., 2020; Vinué et al., 2018). Many of these validation studies rely on small-scale ground-truthing or approaches that heavily depend on interpolation or extrapolation of spatially and temporally fragmented in-situ data points. Therefore, we need to move towards validation of multivariate functional diversity using precisely matched and geo-referenced in-situ measurements for accuracy assessment to truly examine the capabilities for currently operational satellite remote sensing. Alternatively, when such data cannot be acquired, we can explore qualitative assessments indicative of the responsiveness of satellite-based plant diversity estimates against well-studied ecological gradients.

1.5. Research aims

The research objectives of this thesis relate to the scale disparities we observe between ecology and remote sensing observations at conceptual, spatial, spectral and temporal scales which have challenged advances on the application and validity of currently operational satellite earth observation for inferring spatial plant diversity patterns. Overcoming these challenges requires bridging the traditionally separated fields of ‘remote sensing’ and ‘ecology’ to translate the ecological concepts of plant diversity and scaling thereof into the coarse geometric modes of inference presented by satellite remote sensing. This dissertation thesis examines by qualitative and quantitative validation the capabilities of currently operational multispectral satellite remote sensing (Sentinel-2) to estimate scalable spatial patterns of plant community functional diversity without heavy reliance on a priori in-situ measurements. As such, the research objectives can be broken down in two general aims:

1) *To investigate how spatial plant diversity patterns can be captured by currently operational multi-spectral satellite remote sensing (Sentinel-2)*

2) *To address the lack of quantitative and qualitative validation of the capabilities of currently operational multispectral satellite remote sensing (Sentinel-2) to retrieve scalable estimates of in-situ spatial plant diversity patterns.*

Both aims revolve around the operationalization and capabilities of current satellite remote sensing for observational monitoring of terrestrial plant biodiversity at large regional spatial scales. In order to advance the satellite remote sensing information technologies towards scalable, spatially, and temporally explicit methods for plant diversity assessments, I focus on exploring methods that do not heavily rely on *a priori* field measurements. Specifically, I examined two specific methods to assess biodiversity through remote sensing; 1) the direct use of spectral diversity of the remote sensing signal as a proxy of plant diversity, and 2) the use of plant trait estimates derived from spectral reflectance through physics-based RTM inversion. I demonstrate the operationalization of both approaches for space-borne multi-spectral applications and take a closer look at its performance, workings and interpretation in relation to ecological field observations.

To assess the veracity of satellite remote sensing for mapping plant diversity, I explore the remotely sensed metrics of estimated plant diversity that have measurable in-situ equivalents for posterior ground-truthing against ecological field data. I deploy satellite remote sensing for both plot-wise quantitative assessment and for large regional wall-to-wall continuous mapping of plant functional diversity against qualitative environmental gradients. In addition, I highlight how conceptual and spatial scales (i.e. the scale dependency of observations) affect the way we observe spatial patterns of plant diversity and therefore require active and informed methodological decision-making. This relates conceptually to how we grasp ecological concepts of plant diversity through geometric remote sensing metrics. At the same time, this relates, more practically, to how we match and ground-truth remote sensing estimates with in-situ observations towards mature and validated plant diversity indicators derived from satellite remote sensing.

Chapter 1: Introduction

This introductory chapter provides a background on the definitions and scales through which we can look at biodiversity. The chapter outlines the potential and challenges of using satellite remote sensing to monitor plant diversity at large regional scales. The relevance and aim of this thesis are outlined together with the individual research chapters.

Chapter 2: Explaining discrepancies between spectral and in-situ plant diversity in multispectral satellite earth observation

This chapter assesses the viability of the ‘spectral variability hypothesis’ when applied to multispectral satellite remote sensing. Characterization of commonly used spectral diversity metrics further aims to elucidate the mechanisms that explain the presumed spectral diversity – plant (functional/taxonomic) diversity relationship. Hereto, I use Sentinel-2 imagery and in-situ field trait and species count data collected in the Montesinho area in northern Portugal together with RTM simulations. Specifically, I examine which components contribute to the spectral diversity- plant diversity relationship considering in-situ taxonomic and functional diversity, and the role of confounding factors, including vegetation cover, and landscape morphology (slope and elevation).

Chapter 3: Towards scalable estimation of plant functional diversity from Sentinel-2 imagery: in-situ validation in a heterogeneous (semi-)natural landscape

This chapter examines the use of physics-based RTM inversion to derive optical traits from Sentinel-2 spectral reflectance to derive in-situ measurable plant traits to estimate plant functional diversity patterns. Validation is conducted through direct comparison of satellite remotes sensing estimates against precisely matched and scaled in-situ measurements on (aggregate) plant traits and community functional/taxonomic diversity. In-situ measurements were collected during a dedicated fieldwork campaign in the Montesinho national park region (Portugal). The retrieved trait estimates are derived through scalable models trained on the inversion of physically modelled simulations generated by an RTM rather than heavily depending on a priori field data and data-driven statistical learning.

Chapter 4: Linking land use and plant functional diversity patterns in Sabah, Borneo, through large-scale spatially continuous Sentinel-2 inference

This chapter presents a wall-to-wall spatially continuous inference of functional diversity metrics based on RTM inversion derived plant traits retrieved through Sentinel-2 imagery over the biodiverse and heterogenous region of Sabah, Malaysian Borneo. The large-scale application of satellite remotely sensed plant functional diversity is held against a well-studied ecological gradients of land use and historic regional trait measurements as a means of qualitative validation. This qualitative approach allows assessing the responsiveness and potential merits of spatially continuous inference to study large-scale ecological patterns without heavy reliance on dedicated field measurements.

Chapter 5: Sizing up scale dependence of satellite-based plant diversity estimates: Functional diversity-area relationships observed through Sentinel-2 over the Bornean rainforest-plantation matrix

This chapter looks into the spatial scaling of plant community functional diversity patterns considering the scale dependence of both ecological and remote sensing observations and the disparity in scaling concepts in both fields. Based on spatially continuous inference of functional diversity derived from Sentinel-2 over the biodiverse and heterogenous region of Sabah, Malaysian Borneo, I assess how spatial scaling decisions regarding different pixel-based plot area sizes to grasp the ecological ‘community’ concept affects what spatial patterns we observe. The satellite remotely sensed functional diversity-area relationships are studied across different functional diversity metrics in relation to (semi-)random null models and explanatory drivers of diversity.

Chapter 6: General discussion

This chapter brings together the principal findings studied in this dissertation work. It emphasizes the capabilities and advances to map plant biodiversity presented here while considering different approaches, conditions, scales and means for validation. Common across science is that individual research contributes to (small) new advances and initial inquiries are addressed, yet almost without exception, the same research prompts and inspires numerous new questions and venues for future research. Likewise, based on the advances made in this work, the final chapter elaborates on the implications, prompts new discussions and knowledge gaps arising from the synthesized findings and elucidates steps needed to further the field for satellite remote sensing of plant diversity.