# Satellite remote sensing of plant functional diversity

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Leon T. Hauser

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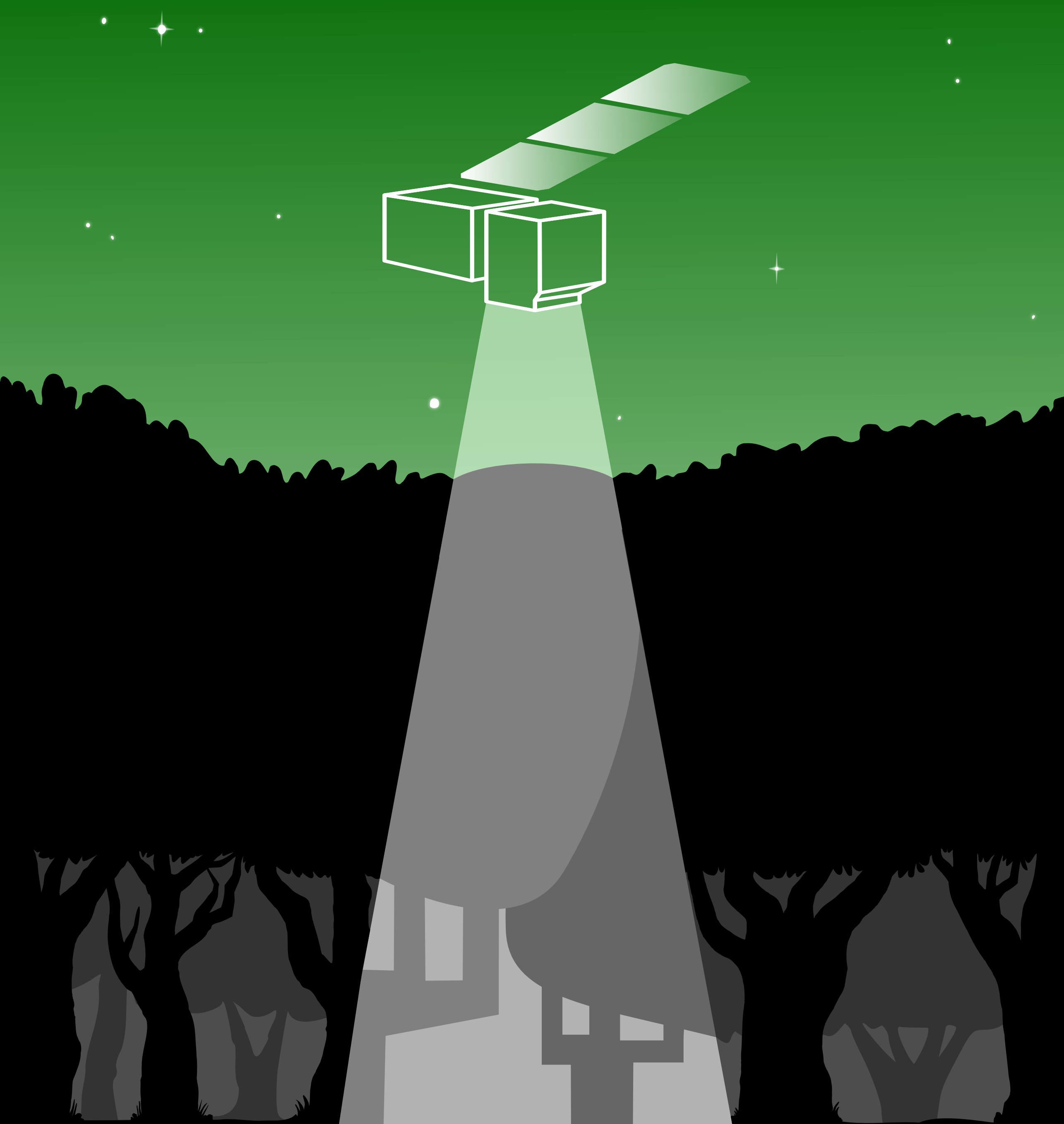

# Satellite Remote Sensing of Plant Functional Diversity

Leon T. Hauser

Satellite Remote Sensing of Plant Functional Diversity

PhD Thesis at Leiden University, The Netherlands

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*To Wil, Otto, and Elke*

*“The most striking feature of earth is the existence of life.*

*The most striking feature of life is its diversity”*

David Tilman (2000)

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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).

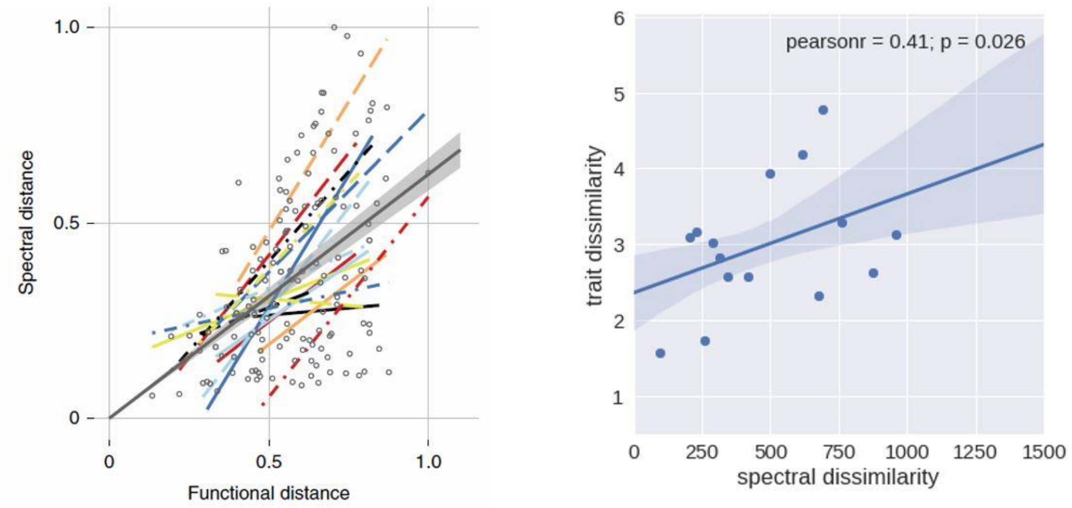
## 1.3. The promise of remote sensing

### 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.

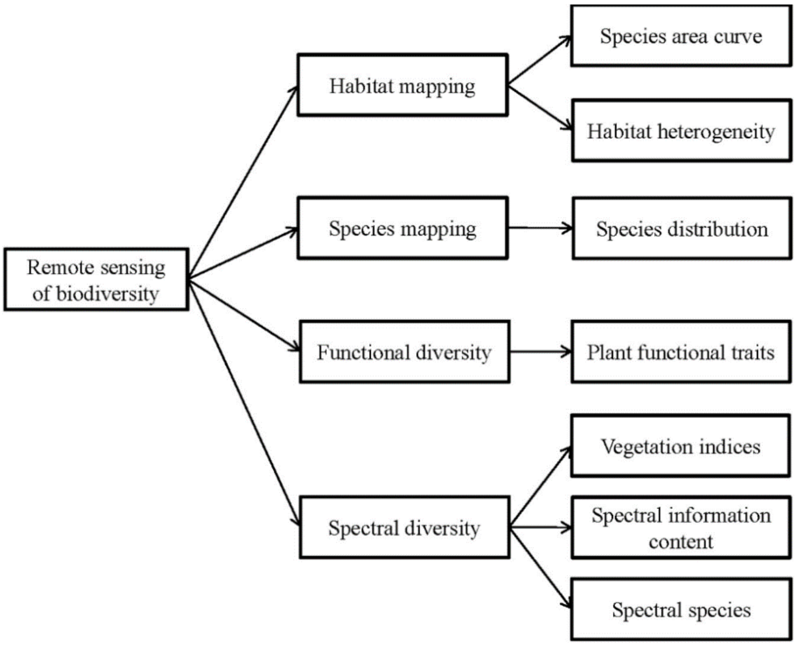


*Fig. 1.2: Classification of different approaches to remote sensing of plant biodiversity developed by Wang and Gamon (2019) which illustrates four broad methodological categories, along with examples of specific sub-methods. In this thesis, the focus lies on the bottom two approaches implemented for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

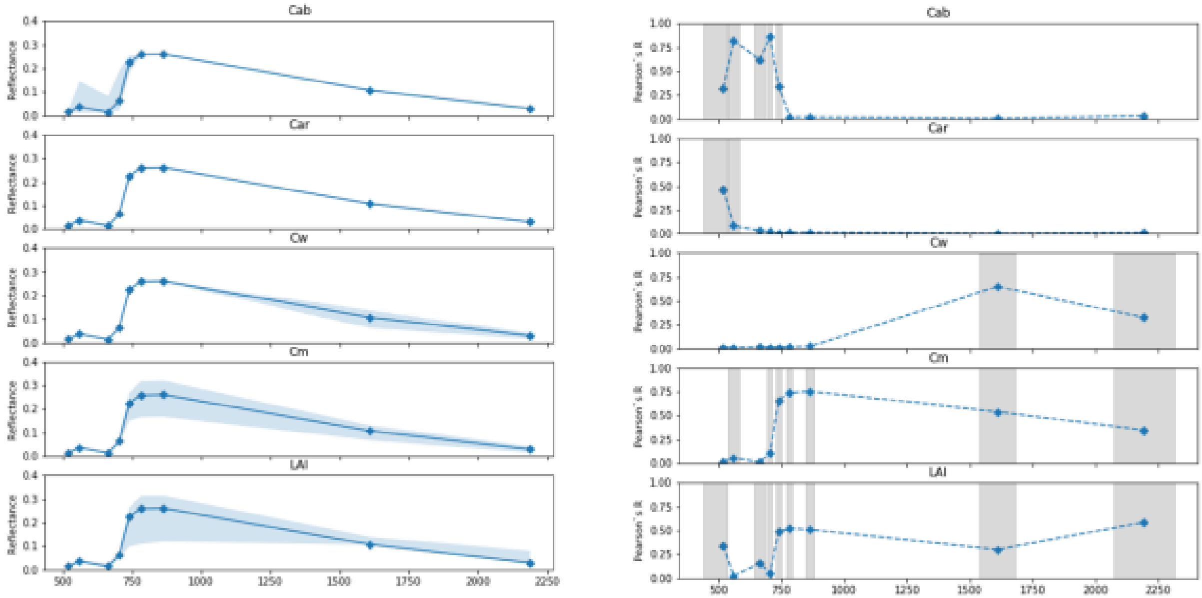


*Fig. 1.3: Sensitivity analysis of PROSAIL's vegetation parameters (Chlorophyll content: (Cab), Carotenoids Content (Car), Leaf water Content (Cw), Leaf Mass per Area (Cm), and Leaf Area Index) to the spectral lay-out of Sentinel-2 MSI 10-20m bands. The left pane illustrates the range of variability 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.

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

**Based on**:

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## Abstract

In light of the ongoing global biodiversity crisis, the urge to monitor and map terrestrial plant biodiversity at large spatial extents has spurred research on adequate quantitative methods. The use of spectral diversity metrics from different remote sensing platforms has emerged as a promising tool for such biodiversity assessments. Satellite remote sensing presents the next frontier for implementation of these methods to assess plant diversity with spatial and temporal continuity at truly regional or global scales. However, the question of what exactly is monitored by spectral diversity metrics from relatively coarse multi-spectral satellite observations has remained largely unanswered.

In this research, we examined which components contribute to satellite remotely sensed spectral diversity. We assessed the relationships between spectral diversity and in-situ taxonomic and trait diversity, and evaluated the role of confounding factors, vegetation cover, and landscape morphology (slope and elevation), in shaping these relationships. Hereto, we used Sentinel-2 imagery and in-situ field trait and species count data collected in the Montesinho-Nogueira Natura 2000 site (Portugal) together with radiative transfer models to quantify the theoretical link between in-situ trait diversity and simulated spectral diversity.

Through the use of linear mixed-effect models, our results highlight that variation in vegetation cover dominates the Sentinel-2's spectral diversity signal (contributing 53-84% of the $R^2_{\text{marginal}}$). The vegetation cover component encompasses spatial variability in canopy architecture traits as well as the fraction of bare soil and plant litter spectra. These elements together strongly impact the overall spectral diversity signal, as shown both in our radiative transfer simulations and empirical comparisons. Next to vegetation cover, we found that taxonomic diversity is a significant predictor and covariate of spectral diversity, while the role of leaf trait diversity appeared insignificant in our multispectral dataset.

Variation in vegetation cover dominated the spectral diversity signal in our study while it is not necessarily correlated with plant diversity. We, therefore, recommend that future applications of multi-spectral diversity metrics consider the impact of vegetation cover, including soil variability and the role of morphological traits, in shaping leaf trait - canopy reflectance relationships to better understand the ambiguous performance of spectral diversity as a proxy

of plant diversity. This will result in higher robustness, consistency, and scalability of spectral diversity metrics for predicting in-situ plant diversity across scales, sensors, and ecosystems in regional biodiversity assessments.

## 2.1. Introduction

Over the past few decades, the threats to global biodiversity have continued to increase. These threats mostly involve anthropogenic pressures, such as habitat loss and fragmentation, overexploitation, climate change, and pollution (IPBES, 2019; Rands et al., 2010). A large consensus exists on the evident importance of biodiversity for vital Earth system processes and the resilience thereof (Cardinale et al., 2012). Consequently, many national governments have set targets and are committed to halting biodiversity losses, as formulated by the Convention of Biological Diversity in the Aichi Biodiversity Targets (O'Connor et al., 2015; Pettorelli et al., 2016), and the Post-2020 global biodiversity framework (CBD, 2020a, 2020b). To reach these ambitious goals, decision-making needs to be supported with well-understood and reliable indicators to track the current trends and state of biodiversity (Jetz et al., 2016; O'Connor et al., 2015; Pettorelli et al., 2016; Rocchini et al., 2015).

Biodiversity is multidimensional and includes the diversity of species (taxonomic diversity), the genetic variation within them (phylogenetic diversity), and the vast variety of traits, i.e. functional attributes, that each organism possesses (functional diversity) (Anderson, 2018; Gaston, 2010). The interactions and diversity of these traits and attributes within a given community shape ecosystem processes - affecting its productivity, adaptability, vulnerability to disturbances, and general functioning (Cadotte et al., 2011; Duncan et al., 2015; Funk et al., 2016; Isbell et al., 2011; Mori et al., 2013; Ruiz-jaen and Potvin, 2010).

Satellite earth observation has gained increased attention as a global and timely technique for monitoring biodiversity dynamics (O'Connor et al., 2015). Satellite remote sensing uses radiative measurements to provide critical information on the features of the Earth's surface using multiple wavelengths to capture detailed spectral information (Jensen, 2013). However, for a long time, remote sensing operated at coarse spatial and spectral resolutions, which hampered local-scale interpretation for biodiversity (Anderson 2018; Butler 2014). With ongoing advances in satellite sensors, a growing body of research examines the capabilities of satellite remotely sensed spectral information as proxies of biological diversity on the ground (Rocchini, 2007; Schmidtlein and Fassnacht, 2017; Torresani et al., 2019).

The use of spectral diversity, e.g. the variability in spectral information content, has become a widely studied approach for estimating terrestrial plant diversity through remote sensing (Wang and Gamon 2019). Initial research on this approach adopted the spectral variability hypothesis (Palmer et al., 2002) as their main premise (Rocchini, 2007; Rocchini et al., 2004). This hypothesis suggests that the diversity in spectral reflectance of an area is representative of in-situ plant diversity through its measurements of the spatial heterogeneity of the environment (Ewers et al., 2005; Palmer et al., 2002; Rocchini, 2007; Rocchini et al., 2010). Two theoretical concepts are central in the link between spectral diversity and in-situ plant diversity, namely 1) radiative transfer theory on vegetation-light interaction, and 2) the surrogacy hypothesis.

Radiative transfer theory for vegetation physically describes how remotely sensed reflectance is determined by a suite of morphological, biochemical, physiological, and structural characteristics of plants and the relative position of the sun and sensor (Chandrasekhar, 1960; Ollinger, 2011). Particularly the impacts of leaf biochemical composition and structural properties of vegetation have been emphasized (Feret et al. 2008; Jacquemoud et al. 1996; Jacquemoud et al. 2009). These properties are not only spectrally important but also relate to plant traits that are of ecological importance and thus can shed light on the functional traits, and diversity thereof, present in an ecological community (Damm et al., 2018; Gamon et al., 2019; Kattenborn et al., 2017). Indeed, links between functional diversity and spectral diversity have been established empirically at the leaf level (Schweiger et al., 2018).

While trait ranges and functional diversity have been used to distinguish among plant functional types (van Bodegom et al., 2014; Verheijen et al., 2016), species spectral discrimination has generally been shown to be challenging 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). Despite these challenges, links between spectral and taxonomic diversity might still apply, but through indirect relationships (Torresani et al., 2019; Villoslada et al., 2020).

The original premise of the spectral variability hypothesis (Palmer et al., 2002) relies on the ‘surrogacy hypothesis’ which suggests that patterns of biodiversity can be captured through its ecological and physical relationships with environmental heterogeneity (Beier and de Albuquerque 2015; Palmer et al. 2002; Stein, Gerstner, and Kreft 2014; Wang and Gamon 2019). In other words, based on this environmental ‘surrogacy’, spectral diversity can capture plant diversity indirectly through spectrally observable landscape heterogeneity, as landscape heterogeneity drives plant diversity.

Based on these theoretical concepts, different metrics and platforms have been deployed to quantify spectral diversity and to assess its link to in-situ plant diversity. Over time, studies have used proximal, airborne, and satellite remote sensing to link spectral diversity to either plant taxonomic, phylogenetic, and/or trait diversity (e.g. Dahlin, 2016; Gholizadeh et al., 2018; Lucas and Carter, 2008; Madonsela et al., 2017; Rocchini, 2007; Schmidtlein and Fassnacht, 2017; Schweiger et al., 2018; Torresani et al., 2019; Wang et al., 2018a). They reported both positive correlations and ambiguous relationships between spectral diversity and field-measured plant diversity. Overall, these studies have shown that scale, sensor, metric and season play a role in how well spectral diversity translates to plant diversity (Gholizadeh et al. 2018; Rocchini 2007; Schmidtlein and Fassnacht 2017; Torresani et al. 2019; Wang et al. 2018).

Despite the advances in applying spectral diversity metrics, the question of what exactly is measured in spectral diversity remains largely unanswered. This is particularly the case for multi-spectral satellite remote sensing in which the relatively coarse spatial resolution does not allow for the direct identification of individual plants and canopy crowns. For instance, European Space Agency’s (ESA) flagship Sentinel-2 Multi-Spectral Instrument (MSI) presents spectral bands scaled at 10m, 20m, or 60m spatial resolution, which implies that spectral signals are aggregates of multiple canopies. Furthermore, even in densely forested areas, the surface reflectance spectral signal at these scales comprises a number of different constituents, each contributing to the overall signal: vegetation cover (including plant size and density, canopy architecture, and understory layers), the soil/litter/background signal, vegetation biochemical and biophysical composition (trait diversity) as well as landscape morphology (Asner, 1998;

Van Leeuwen and Huete, 1996; Zarnetske et al., 2019). Better characterization and quantification of the components contributing to satellite remotely sensed spectral diversity is therefore needed to further advance the use and interpretation of spectral diversity in assessing in-situ plant diversity.

In this paper, we tested the hypothesis that spectral diversity from multispectral satellite observations is able to capture in-situ measured plant diversity directly, through spectral responses of plant traits as expected based on radiative transfer theory, or indirectly, through environmental 'surrogacy'. Firstly, the theoretical physics-based expectations from radiative transfer were quantified through radiative transfer model (RTM) simulations, providing a theoretical reference. This helped assessing the extent to which modeled spectral diversity based on radiative transfer actually relates to the empirical data; in-situ measured traits as well as Sentinel-2 observed spectral diversity.

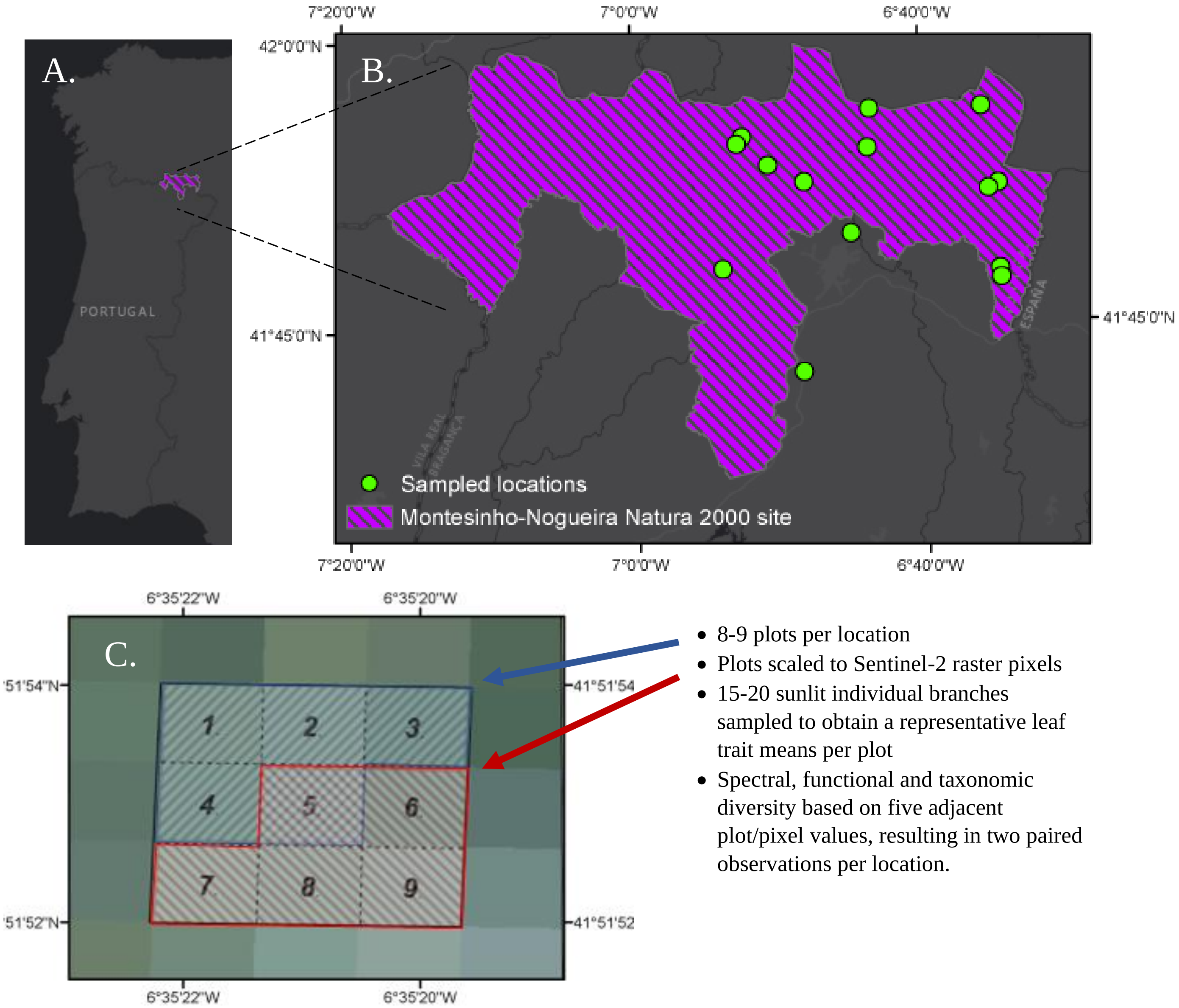
Secondly, the empirical relationships between spectral, taxonomic, and trait diversity and confounding factors were examined using Sentinel-2 imagery and in-situ field data collected in the Montesinho Natural Park and Montesinho-Nogueira Natura 2000 sites in northern Portugal. The analysis of bivariate correlations and linear mixed-effect models allowed us to characterize the extent to which observed Sentinel-2 spectral diversity covaries with in-situ observed taxonomic and trait diversity, but also of confounding variation in vegetation cover and landscape morphology. Ultimately, our findings feedback into the discussion on how to assess plant diversity from satellite remote sensing and the considerations needed for spectral diversity approaches in multi-spectral applications.

## 2.2. Methodology

### 2.2.1. Study area

The study area includes the Montesinho Natural Park and the Natura 2000 sites of Montesinho-Nogueira (PTZEP002 and PTCON0002), located in the Northeast of Portugal along the Spanish border (latitude 41°70′ - 41°94′N, longitude 6°57′ - 6°90′W) (See Fig. 2.1). With a size of over 1000 $km^2$, the area plays an important role in the conservation of regionally endemic biodiversity (Aguiar, 2001; Bastos et al., 2018). The study area is a natural mountainous area with an elevation between 371 and 1488m, characterized by high landscape richness and heterogeneous topography (Sil et al., 2016). This corresponds to a relatively wide range of climatic conditions between the highlands versus lowlands respectively with average annual temperature varying between 8.6°C and 12.9°C, and average annual precipitation between 1262mm and 806mm (Sil et al., 2016).

Semi-natural areas comprising of highly diverse shrub communities dominate the landscape, particularly in the highlands (Fonseca et al., 2012). Native deciduous Pyrenean oak forests are well represented, particularly in the Nogueira site (Rego et al., 2011), while Holm-oak woodlands occur mostly in rock outcrops, shallow soils, and steep slopes (Azevedo et al., 2013). The lowlands consist of agriculture intermingled with chestnut groves, while pine forest plantations occur at mid-elevation in the eastern part of the area (Sil et al., 2017). The landscape is heterogeneous, dynamic, and anthropogenic fires play an important role as drivers of landscape change (Azevedo et al., 2011; Sil et al., 2019).



- 8-9 plots per location
- Plots scaled to Sentinel-2 raster pixels
- 15-20 sunlit individual branches sampled to obtain a representative leaf trait means per plot
- Spectral, functional and taxonomic diversity based on five adjacent plot/pixel values, resulting in two paired observations per location.

*Fig. 2.1 Map of the study area depicting the location of the Montesinho-Nogueira Natura 2000 site in Portugal (panel A.), the distribution of the 14 individual sampling locations characterized by woody vegetation across the wider national park and Natura 2000 site (panel B.), and an exemplar individual location (panel C.) consisting of eight to nine plots scaled and georeferenced to Sentinel-2's pixel raster which is illustrated by surface reflectance at 20m spatial resolution as background. Diversity metrics (spectral, trait, and taxonomic) were calculated per five adjacent plot/pixel values resulting in two paired observations per location. For each plot (total N=115), an average of 17 individual sunlit branches was sampled to collect leaves representative of trait means of the overstory areal composition.*

A total of 28 multi-plot sites were sampled across 14 representative vegetated locations in the Montesinho area (Fig. 2.1), covering three different land use types; shrublands, forested areas, and chestnut plantations. Photographs indicative of the different sampling locations and land use types can be found in Suppl. Mat. Fig. S. 1. Each location consisted of multiple adjacent 20m x 20m sampled plots. Each plot (total N = 115) was precisely scaled and georeferenced in the field to match Sentinel-2's pixel raster using a Trimble Catalyst GPS with Global Navigation Satellite System service of <1m precision. Therefore, Sentinel-2 observations match field measurements in terms of the scale of the plots as well as the size of the clustered plots. Within each plot, we sampled leaves following the sampling protocol described in section 2.2.1. All diversity metrics, both in-situ and remotely sensed, were calculated for clusters of five adjacent plots resulting in two paired observations per location. The diversity metrics quantify the relative distance between trait combinations rather than the individual traits itself. As such, each observation of diversity is unique despite the overlap in pixels illustrated in Fig. 2.1C.

### 2.2.2. Data collection

#### 2.2.2.1. Field data collection

A field data collection campaign was conducted from 12/06 until 05/07 of 2019. The prime objectives of the campaign were to collect for each plot individually; in-situ leaf trait data, conduct a species inventory, and assess the vegetation cover.

For leaf trait analysis, we collected samples from 15-20 individual branches of the healthy unshaded top of the canopies of each plot to capture a representative plot-level composite trait means. Prior visual and geometric inspection guided sampling choices to select the most dominant canopy types in terms of areal coverage of each plot. Collected leaves were weighted fresh, then transported on ice, and stored in a -18 °C freezer until further analysis in the lab. In total, 1955 leaf samples were analysed to derive four leaf traits (section 2.2.2.2) from 115 plots across 14 locations. Simultaneous with the collection of leaf samples, a species inventory was made for the sampled canopies for each plot of each site. This resulted in an area-based species count survey representative of the top of canopy/overstorey vegetation.

In addition to leaf sampling and the species inventory, we quantified the structural vegetation cover for each plot. Vegetation cover was characterized through the Plant Area Index (PAI), which is defined as the area of living plant material per unit of ground surface area. We used hemispherical photography to specify PAI similar to approaches by Garrigues et al. (2008), Hadi et al. (2017), and Weiss et al. (2004). For consistent measurements across all sites, we took five hemispherical photos per plot, one from the plot centroid and one from the center of each quadrant. Images were retaken in case of the presence of sunbeams or sun fleck problems. After the field campaign, we processed the RGB hemispherical photographs using CAN-EYE v6.4 open-source software to retrieve effective PAI estimates (Weiss and Baret, 2010).

We cross-validated the PAI measurements from hemispherical photography with above and below canopy measurements taken with Photosynthetically Active Radiation (PAR) sensor (Apogee MQ-301; handheld device), quantifying the relative quantity of incident solar radiation absorbed by vegetation. Further, cross-validation was performed through comparison of PAI measurements against the fraction of vegetation through spectral unmixing based on in-situ soil spectral reflectance measurements, and leaf spectral reflectance signals as generated by the PROSPECT model (Lehnert et al., 2018; Sohn and McCoy, 1997). The PAI observations strongly correlated with the PAR measurements as well as with the fraction of vegetation in the spectral signal derived from spectral unmixing (Fig. S. 2. in Suppl. Mat.).

#### 2.2.2.2. Leaf biochemical traits

The collected field samples were analyzed in the lab to obtain relevant plot-level community means of leaf biochemical traits to ultimately assess site-level leaf trait diversity. The selection of traits was based on 1) their ecological importance in terms of plant functioning (Croft et al., 2017; Damm et al., 2018; Díaz et al., 2016; Wright et al., 2004), and 2) their importance in the spectral response of leaves and our understanding thereof. Specifically, the four selected leaf traits are the input parameters of the widely applied PROSPECT radiative transfer model that links leaf traits and biochemistry to spectral responses using physical laws (Feret et al. 2008; Jacquemoud and Baret 1990).

Chlorophyll A and B content ($\mu g/cm^2$; CAB) is the area-based leaf content of green photosynthetic pigments in chloroplasts. Chlorophyll plays an important role in the photosynthetic capacity and resource strategy of plants (Croft et al., 2017). Carotenoid content ($\mu g/cm^2$; CAR) is the amount of orange and yellow photosynthetic pigments in chloroplasts. CAR serves a number of roles in the functioning of plants, including light harvesting for photosynthesis and dissipating energy to avoid damage by excess light (Croft et al., 2017). Both CAB and CAR were derived using a protocol based on Lichtenthaler (1987).

Equivalent water thickness ($g/cm^2$; EWT) is the amount of water present in a leaf or canopy divided by its area. EWT plays a role in the physiological plant performance and regulatory mechanisms important for drought and stress tolerance (Damm et al. 2018; Lawlor and Cornic 2002; Saura-Mas 2007; Weiher et al. 1999). Leaf mass per area ($g/cm^2$; LMA) is the amount of dry mass of a leaf per leaf area. LMA is a key feature in capturing leaf economics, reflecting trade-offs between carbon gain and longevity of a plant (Díaz et al., 2016; Wright et al., 2004). Both EWT and LMA were calculated based on fresh and dry leaf weight and leaf area (as determined in Image J 1.52a software (Schneider, Rasband, and Eliceiri 2012)).

#### 2.2.2.3. Sentinel-2 surface reflectance

Spectral diversity metrics were calculated based on the optical surface reflectance retrieved by ESA's Sentinel-2 MSI sensor. The Sentinel-2a/b constellation consists of a wide-swath, medium-high spatial resolution (10, 20, and 60m), multi-spectral (13 bands) imager with 5–10 days revisit time (ESA, 2015). Sentinel-2 surface reflectance (level-2a) imagery was downloaded from the Copernicus Scientific Hub which comes as atmospherically corrected by ESA using the Sen2Cor algorithm (Gascon et al., 2014; Louis et al., 2016). Only one scene (29th of July 2019) covering all sampled locations was completely free of quality flags (cloud cover, cloud shadow, cirrus, and other atmospheric contamination) and corresponded with the time of our field campaign. We excluded the 60m bands from the analysis and resampled the 10m bands to 20m spatial resolution using a nearest neighbour resampling method to match the scaling of our 20m×20m georeferenced field plots. This resulted in nine spectrally non-overlapping bands which were used to calculate the spectral diversity metrics (See Table S. 3 for the spectral layout of the Sentinel-2 bands used).

### 2.2.3. Data analysis

#### 2.2.3.1. Diversity metrics

The relationship between plant diversity and spectral diversity is metric-dependent (Gholizadeh et al., 2018). Therefore, we implemented a multi-metric analysis with two of the most commonly used diversity measures in current research on both spectral diversity and trait diversity; Convex Hull Volume (CHV) and Rao's quadratic entropy index (Rao's Q) (Table 2.1). These metrics have been commonly used to capture plant trait diversity (Mouchet et al., 2010; Rocchini et al., 2017; Torresani et al., 2019; Villéger et al., 2008). The use of the same metrical concepts for both spectral and trait diversity allows for consistency in the analyses. The spectral diversity metrics were based on spectra from pixel-based Sentinel-2 observations (section 2.2.2.3). For the trait diversity metrics, we relied upon plot-wise means of leaf trait samples acquired in-situ, scaled, and georeferenced to the Sentinel-2's pixel observations. The diversity metrics used allow for consideration of abundance. However, since we are using homogenously sized pixel/plot-wise (composite) values, the abundance is equal across plots (abundance = 1).

In addition to these spectral and trait diversity indices, we calculated taxonomic diversity using in-situ plot-wise species count data. We relied on Shannon's H diversity index as a commonly applied indicator of local taxonomic diversity of each site;

$$H = -\sum_{i=1}^{s} (p_i \times \log_2 (p_i))$$

where s is the total number of species and $P_{\mathrm{i}}$ the proportion of the community represented by species i. Taxonomic diversity calculations based on Shannon's H were calculated using the scikit-bio 0.5.6 (http://scikit-bio.org/) package in Python. Min-max normalization of all metrics ensured all values were scaled between 0 and 1.

*Table 2.1: Overview of the properties of the trait and spectral diversity metrics used in this study.*

| Metric | Concept | Algorithm | References | |
|---|---|---|---|---|
| | | | Spectral Diversity | Trait Diversity |
| Convex Hull Volume (CHV) | Volume in an n-dimensional space[1] | Quickhull Algorithm | (Dahlin, 2016; Gholizadeh et al., 2018) | (Cornwell et al., 2006) |
| Rao's quadratic entropy index (Rao's Q) | Mean squared pairwise distances[2] | $Q = \sum_{i=1}^{L-1} \sum_{j=i+1}^{L} d_{ij\times} p_{i\times} p_j$<br>$d_{ij}$ = *multivariate distance matrix comprising i-th to j-th pixel*<br>$p_{ij} = pixel\ \ or\ plot\ value\ abudance\ (= 1)$<br>$L$ = *collective of pixel or plots in site* | (Rocchini et al., 2017; Torresani et al., 2019) | (Botta-Dukat, 2005) |

[1] We used the first three principal components to calculate the convex hull volume to have an equal number of dimensions among spectra or traits metrics.

[2] Traits and spectra were normalized prior to calculation of the index.

### 2.2.3.2. Simulating spectral diversity through radiative transfer models

In addition to the empirical data collected, we made use of theoretical models to assess how spectral diversity and the diversity of in-situ measured traits related according to radiative transfer processes. From radiative transfer models, simulated leaf and canopy spectra were generated based on in-situ trait information and, ultimately, used to calculate a simulated spectral diversity based on the metrics described in section 2.2.3.1. The simulated spectral diversity served as a theoretical physics-based reference to evaluate its relationship to in-situ trait diversity based on radiative transfer theory and, in addition, were compared against Sentinel-2 spectral diversity to assess its correspondence to empirical observations.

The simulations were based on two radiative transfer models; the leaf-based PROSPECT-5 model (Feret et al., 2008) and the canopy-scaled PROSAIL model (Jacquemoud et al., 2006). For full compatibility with our empirical observations based on Sentinel-2, we ran a spectral convolution to resample the RTM-simulated spectra to the same spectral band layout as

Sentinel-2 following ESA's spectral response table (ESA, 2020). Based on the plot-wise spectra, the spectral diversity was calculated for five adjacent plots like done for the calculations for the observed Sentinel-2's pixel-based spectra and similar to the trait and taxonomic metrics.

First, we modelled leaf spectra using the commonly applied PROSPECT-5 model (Feret et al., 2008) based on plot-wise aggregated observed trait values. This model uses well-established physical principles of light-matter interaction to simulate how light interacts with a single leaf and serves numerous more complex vegetation radiative transfer model models (such as PROSAIL, INFORM, SCOPE) (Feret et al., 2008). It requires relatively few input parameters to determine spectral responses; leaf structure parameter (N), chlorophyll a+b (CAB), equivalent water thickness (EWT), leaf mass per area (LMA), brown pigment (CBP), and carotenoid concentration (CAR). The spectra were simulated for each plot individually on the basis of the mean leaf trait in-situ plot-wise measurements, with only the leaf structural parameter and brown pigments fixed to $N = 1.6$, and $C_{brown} = 0.01$, respectively (Bacour et al., 2002). A strong correlation was expected between leaf trait diversity and spectral diversity calculated with PROSPECT-5 given that we related the diversity of simulated spectra based on in-situ derived trait information to the diversity of that same trait information. Nevertheless, non-linearity in the relationship between traits and spectra and its representation in diversity metrics may have impacted the strength of this correlation (Verrelst et al., 2015).

Secondly, we scaled the leaf trait characteristics to canopy reflectance using the PROSAIL radiative transfer model, which combines the leaf model PROSPECT (Feret et al., 2008; Féret et al., 2017) and the canopy model 4SAIL (Verhoef 1984; Verhoef et al. 2007). Canopy reflectance is more equipped to link directly to the Sentinel-2 observations. However, PROSAIL requires a larger number of parameters beyond what we could collect during the field campaign, with leaf angle distributions and plot-wise soil characteristics not measured. Instead, we modelled canopy reflectance i) by artificially fixing these values (based on Jay et al. 2017; Spitters, Toussaint, and Goudriaan 1986; Bacour et al. 2002), and ii) local optimization of soil and leaf angle parameters to the observed Sentinel-2 spectra through a genetic algorithm (GA). In recent years, GA has been successfully applied to a variety of optimization problems in remote sensing (Fang et al., 2003). The most significant advantage of GA is that it provides a systematic scanning of both the entire solution space as well of local minima to find the global optimum solution (Bozorg-Haddad et al., 2017). An overview of the two implementations of PROSAIL including its input parameters and search ranges is presented in Table S. 4. The spectral diversity obtained from these two implementations of PROSAIL was again compared to the observed Sentinel-2 spectral and in-situ trait diversity.

#### 2.2.3.3. Statistical analysis

Our study design is spatially nested with a total of 28 observations, each consisting of 5 clusters of adjacent plots/pixels, distributed in pairs across 14 independent locations. To avoid autocorrelation in this design, we opted for two solutions; 1) the use of average values between paired observations, and 2) the use of linear mixed-effect models. The first allowed us to integrate paired observations into single independent values without losing information. This increased robustness against outliers in either set of observations and robustness against possible noise in spectral and/or field measurements. Furthermore, it facilitates straightforward bivariate comparisons. The linear mixed-effect approach, on the other hand, allowed us to maintain power of the nested sample size (N=28) facilitating multivariate analysis while accounting for the effect of location on the empirical relationships (Zuur et al., 2009).

Our statistical analyses consisted of three main parts. In the first part, we evaluated the bivariate relationships between simulated spectral diversity, either at leaf or canopy scale (section 2.2.3.2), compared against the observed Sentinel-2 spectral diversity and in-situ trait diversity. The second part focussed on the empirically observed bivariate relationships between spectral-trait-taxonomic diversity. Both the first and second parts of our analysis relied on bivariate rank correlations operationalized through Spearman's rho (ρ) as the non-parametric and rank-based alternative to Pearson's r (Khamis, 2008; Schober and Schwarte, 2018). Spearman's ρ does not assume normality and is robust against outliers in our small sample size (Fowler, 1987).

The third part assessed the constituents of spectral diversity through a multivariate analysis. We used linear mixed-effect models to assess the relationship between in-situ plant diversity and spectral diversity while accounting for the role of (assumed) confounding factors; vegetation cover and landscape morphology. Models were run using the ‘lme4’ package in R and model outputs were visualised using the ‘sjPlot’ package in R v3.6.1 (R Core Team, 2019). The $R^2$ values implemented were split into marginal and conditional $R^2$ statistics based on Nakagawa et al. (2017). The underlying assumptions of the linear mixed-effect regression models were checked (Suppl. Mat. Fig. S. 5) and considered as satisfactory. Landscape morphology was quantified as the elevation and slope (resampled to 20m resolution using bilinear interpolation) derived from the Shuttle Radar Topography Mission (25m spatial resolution). Vegetation cover was characterized through Plant Area Index (PAI). Both the mean and variance of landscape morphology and vegetation cover were included in the models. The dependent variable in these mixed-effect models was spectral diversity. The independent variables were the matching metric of in-situ leaf trait diversity in combination with the mean and variance of landscape morphology and vegetation cover. We repeated the same design of models for taxonomic diversity, using Shannon’s H index instead of trait diversity metrics.

In addition to the linear mixed-effect models, a relative weights analysis was conducted to assess the relative importance of predictors to supplement effect sizes and statistical significance (Johnson 2000; Kraha et al. 2012). Relative importance is defined as the contribution each predictor makes to the total explained variance – while taking into consideration both its unique contribution and its contribution in the presence of the other predictors (LeBreton et al., 2007). The calculation of relative weights followed Tonidanel and LeBreton (2011).

## 2.3. Results

### 2.3.1. Assessing links and discrepancies between spectra and in-situ traits through RTM simulations

When using PROSPECT, a strong relationship was found between simulated spectral diversity and in-situ observed leaf trait diversity (CHV: ρ=0.72; Rao’s Q: ρ=0.75, Fig. 2.2). In contrast to these simulated spectral-leaf trait relationships, no significant correlation was found between PROSPECT-simulated spectral diversity and the observed spectral diversity from Sentinel-2 (CHV: ρ=0.21; Rao’s Q: ρ=0.28, Fig. 2.2). The latter can be understood through the mismatch in scale that exists between the PROSPECT simulated leaf spectra and the actual Sentinel-2 spectra which represent aggregate canopy-soil-understory observations.

When using PROSAIL with fixed estimates of the unmeasured canopy properties, the relationships with in-situ trait diversity weakened (CHV: ρ=0.46; Rao's Q: ρ=0.54, Fig. 2.2), as expected given the additional inclusion of canopy parameters, while the relationship with observed spectral diversity became equivocal (CHV: ρ=0.51; Rao's Q: ρ=0.09, Fig. 2.2). When using an optimized PROSAIL with variable leaf angle distribution and soil characteristics determined by GA optimization, the simulated spectral diversity correlated strongly with observed spectral diversity from Sentinel-2 (CHV: ρ=0.67; Rao's Q: ρ=0.86, Fig. 2.2) while the relationship with in-situ trait diversity was no longer clearly correlated (CHV: ρ=0.23; Rao's Q: ρ=0.07, Fig. 2.2).

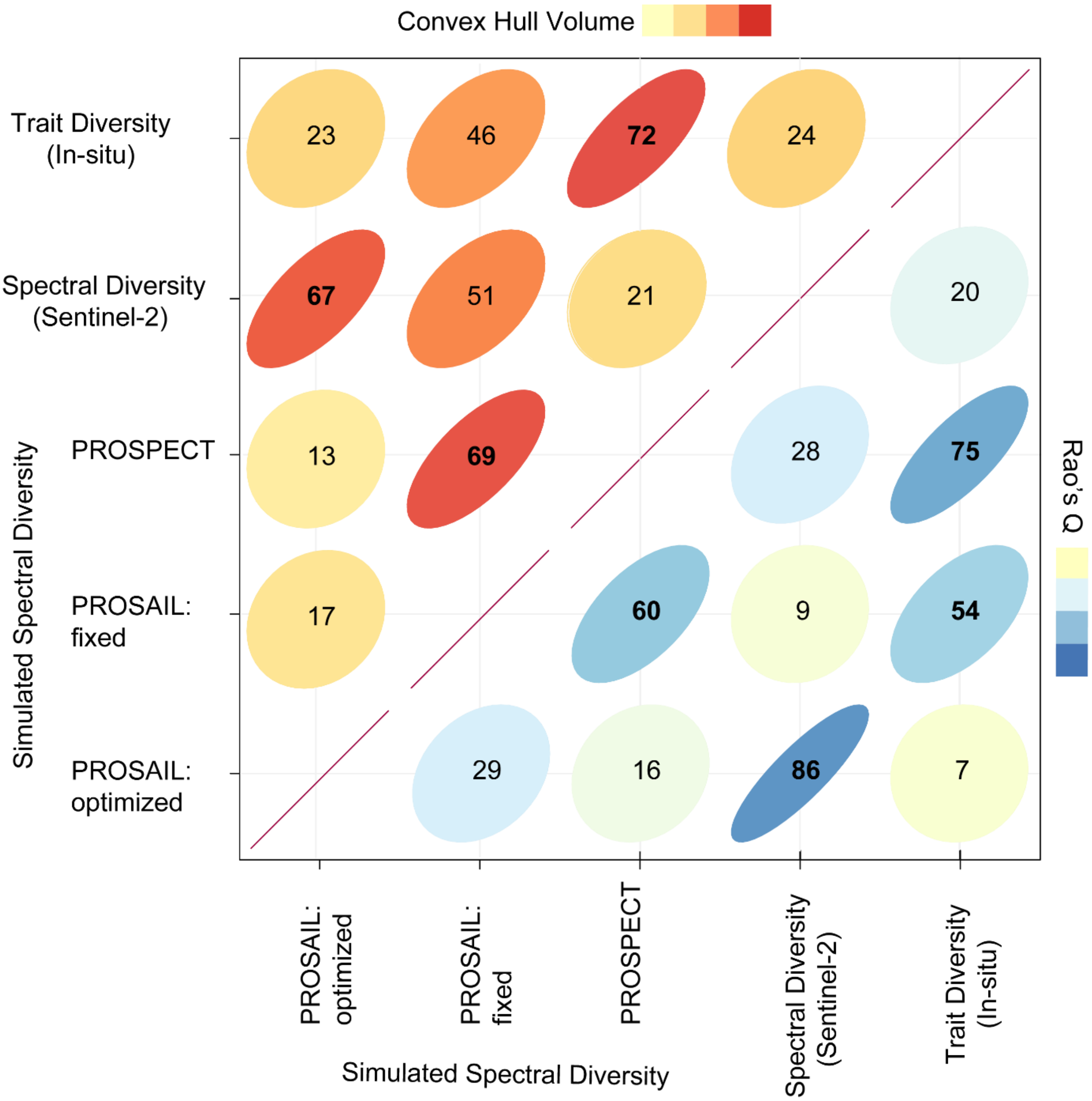


*Fig. 2.2: Correlogram presenting the bivariate associations (Spearman's ρ × 100) between in-situ trait diversity, observed Sentinel-2 spectral diversity, and simulated spectral diversity as modelled by PROSPECT, PROSAIL (with fixed parameters), PROSAIL (variable with GA-optimized parameters) respectively. Diversity metrics based on the Convex Hull Volume (CHV) are in the upper left half, and Rao's Quadratic Entropy (Rao's Q) in the lower right half, which are displayed in yellow to red, and yellow to blue, respectively. Values presented in bold are significant ($p < 0.05$).*

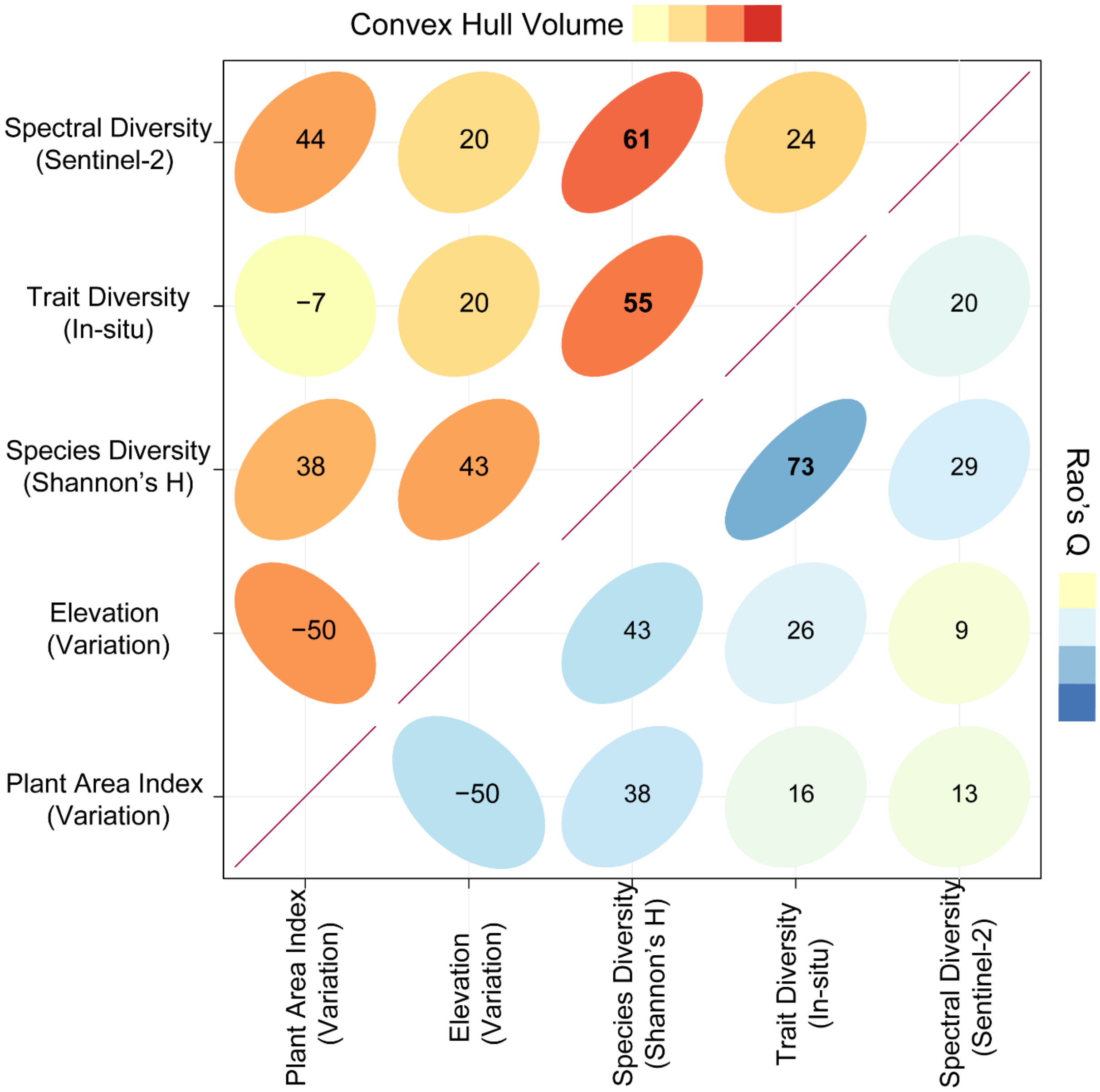


*Fig. 2.3: Correlogram presenting the empirical bivariate relationships (Spearman's ρ × 100) between in-situ plant diversity (Taxonomic; Shannon's H, Traits), the observed Sentinel-2 spectral diversity, and environmental predictors of variation in elevation and variation in vegetation cover (PAI). Diversity metrics based on the Convex Hull Volume (CHV) are in the upper left half, and Rao's Quadratic Entropy (Rao's Q) in the lower right half, which are displayed in yellow to red, and yellow to blue, respectively. Values depicted in bold are considered significant ($p < 0.05$).*

### 2.3.2. Trait-, Taxonomic and Spectral diversity relationships in empirical data

Moving from simulated to entirely empirical data, the field measurements showed that in-situ trait and taxonomic diversity were significantly correlated with each other (CHV: ρ=0.55; Rao's Q: ρ=0.73, Fig. 2.3). We also observed a positive relationship between spectral diversity (CHV) and taxonomic diversity (Shannon's H) (ρ = 0.61, Fig. 2.3) while for Rao's Q this correlation was absent (ρ=0.29). Bivariate correlations between leaf trait diversity and spectral diversity were weak (CHV: ρ=0.25; Rao's Q: ρ=0.20), despite correlations found between taxonomic diversity and leaf trait diversity and the correlation of taxonomic diversity with spectral diversity (CHV).

Fig. 2.3 also gives insight into relationships between taxonomic, trait, and spectral diversity versus confounding factors of landscape morphology and vegetation cover. No significant correlations were found in our relatively small sample set. However, linear mixed-effect models (section 2.3.3) allowed us to include a larger set of spatially nested observations and to look into the underlying multivariate and potentially confounding relationships with spectral diversity.

### 2.3.3. Multivariate constituents of spectral diversity through linear mixed-effect models

Fig. 2.4 offers a summarized breakdown of the linear mixed-effect models that assessed the role of plant diversity in combination with landscape morphology and vegetation cover as predictors and constituents of Sentinel-2's spectral diversity. Four linear mixed-effect models were specified with spectral diversity operationalized by either CHV or Rao's Q and relying on either trait or taxonomic diversity as predictors in combination with confounding factors. Each of the individual model summaries is shown in the Suppl. Mat. Table S. 6a-d.

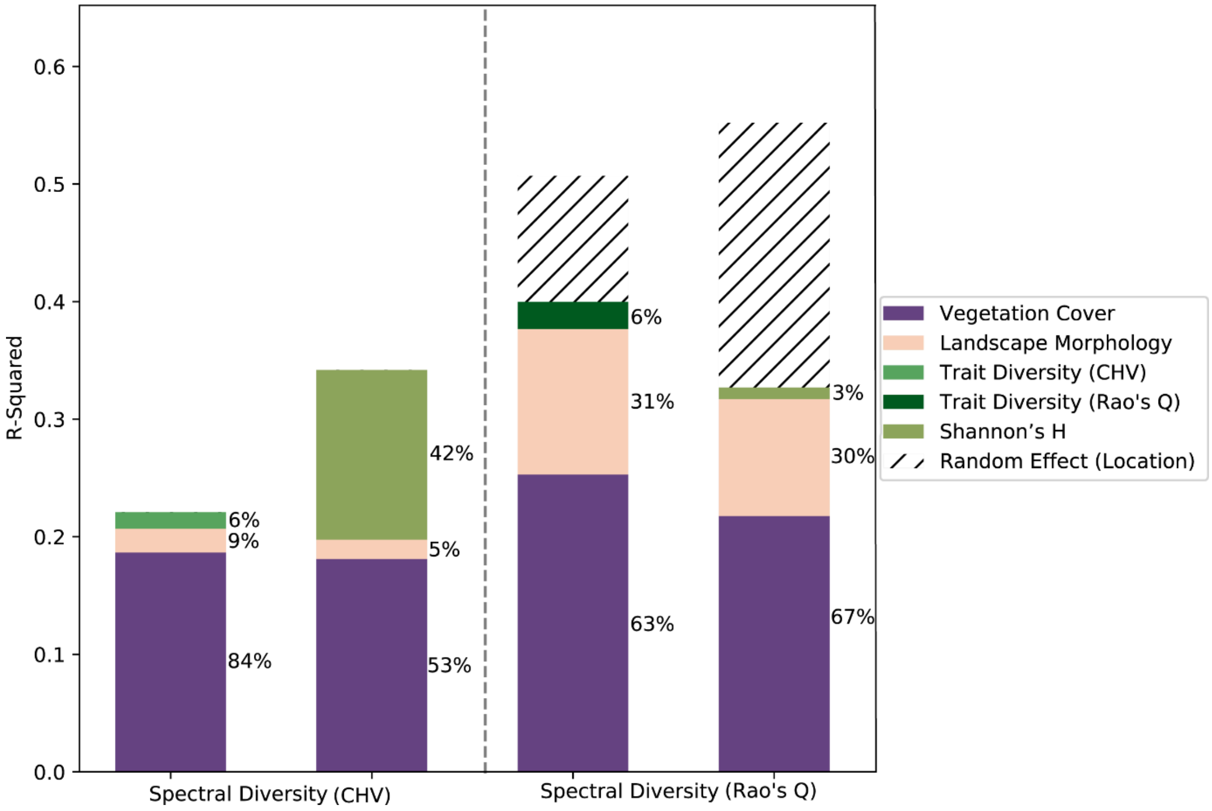


*Fig. 2.4: Summary of four linear mixed-effect models with Sentinel-2 observed spectral diversity as the dependent variable and vegetation cover, landscape morphology, and either trait or taxonomic diversity as predictors, while the location was set as the random effect (N=28). Results from the relative weights analyses of each of the four sets of predictors are annotated in percentages and relate to the relative contribution of the fixed effects (excluding random effect).*

The role of location as a random effect was minimal for CHV, as revealed by the low values of the random factor intraclass correlation coefficient (ICC) (Table S. 6a-6b). In contrast, Rao's Q revealed moderate effects of location on the proportion of the variance explained, ranging between one-fifth to one-third of the explained variance (ICC: 0.18-0.33) (Fig. 2.4, Table S. c-6d).

Controlling for the effect of paired observations per location, the models explained between 22% and 40% of the variance found in spectral diversity (Fig. 2.4). These fixed effects were consistently stronger than the random effects of location. Across models, we found that vegetation cover is a particularly significant predictor. The relative weights analysis further highlighted the dominance of vegetation cover in predicting spectral diversity among fixed effects - contributing from 53 to 84% of the explained variance ($R^2_{\text{Marginal}}$).

Trait diversity did not significantly contribute as a predictor of spectral diversity in either CHV or Rao's Q models. The relative importance of leaf trait diversity in explaining variation in spectral diversity was largely inferior to the predictive power of vegetation cover. Shannon's H, on the other hand, constituted as a significant predictor in CHV-based spectral diversity and accounted for as much as 42% of the fixed effects (Fig. 2.4). This was in line with the earlier bivariate correlation found between Shannon's H and spectral diversity (CHV) (Fig. 2.3). No significant role of taxonomic diversity was observed in Rao's Q calculations of spectral diversity. Instead, landscape morphology appeared as a significant explanatory variable in the Rao's Q calculations, with a relative importance accounting for 30-31% of the fixed effects (Fig. 2.4).

## 2.4. Discussion

This paper examined the question of what exactly is measured in spectral diversity obtained from multi-spectral satellite observations, considering; 1) direct responses of physical mechanisms between plant traits and spectral reflectance, and 2) proxies of plant diversity through environmental heterogeneity. The combination of coordinated field data and Sentinel-2 information allowed for direct empirical comparisons between spectral, taxonomic, and trait diversity, as well as confounding factors, while the RTM simulations evaluated the theoretical physical relationship between spectral and leaf trait diversity based on radiative transfer theory.

### 2.4.1. Leaf and canopy simulations show large differences in relation to empirical observations

Our empirical observations showed a minimal correlation between in-situ leaf trait diversity and Sentinel-2's spectral diversity. This departed from the strong theoretical relationships of spectral diversity and trait diversity modelled in the leaf-level PROSPECT simulations ($\rho$=0.72-0.75) (Fig. 2.2) and earlier reported empirical relationships at the leaf scale (Schweiger et al. 2018). Notably, the discrepancy between in-situ leaf trait diversity and simulated leaf spectra versus the actual Sentinel-2 spectral diversity as observed in our study, presents a scaling mismatch between leaf and canopy scales. Sentinel-2 observations represent aggregate complex canopy and background reflectance which limits the transferability of the leaf simulations (PROSPECT) to these empirical multi-spectral observations.

To address the scaling mismatch, PROSAIL simulations were implemented to model canopy reflectance for which we either fixed or varied (using optimization) the missing canopy and soil parameters. Despite the RTM's relative simplicity, our GA-optimized PROSAIL simulations illustrated the possibility to closely model observed Sentinel-2 spectral diversity ($\rho$=0.67-0.86) based on the inclusion of variability in soil and canopy variables (Fig. 2.2).

Specifically, the differences in the configurations of the RTM simulations used for modelling spectral diversity indicated a trade-off in describing either the in-situ trait diversity or the actual Sentinel-2 spectral diversity (Fig. 2.2). These findings assert the importance of soil and understory variability and canopy traits like leaf angle distribution in shaping and modelling spectral diversity in multi-spectral applications.

### 2.4.2. Vegetation cover is dominant in spectral diversity signal

The dominance of vegetation cover in the spectral diversity signal is manifested through its significance as a predictor in the linear mixed-effect models. The relative weights analysis highlighted that vegetation cover contributes 53-84% of the explained variance by fixed effects ($R^2_{marginal}$) in the Sentinel-2's spectral diversity signal (Fig. 2.4). Vegetation cover, measured through PAI, influences the extent to which soil, litter, and understory appear in the spectral reflectance signal of a Sentinel-2 pixel. The widely different spectral signatures of soil versus that of vegetation further contribute to the importance of vegetation cover in spectral diversity. Variation in the contribution of soil and vegetation to the overall spectral reflectance can result in relatively large spectral dissimilarities between corresponding plots (Gholizadeh et al., 2018; Villoslada et al., 2020; R. Wang et al., 2018c), even if plots are functionally relatively similar.

Additionally, vegetation cover is tied to the present canopy architecture as dictated by morphological traits. Canopy traits tend to dominate the spectral signal of vegetation across a broad range of the electromagnetic spectrum (Asner, 1998; Gu et al., 2016). Asner (1998) demonstrated that leaf area index (LAI) and leaf angle distribution, as relevant descriptors of the canopy morphology, strongly control the relationship between leaf traits and canopy spectral characteristics. Similarly, Roelofsen et al. (2013) showed the importance of LAI in linking leaf traits to canopy-level reflectance. The multispectral broadband setup may further increase the dominance of canopy, soil, and biomass characteristics as opposed to expressions of biochemical and biophysical leaf traits found in narrower ranges of the electromagnetic spectrum that benefit from hyperspectral measurements (Durán et al., 2019; Schneider et al., 2017; Schweiger et al., 2018).

The dominance of variation in vegetation cover as a driver of the spectral diversity signal requires further attention in future applications of spectral diversity. Diversity in vegetation cover density, biomass, and canopy architecture captured in PAI might not necessarily relate to plant diversity. For example, our dataset revealed no clear bivariate relationships between vegetation cover (variation in PAI) and trait diversity ($\rho$=-0.07-0.16), or taxonomic diversity ($\rho$=0.38) (Fig. 2.3). Similar to our findings, yet at a much higher (airborne) spatial resolution, Villoslada et al. (2020) reported that the sensitivity of spectral diversity to vegetation cover density could mask the effect of plant diversity.

In combination, our evidence shows that while spectral diversity approaches allow circumventing the challenges and difficulties in isolating direct plant diversity signals, the approach risks the spectral diversity signal to be dominated by other factors, like vegetation cover (Fig. 2.4), instead of plant diversity directly. Our ability to account for spectrally dominant confounding factors, such as vegetation cover and soil, could improve the robustness and relationship of spectral diversity approaches to in-situ plant diversity across spatial, spectral, geographic, and temporal resolutions.

Several approaches are already in place to assist in further dissection of the spectral signal to isolate plant diversity (Musavi et al., 2015). These techniques include spectral unmixing (Asner and Heidebrecht, 2002; Clasen et al., 2015; Gholizadeh et al., 2019; Sohn and McCoy, 1997), separate vegetation indices (Delegido et al., 2011; Schneider et al., 2017), radiative transfer model inversion (Ali et al., 2020b, 2020a; Brown et al., 2019; Hauser et al., 2021; Rossi et al., 2020), statistical learning (Berger et al., 2021; Durán et al., 2019; Ma et al., 2019) and data fusion approaches (Combal et al., 2002; Hakkenberg et al., 2018; Koetz et al., 2007; Lahoz and Schneider, 2014; Lewis et al., 2012). In Suppl. Mat. S. 7, we elaborate on the potential of these approaches.

### 2.4.3. Spectral Variability Hypothesis works for taxonomic diversity, the underlying mechanism remains unexplained

Despite the influence of vegetation cover, our empirical results revealed a direct correlation between taxonomic diversity and spectral diversity for CHV calculations ($\rho = 0.61$, Fig. 2.3). Furthermore, linear mixed-effect models and the relative weights analysis confirmed taxonomic diversity as an important contributor (42% of the fixed effects) to the explained variance ($R^2_{\text{marginal}}$) in CHV calculations (Fig. 2.4). Although species are spectrally difficult to separate based on multi-spectral broadbands (Cochrane, 2000), our findings suggest that indeed spectral diversity (CHV) can be meaningful as a proxy of taxonomic diversity using Sentinel-2 observations.

The relationship between spectral diversity and taxonomic diversity is often linked to Palmer’s (2002) Spectral Variation Hypothesis which states that the spectral diversity in an area is expected to relate to the diversity of species through environmental heterogeneity (Dauber et al., 2003; Ewers et al., 2005; Palmer et al., 2002). Empirical demonstration of this relationship in satellite-based multispectral applications was found by, e.g. Torresani et al. (2019), Madonsela et al., (2017), and Rocchini et al. (2004; 2007). The underlying argumentation builds on the surrogacy hypothesis which suggests that higher environmental variation relates to higher species richness (Beier and de Albuquerque 2015; Stein, Gerstner, and Kreft 2014; Wang and Gamon 2019). However, thus far, studies on the spectral variability hypothesis tended to omit a characterization of the exact drivers of ‘surrogacy’ that align spectral diversity, environmental heterogeneity, and the diversity of species.

Here, we confirm the correlation of spectral diversity (CHV) and taxonomic diversity in a mountainous and heterogenous Mediterranean landscape using Sentinel-2 observations ($\rho = 0.61$; relative importance of 42% for $R^2_{\text{marginal}}$). Despite our attempt to incorporate leaf trait diversity and confounding factors in multivariate models, the exact workings of this relationship remain unexplained in our study. While taxonomic and leaf trait diversity were strongly correlated in-situ, only the former showed a correlation with spectral diversity. In addition, neither variation in elevation or vegetation cover were clearly correlated to taxonomic diversity as confounding mechanisms of ‘surrogacy’ (Fig. 2.4).

Hence, further research is needed to explore the exact mechanisms through which the relationship between spectral and taxonomic diversity is established. A more elaborate analysis of components of environmental heterogeneity at relevant spatial scales may allow a better understanding of the stronger association of taxonomic diversity compared to leaf trait diversity. For instance, taxonomic diversity observed here might covary with spectral diversity metrics through unmeasured canopy structure traits, not related to PAI, or through aspects of environmental heterogeneity not considered here. Given that we could explain only a moderate share of variance in spectral diversity ($R^2_{\text{Marginal}} = 0.22\text{-}0.40$), the role of variables like fire regimes, plant phenology, grazing, dead biomass, and soil types in multi-spectral spectral diversity deserves further attention (Pausas and Vallejo, 1999; Schneider et al., 2017; Vivian and Cary, 2012; Zarnetske et al., 2019). Despite our substantial field campaign efforts, our sample size remained relatively small for multivariate analyses (N=28).

Differences in the significance of predictors depending on the metric (CHV versus Rao's Q) underpin that the choice of metric is highly relevant in the relationship between spectral diversity and in-situ plant diversity (see also Gholizadeh et al. 2018 for hyperspectral observations). Noteworthy in understanding differences between CHV and Rao's Q is that the latter also incorporates elements of divergence in quantifying diversity (Botta-Dukat, 2005; Mouchet et al., 2010). Furthermore, Wang, Gamon, Schweiger et al. (2018) highlighted the role of species evenness in metrics of spectral diversity. The authors suggested that the combined spectral effects of species richness and evenness are better captured with Shannon's H index than the trait diversity metrics as expressed by CHV. Moreover, data dimensionality plays a role in the patterns observed (Gholizadeh et al., 2018). Our operationalization of CHV runs on three axes (PCA dimensions) of spectra and traits while Rao's Q uses all standardized traits and spectral bands. The latter therefore does not reduce data dimensionality and could give more weight to signals that are expressed across a broad range of the observed spectral bands/trait space.

### 2.4.4. Absence of leaf trait diversity in spectral diversity signal

We expected trait diversity and spectral diversity to relate based on radiative transfer theory. Our simulations (Fig. 2.2) confirmed a direct theoretical relationship, yet only at the leaf level as much less association was observed when scaled to the canopy level. In addition, given the correlation between taxonomic and trait diversity in-situ, an indirect relationship was still expected. After all, environmental heterogeneity creates diversity in the optimal environmental fitness and conditions of resource availability (Dézerald et al., 2018; Kraft et al., 2008; Read et al., 2014). Nevertheless, the overall relationship of leaf trait diversity with spectral diversity appeared to be insignificant, even in consideration of confounding variables of vegetation cover and landscape morphology (Fig. 2.3 and Fig. 2.4).

Based on the aforementioned arguments, we forward three non-mutually exclusive explanations for the observed underrepresentation of leaf trait diversity and the dominance of the vegetation cover signal in the Sentinel-2 spectral diversity measurements; (1) the spectral dominance of variability in soil and morphological traits (Asner, 1998; Gholizadeh et al., 2018), (2) the underrepresentation of leaf optical properties at low vegetation density (Asner, 1998; Baret et al., 1994), and (3) the limitations of the multispectral broadbands at aggregate 20m resolution (Nagendra et al., 2010; Rocchini, 2007).

### 2.4.5. Expanding spectral diversity applications

The sites considered in this study consist of multiple land-cover types, growth forms, and a relatively heterogeneous abiotic environment to provide an important test for the implementation of spectral diversity metrics needed in biodiversity assessments at larger scales (Dahlin, 2016; R. Wang et al., 2018c). Stratification of our sampled sites in different levels of vegetation cover density, fractional cover, growth form, or land use type might have helped to further examine the importance of each of the above-mentioned explanations. Our sample size posed limitations on the type of analyses possible and the conclusions to be drawn. The sampling effort was strongly constrained by the labour-intensiveness of comprehensive field campaigns at the scale of satellite remote sensing. Future research efforts and/or combined analyses of the data already out there might provide further stratification of spectral diversity relationships and ensure a better representation across time and biomes.

Further testing across different ecosystem types remains crucial. We anticipate the constituents of spectral diversity to be ecosystem-dependent, at least for multispectral spectral diversity metrics (Schmidtlein and Fassnacht, 2017). For instance, in some ecosystem types, variation in vegetation density might align more strongly with leaf trait diversity (Sheil and Bongers, 2020; Walter et al., 2020), while in other ecosystems vegetation cover density could mask or be ordinal to the effect of plant diversity (Hauser et al., 2021; Villoslada et al., 2020). Moreover, denser ecosystem types tend to allow for multiple-scattering, enhancing the contribution coming from leaf-level biochemical and biophysical information within canopy scale reflectance (Asner, 1998; Baret et al., 1994). Even temporally, within the same ecosystem, the impact of vegetation cover on the signal of plant diversity in spectral diversity metrics may vary. For instance, in Torresani et al. (2019)'s temporal study in an alpine conifer forest, the highest correlations between spectral diversity and in-situ plant diversity were found at the peak of the growing season in June and July.

The spectral resolution of the sensors also plays a role in our ability to detect in-situ plant diversity from remote sensing, as repeatedly pointed out in previous studies (Nagendra et al., 2010; Rocchini, 2007). Sentinel-2 MSI's spectral configuration offers rich spectral coverage compared to its predecessors yet is still largely inferior to hyperspectral sensors. While the spectral responses of leaf traits included here (LMA, EWT, CAB, CAR) show sensitivity to the wavelengths present in Sentinel-2's MSI sensor (de Sá et al., 2021; Gu et al., 2016; Verrelst et al., 2019b), the aggregation of signals across 20m spatial resolution through multi-spectral broadbands could have reduced the ability to pick up leaf trait diversity. Nevertheless, the forthcoming launch of hyperspectral satellite imagers (e.g. EnMAP, SBG, CHIME; Cavender-Bares, Gamon, and Townsend 2020) offers prospective that might benefit plant diversity assessments from space with more versatile spectral and spatial resolutions allowing for more detail.

## 2.5. Conclusions

While the spectral variability hypothesis has been proposed to capture patterns of plant diversity through the relationship between environmental ‘surrogacy' drivers and spectral drivers, the identity of those environmental drivers had not yet been characterized. Our analysis shows that vegetation cover served as the most dominant constituent in Sentinel-2 observed spectral diversity, thus providing important insights in the working of the spectral variability hypothesis. Effects of plant functional diversity, here examined as leaf trait diversity, remained obscured due to the dominant impacts of vegetation cover, possibly due to the low vegetation density in various plots of this study and the spectral dominance of canopy traits in multi-spectral configurations.

In contrast, spectral diversity based on Sentinel-2 observations was capable of predicting taxonomic diversity in accordance with the spectral variability hypothesis. Nevertheless, despite our consideration of leaf trait diversity and confounding factors of vegetation cover and landscape morphology, the exact workings (or ‘surrogacy’) of this relationship remained hidden and will require a broader investigation of environmental heterogeneity and canopy traits.

We recommend that future applications of satellite-based spectral diversity metrics consider the impacts of vegetation cover. As illustrated in our study, variation in vegetation cover can dominate the spectral diversity signal while it is not necessarily correlated with plant diversity. We, therefore, think it is important to account for vegetation cover to compare across ecosystems and study areas and understand the potentially ambiguous performance of spectral diversity as a proxy of plant diversity. In the future, a practice of better characterization of constituents of spectral diversity may result in more robust interpretations, consistency, and scalability of spectral diversity metrics in predicting in-situ plant diversity across scales, sensors, ecosystems, and other external drivers for regional biodiversity assessments.

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

**Based on**:

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## Abstract

Large-scale high-resolution satellite observations of plant functional diversity patterns will greatly benefit our ability to study ecosystem functioning. Here, we demonstrate a potentially scalable approach that uses aggregate plant traits estimated from radiative transfer model (RTM) inversion of Sentinel-2 satellite images to calculate community patterns of plant functional diversity. Trait retrieval relied on simulations and Look-up Tables (LUTs) generated by an RTM and hybrid approaches rather than heavily depending on a priori field data and data-driven statistical learning. This independence from in-situ training data benefits its scalability as relevant field data remains scarce and difficult to acquire. We ran a total of three different inversion algorithms that are representative of commonly applied approaches and we used two different metrics to calculate functional diversity.

In tandem with Sentinel-2 image-based estimation of plant traits, we measured Leaf Area Index (LAI), leaf Chlorophyll content (CAB), and Leaf Mass per Area (LMA) in-situ in a (semi-)natural heterogeneous landscape (Montesinho region) located in northern Portugal. Sampling plots were scaled and georeferenced to match the satellite observed pixels and thereby allowed for a direct one-to-one posterior ground truth validation of individual traits and functional diversity.

Across approaches, we observe a reasonable correspondence between the satellite-based retrievals and the in-situ observations in terms of the relative distribution of individual trait means and plant functional diversity across locations despite the heterogeneity of the landscape and canopies. The functional diversity estimates, based on a combination of canopy and leaf traits, were robust against estimation biases in trait means. Particularly, the convex hull volume estimate of functional diversity showed strong concordance with in-situ observations across all three inversion methods (Spearman's ρ: 0.67–0.80). The remotely sensed estimates of functional diversity also related to in-situ taxonomic diversity (Spearman's ρ: 0.55–0.63).

Our work highlights the potential and challenges of RTM-based functional diversity metrics to study spatial community-level ecological patterns using currently operational and publicly

available Sentinel-2 imagery. While further validation and assessment across different ecosystems and larger datasets are needed, the study contributes towards a further maturation of scalable, spatially, and temporally explicit methods for functional diversity assessments from space.

## 3.1. Introduction

Worldwide biodiversity declines are affecting ecosystem functioning and pose risks to humankind as our existence heavily relies on healthy ecosystems (Cardinale et al., 2012; IPBES, 2019; Rands et al., 2010). In light of this ongoing global biodiversity crisis, the urgency to monitor and map terrestrial biodiversity at large scales has spurred research on adequate quantitative methods for biodiversity assessments (Anderson, 2018; Pereira et al., 2013). Improved monitoring of biodiversity dynamics can equip us to better understand and act upon changes, and halt further exacerbation of the current alarming rates of biodiversity loss (O'Connor et al., 2015; Skidmore, 2015).

A growing body of research highlights the role of functional diversity - rather than species diversity – in linking biodiversity to the functioning of ecosystems (Diaz and Cabido, 2001; Hooper et al., 2005; Violle et al., 2014). Functional diversity describes the range, value, and abundance of organismal traits. Traits are the measurable features of an organism that potentially affect performance, fitness, or resource acquisition strategies (Cadotte et al., 2011). Plant functional diversity integrates both inter- and intraspecific trait variation and has been found enhance ecosystem productivity, stability and resilience (Cardinale et al., 2011; Díaz et al., 2007; Duncan et al., 2015; Funk et al., 2016; Grime, 1998; Hooper, 2002; Isbell et al., 2011; Mori et al., 2013; Ruiz-jaen and Potvin, 2010). As such, the assessment of plant functional diversity patterns is highly relevant to monitoring the health (productivity, stability) and biodiversity of our ecosystems.

Traditionally, trait measurements are acquired by elaborate field campaigns (Baraloto et al., 2010). Such field campaigns are highly valuable but laborious, costly, and inefficient in dealing with the ecological complexity that comes with monitoring spatial and temporal variation of functional diversity (Májeková et al., 2016; Scholes et al., 2012). Field campaigns are particularly laborious if we aim to gather detailed spatially continuous information across large spatial extents for mapping and understanding the spatio-temporal dynamics of functional diversity.

To overcome this challenge, an increasing number of studies has explored the applicability of remote sensing techniques in assessing regional plant functional diversity for different ecosystems to scale up our biodiversity monitoring capabilities (Aguirre-gutiérrez et al., 2021; Jetz et al., 2016; Wang and Gamon, 2019). State-of-the-art studies used airborne data to map multivariate forest functional types (Asner et al., 2017) and plant functional diversity using both optical and LiDAR observations in combination with statistical approaches (Durán et al., 2019) and spectral indices (Schneider et al. 2017). Despite the value of these airborne remote sensing observations, its potential for application at larger extents is limited as airborne campaigns remain costly to organize and are bound in spatial extent and repeatability.

With ongoing technological advances and the launch of higher spatial and spectral resolution sensors in orbit, satellite-based observations present global and timely information that holds large potential as the next frontier to monitor functional diversity patterns across space and time (Aguirre-gutiérrez et al., 2021; Jetz et al., 2016; Ma et al., 2019). Spaceborne remote sensing, however, generally relies on sensors that operate at spatial and spectral resolutions that are inferior to airborne hyperspectral instruments. These constraints challenge the fine-grained local-scale interpretation and in-situ validation of biodiversity estimates, and increase ill-posedness in retrieving biophysical traits from the spectral broadbands of satellites (Baret and Buis, 2008; Wang and Gamon, 2019).

The search for adequate quantitative methods to monitor functional diversity exploiting satellite earth observations remains in need of further research and development (Ma et al., 2019; Rossi et al., 2020; Torresani et al., 2019). Ideally, these research efforts will provide methods that allow us to accurately retrieve plants traits for functional diversity 1) with current satellite sensors, 2) without heavy reliance on scarce comprehensive ancillary field measurements, and that are 3) scalable across time and location including across vegetation types, and 4) measurable in-situ for validation against ecological field data. To meet these requirements, the use of optical traits that are physically related to spectra is particularly appealing given its universal applicability as opposed to statistical learning approaches and/or spectral indices that 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, Darvishzadeh, Skidmore, Gara, et al. 2020).

The physical basis of trait retrieval is commonly ensured through the use of Radiative Transfer Models (RTMs) which relate incident radiation to vegetation canopies through angular, structural, biochemical, and biophysical characteristics (Verhoef 1998; Jacquemoud et al. 2009; Jacquemoud and Ustin 2019). These model parameters include leaf or canopy characteristics of ecological relevance (Anderson, 2018; Feilhauer et al., 2018; Homolová et al., 2013; Ollinger, 2011; Roelofsen et al., 2013). However, the universality of these models is bound by strong assumptions and heavy parameterization, simplifying the heterogeneous canopies and vegetation types encountered in the field. In the end, the practice of canopy RTM inversion to estimate plant traits from vegetation spectral reflectance is not trivial, but ill-posed and prone to a range of equally possible solutions, especially in multispectral settings (Combal et al., 2003; Koetz et al., 2007; Musavi et al., 2015).

Recently, a number of studies have shown success in applying RTM inversion on satellite earth observations (Sentinel-2) to estimate key plant traits in (semi-)natural ecosytems (e.g. Ali, Darvishzadeh, Skidmore, Gara, et al. 2020; Ali, Darvishzadeh, Skidmore, Heurich, et al. 2020; Rossi et al. 2020; Vinué, Camacho, and Fuster 2018). Unfortunately, the step from using trait estimates that are consistent among each other to deriving functional diversity from satellite remote sensing is undertaken less often (Ma et al., 2019; Rossi et al., 2020). To our knowledge, none of the existing satellite-based approaches so far has used RTM inversion to derive multiple traits simultaneously to obtain functional diversity estimates in heterogeneous (semi-)natural landscapes.

In this study, we present satellite-based functional diversity estimates using Sentinel-2 imagery. Our main objective is to examine our current ability to derive multiple plant traits, the local variation in trait aggregates, and ultimately estimate community patterns of functional diversity metrics across a heterogeneous and biodiverse (semi-)natural landscape. Our approach focuses on the use of RTM inversion that does not heavily rely on 'data-intensive' or ‘a priori’ in-situ training data. In support of our main objective, we 1) validated functional diversity estimates as derived by satellite observations using appropriately scaled in-situ measurements, 2) evaluated the robustness of different functional diversity indicators in light of uncertainties in the retrieval of trait values, and 3) assessed how remotely sensed community-based patterns of functional diversity aligns with in-situ community taxonomic diversity, as species are still the most commonly used units of assessment in conservation planning (Gaston, 2010; Meatyard, 2005; Petchey and Gaston, 2002). We ran three different implementations of commonly used RTM inversion approaches to estimate plant traits to more generically evaluate the performance, applicability and robustness of RTM-based functional diversity estimates instead of focusing on tweaking a single inversion method. Taken together, the demonstration and validation of Sentinel-2-derived functional diversity gives insight into the potential of scalable and operational RTM approaches to serve plant functional diversity monitoring from satellite earth observations across large-scale heterogeneous landscapes.

## 3.2. Methods

### 3.2.1. Study area

A comprehensive field data campaign was conducted in the Montesinho Natural Park and the Natura 2000 sites in Montesinho-Nogueira located in the Northeast of Portugal along the Spanish border (See Fig. 3.1). With a size of over 1000 km$^2$, the area plays an important role in the conservation of regionally endemic biodiversity (Aguiar, 2001; Bastos et al., 2018). The study area is characterized as a natural mountainous area with elevation ranging between 371m and 1488m above sea level. The highlands are dominated by a patchy landscape of shrublands, mixed with occasional Pyrenean oak forests and Holm-oak woodlands of which the latter mostly occur on rock outcrops, shallow soils, and steep slopes (Azevedo et al., 2013; Fonseca et al., 2012; Rego et al., 2011). The lowlands consist of agriculture intermingled with chestnut plantations, while pine forests plantations occur at mid-elevation in the eastern part of the area (Sil et al., 2017).

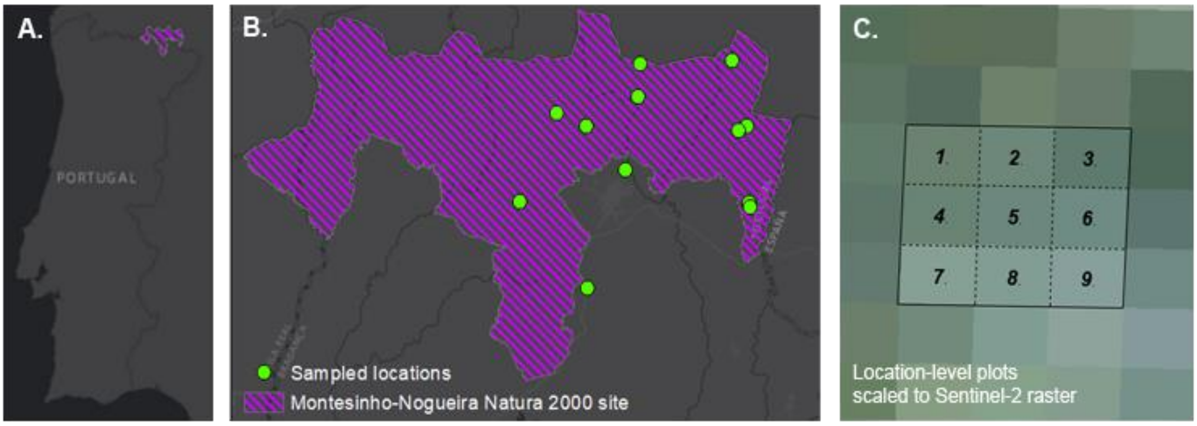


*Fig. 3.1: Map of the study area depicting the location of the Montesinho-Nogueira Natura 2000 site in Portugal (panel A.), the distribution of the twelve individual sampling locations characterized by (semi-)natural woody vegetation across the wider national park and Natura 2000 site (panel B.), and an exemplar individual location (panel C.) consisting of nine individual adjacent plots scaled and georeferenced to Sentinel-2’s pixel raster which is illustrated by the panchromatic reflectance at 20m spatial resolution as*

*background. For each plot (total N=97), an average of 17 individual sunlit branches were sampled to collect leaves representative of trait means of the overstory areal composition.*

A total of twelve vegetated locations were selected in the Montesinho area (Fig. 3.1). The selection of the locations is representative of the territorially abundant extensively managed (semi-)natural areas dominated by woody vegetation that are of importance to the endemic biodiversity. These twelve locations include six forested and six shrubland locations and include sites that are dominated by single-species canopies as well as sites with a heterogeneous mix of species. Each location consisted of eight to nine plots (8-9×(20m×20m)) that correspond to georeferenced and scaled Sentinel-2 pixels. Fig. S. 8 depicts photos taken during the field campaign illustrative of the typical sampling locations.

### 3.2.2. Field measured plant traits

In-situ species inventories and leaf and canopy traits of each plot across the twelve locations were assessed during a field study that lasted from 12/06 until 05/07 of 2019. The trait collection resulted in ground measurements of Leaf Area Index (LAI), Chlorophyll A and B content (µg/cm²; CAB) and Leaf Mass per Area (g/cm²; LMA) operationalized in units directly comparable to the implementation of these traits in the PROSAIL RTM (Jacquemoud et al. 2009). The selection of traits was based on their ecological importance in terms of plant functioning (Croft et al. 2017; Wright et al. 2004; Díaz et al. 2016; Asner, Scurlock, and Hicke 2003; Zheng and Moskal 2009), and their importance in the spectral response of vegetation and our understanding thereof (Feret et al. 2008; Jacquemoud and Baret 1990; Serbin et al. 2019). Selected traits include;

- LAI, defined as the area of leaf material per unit of ground surface area, is considered an important canopy trait, both by itself as well as an important characteristic to scale up leaf traits to canopy traits (Asner 1998; Roelofsen et al. 2013). LAI relates directly to primary productivity and to competitive and complementary light use, transpiration, and energy exchange (Asner et al., 2003; Castillo et al., 2017; Fang et al., 2019; Zheng and Moskal, 2009).
- CAB is the surface-based leaf content of green photosynthetic pigments in chloroplasts and plays an important role in the photosynthetic capacity and resource strategy of plants (Croft et al. 2017).
- LMA is the amount of dry mass of a leaf per leaf area and a key feature in capturing leaf economics, reflecting trade-offs between carbon gain and longevity of a plant (Díaz et al., 2016; Wright et al., 2004).

We used hemispherical photography to specify LAI similar to approaches by Garrigues et al. (2008), Hadi et al. (2017), and Weiss et al. (2004). For consistent measurements across all sites, we took five hemispherical photos per plot that we combined to plot-wise mean LAI measurements: one from the centroid and one from the center of each quadrant. Images were retaken in case of the presence of sunbeams or sun fleck problems. After the field campaign, we processed the RGB hemispherical photographs using CAN-EYE v6.4 open-source software to retrieve effective LAI measurements comparable to PROSAIL’s interpretation (Weiss and Baret 2010). We cross-validated the LAI measurements from hemispherical photography with above and below canopy measurements taken with a Photosynthetically Active Radiation (PAR) sensor (Apogee MQ-301; handheld device), quantifying the relative quantity of incident solar radiation absorbed by vegetation. The LAI observations strongly correlated with the PAR measurements (See Fig. S. 9).

For the leaf trait analysis, we collected 17 leaf samples from the healthy unshaded top of the canopy of each individual plot. Prior visual and geometric inspection guided choices to select the most appropriate samples in terms of areal representativeness. As such, the collected samples approximated a representative composite trait mean of the plots' upper canopy layer. Collected leaves were transported on ice after which they were either dried for LMA analysis or stored in a ≤ -18 °C freezer until CAB analysis in the lab. LMA was calculated based on the dry leaf weight and fresh leaf area (as determined in Image J 1.52a software (Schneider, Rasband, and Eliceiri 2012)). CAB was derived using a protocol based on Lichtenthaler (1987).

Simultaneously with the collection of leaf samples and hemispherical photography, an inventory of the overstorey plant species composition and species number was made of each plot of each location. Parallel to trait and species assessments, local soil spectra were collected using an RS-3500 spectroradiometer (350-2500nm, ~8nm average spectral resolution) developed by Spectral Evolution. These soil spectra aid a representative approximation of PROSAIL's soil parameters for the study site.

### 3.2.3. Remotely sensed plant traits

#### 3.2.3.1. Sentinel-2 data

The Sentinel-2 constellation consists of two wide-swath, medium-high spatial resolution (10, 20, and 60 m), multi-spectral (13 bands) imaging instruments with a combined 5-day revisiting time (ESA, 2015). Corresponding to the study area and timeframe of our field campaign, one scene (29/07/2019) was completely free of problematic quality flags (cloud cover, cloud shadow, cirrus, and other atmospheric contamination). The availability of a single could-free image prevented complications of having to combine scenes from different timestamps and introducing temporal variability. The Sentinel-2 Level-2a (L2a) imagery for this data was acquired atmospherically corrected (Sen2Cor software) and obtained through the European Space Agency (ESA)'s Copernicus open-access Scientific Hub (Gascon et al., 2014; Louis et al., 2016). We excluded the 60m broad bands from the analysis and resampled the 10m spectral bands to 20m spatial resolution to match the scaling of our georeferenced field plots. Ultimately, ten out of thirteen available spectral bands of Sentinel-2 were used.

#### 3.2.3.2. Radiative transfer model inversion

Sentinel-2 L2a reflectance data served as the foundation for estimating key plant traits. The relationship between spectra, geometry, and soil and vegetation biophysical parameters was modelled with the use of the PROSAIL radiative transfer model inversion, which combines the leaf model PROSPECT (Feret et al. 2008; Féret et al. 2017; Jacquemoud and Baret 1990) and the canopy model 4SAIL (Verhoef 1984; Verhoef et al. 2007). PROSAIL assumes the canopy to be a homogenous turbid medium where absorption is defined by soil, canopy, and leaf properties (Jacquemoud et al. 2006). Such homogeneous canopies are an idealized approximation for many ecosystems. Inversion results are therefore subject to discrepancies between underlying assumptions of the extended 1-D columnar model and the complex reality of the heterogeneous canopies observed in the field (Jacquemoud et al., 2009). PROSAIL's relative simplicity with few but ecologically relevant input parameters avoids further complication of ill-posedness in the non-trivial inversion of multispectral reflectance data acquired by Sentinel-2 (Verrelst et al., 2019b; Yin et al., 2015). Spectral sensitivity of Sentinel-2 for retrieval of PROSAIL's traits under study (LAI, CAB, and LMA) has been demonstrated in previous sensitivity analyses (Gu et al. 2016; Rossi et al. 2020; Verrelst, Vicent, et al. 2019; de Sá, Baratchi, and Hauser 2021). Considering the model's widespread application, research on its generality across different vegetation types is relevant to a growing body of applications (Jacquemoud et al. 2006; Yin et al. 2015).

We implemented three approaches for inversion of the PROSAIL RTM on Sentinel-2 reflectance data representative of different common approaches found in remote sensing (Ali et al., 2020b; Verrelst et al., 2015); a Look-up Table (LUT)-based inversion based on a non-normalized "least-squares estimator" (LSE) cost function (Rivera et al., 2013; Rossi et al., 2020), the biophysical processor module from the ESA's Sentinel application platform (SNAP toolbox) (Weiss and Baret 2016), and a hybrid PROSAIL-D Support Vector Regression approach (SVR) (Féret et al., 2018, 2017).

*Table 3.1: Ranges of variable input parameters of the PROSAIL model used to generate the LUTs.*

| Domain | Parameter | Symbol | Unit | Distribution | Range |
|---|---|---|---|---|---|
| Leaf | Leaf structural parameter | N | – | Uniform | 1.4-1.7 |
| | Chlorophyll a+b content | CAB | μg/cm$^2$ | Gaussian | 10-60 |
| | Equivalent water thickness | EWT | g/cm$^2$ | Uniform | 0.001-0.045 |
| | Leaf dry mass per area | LMA | g/cm$^2$ | Uniform | 0.001-0.040 |
| | Brown pigments content | Cbrown | – | Fixed | 0.01 |
| Canopy | Leaf area index | LAI | m$^2$/m$^2$ | Gaussian | 0.01-3.5 |
| | Mean leaf inclination angle | ALA | deg | Uniform | 30-70 |
| | Hot spot size parameter | hot | m/m | Fixed | 0.01 |
| Abiotic | Ratio of diffuse to total incident radiation | SKYL | – | Fixed | 18% |
| | Soil brightness | psoil | – | Fixed | Spectroradiometer |
| Positional | Solar zenith | tts | o | Fixed | Sentinel-2 geometry |
| | Observer zenith | tto | o | Fixed | Sentinel-2 geometry |
| | Relative azimuth | phi | o | Fixed | Sentinel-2 geometry |

#### 3.2.3.2.1. Look-up Table (LUT)-based inversion

The Look-up Table (LUT)-based inversion is a two-step approach entailing:

i. generating a large number of simulations using a RTM, using a given sampling strategy for the input parameter ranges, and
ii. identifying the sample or the set of samples minimizing a cost function.

The estimated biophysical parameter corresponding to a reflectance spectrum is deduced from the value or mean value of the LUT samples minimizing the cost function. Here, we first created an extensive LUT of a subset of 10 000 simulations using Latin hypercube sampling to capture an optimal representation of all possibilities within the relevant trait space based on constrained search ranges defined by minimum and maximum trait values found in the field. Fixed values and ranges of parameters not measured in the field were selected based on literature (Bacour et al., 2002; Jay et al., 2017; Spitters et al., 1986). We used PROSPECT-4 coupled with 4SAIL in order to simulate canopy reflectance. The value, range, and distribution followed for each input parameter of the models are provided in Table 3.1.

For the inversion, we used a non-normalized "least-squares estimator" (LSE) cost function (Rivera et al., 2013; Rossi et al., 2020) and implemented the LUT inversion with the ARTMO toolbox V1.14 in Matlab (Verrelst et al. 2011). We applied the LUT inversion approach to estimate leaf CAB, LMA, and LAI. For optimization of its performance, we applied Gaussian noise (0-18%) to account for model and measurement uncertainties (Rivera et al., 2013). We used ARTMO's default parameterization for the noise and the multiple solution binning.

#### 3.2.3.2.2. Sentinel Application Platform Biophysical processor

The Sentinel Application Platform (SNAP) biophysical processor (Weiss and Baret 2016) is based on a hybrid approach combining physical modeling and machine learning. This type of approach consists of training the machine learning algorithm with a LUT to produce regression models for the estimation of a set of parameters. SNAP uses an artificial neural network (ANN) inversion pre-trained on a PROSAIL simulated database including canopy reflectance and the corresponding set of input parameters. The value, range and distribution followed for each input parameter of the models are described in Weiss and Baret (2016). SNAP can be considered as the standard approach and first port of entry for the estimation of vegetation biophysical parameters, as it is publicly available and easily applicable without strong expertise. SNAP includes an unreleased version of PROSPECT prior to PROSPECT-4, coupled with the SAIL model (Fourty and Baret, 1997). Traits retrieved in SNAP are scaled at canopy-level and include LAI, canopy chlorophyll (CAB*LAI) and canopy water (EWT*LAI). We reversed the multiplication by LAI to arrive at leaf trait estimates (CAB, EWT). In order to derive LMA, we coupled LMA to EWT (fixed factor; EWT*0.79=LMA), a strategy adopted more commonly in RTM inversion exercises given the large spectral overlap of LMA and EWT (e.g. Combal et al. 2003; Weiss et al. 2000; Kattenborn et al. 2017). The strong association between EWT and LMA has been found repeatedly in relevant datasets; in our own in-situ observations, but also the LOPEX/ANGERS, and NEON datasets (Hosgood et al. 1994; Jacquemoud et al. 2003; NEON, 2020).

#### 3.2.3.2.3. PROSAIL-D/Support Vector Regression hybrid approach

We tested an alternative hybrid approach including a physical modeling layer and a machine learning algorithm differing from those used in SNAP. The physical modeling layer included the newer leaf model PROSPECT-D (Féret et al., 2017) coupled with the 4SAIL canopy model (Verhoef et al. 2007). The Support Vector Regression (SVR, Vapnik 1998) algorithm was used as a regression model.

This hybrid inversion consists of bagging prediction of biophysical properties: a LUT is simulated with PROSAIL and resampled in order to produce multiple datasets including a limited number of samples. Then a set of individual support vector regression (SVR) models is trained from each reduced dataset. In our study, we produced 5000 samples and trained 50 SVR models of 100 samples with repetition for each biophysical property. The sampling used to produce the LUT followed the same distribution as showed in Table 3.1, with a few exceptions; as opposed to the fixed soil parameter in the ARTMO LUT implementation, the variability of the soil reflectance was introduced by defining minimum and maximum soil reflectance from experimental data. Soil spectra corresponding to weighted sum of these minimum and maximum soil spectra were generated, with the weight defined by the $psoil$ parameter (Table 3.1), which was randomly sampled following a uniform distribution between 0 and 1.

The geometry of acquisition, including solar zenith, observer zenith and relative azimuth was defined based on a random sampling following a uniform distribution between the minimum and maximum angles corresponding to the different acquisitions. The ratio of diffuse to total incident radiation (SKYL) was defined based on the sun zenith angle under clear sky conditions, following the equations proposed by Spitters, Toussaint, and Goudriaan (1986).

Two additional pigments are included in PROSPECT-D compared to the PROSPECT-4 parameterization: carotenoids and anthocyanins. Both pigment contents were defined based on a random sampling following a uniform distribution. The range for carotenoid content was defined between 0 and 15 $\mu g/cm^2$, which corresponds to the extended range observed in-situ, while the range for anthocyanin content was defined between 0 and 10 $\mu g/cm^2$, which corresponds to the range measured for mature leaves, yellow and reddish senescent leaves (Feret et al., 2017).

Finally, a random Gaussian noise was applied on the reflectance data, in order to account for the uncertainty originating from multiple origins, such as atmospheric conditions, sensor calibration, and the radiative transfer model itself (Berger et al., 2018b), or its improper parameterization (Danner et al., 2019).

### 3.2.4. Functional and taxonomic diversity estimations

The inversion of PROSAIL with Sentinel-2 spectra allowed us to estimate pixel-based (aggregated) trait values of plant canopies. For both in-situ and remote sensing datasets, functional diversity metrics were calculated for each location. While numerous functional diversity metrics exist, we opted for two commonly used metrics of functional diversity: the convex hull volume (CHV) and Rao’s quadratic entropy (Rao’s Q) (Dahlin, 2016; Gholizadeh et al., 2018; Rocchini et al., 2017; Torresani et al., 2019). Both metrics are straightforward to compute with relatively few observations, relatively easy to interpret and particularly equipped in characterizing multivariate trait space.

The CHV, a construct from computational geometry, provides an n-dimensional measure of the volume of canopy plant trait space within a community. CHV is commonly proposed as an adequate method to capture continuous trait space (Cornwell et al., 2006) and provides the smallest convex hull that encloses all observed traits. The measure is relatively sensitive to outliers and anomalies (Blonder et al., 2014; Schleuter et al., 2010). Functional richness calculated through the CHV has generally been found to hold a strong relationship to species richness (Mouchet et al., 2010; Schleuter et al., 2010).

Rao’s Q is one of the most commonly used multivariate measures of functional diversity and its calculation offers relative mathematical simplicity (Botta-Dukat, 2005; Mouchet et al., 2010; Ricotta and Moretti, 2011; Rocchini et al., 2017; Schleuter et al., 2010). A trait-based implementation of Rao’s Q depends both on the range of functional space occupied and on the similarity between trait combinations weighted by abundance (Botta-Dukat, 2005). Hence, elements of both functional richness and functional divergence are part of Rao’s Q (Mouchet et al., 2010). Rao’s Q has been widely applied to analyse patterns of trait convergence or divergence, i.e. quantifying trait dissimilarity compared to a random expectation (Ricotta and Moretti, 2011). In the remote sensing setting here, Rao’s Q describes the sum of pairwise distances between pixel-based multivariate values representing trait estimates while accounting for pixel abundance (in this case; $p = 1$) (Botta-Dukat, 2005; Rocchini et al., 2017):

$$Q = \sum_{i=1}^{L-1} \sum_{j=i+1}^{L} d_{ij}{}^{*}p_i{}^{*}p_j \quad (1)$$

where $d_{ij}$ corresponds to the multivariate distance matrix comprising $i$-th to $j$-th pixel, $p$ is the pixel or plot value abundance (=1 in our case), and $L$ corresponds to the number of pixels or plots sampled per location.

For the calculation of functional diversity, we took the combination of canopy (LAI) and leaf traits (CAB and LMA) given the ecological importance of these traits for plant functioning (see section 2.2). The combination of these traits allows us to partition canopy reflectance through RTM inversion and focus on canopy structure through LAI, foliar morphology through LMA and leaf chemistry (pigments) through CAB (Rossi et al. 2020; Serbin et al. 2019; Croft et al. 2017; Díaz et al. 2016). Functional diversity was calculated per location in the study area based on the eight to nine plot/pixel-wise trait mean estimates. All three traits were standardized prior to the calculations to assure equal weight to each trait.

Lastly, we calculated taxonomic diversity using in-situ species count data. We relied on the commonly applied Shannon's H diversity index as an indicator of local taxonomic diversity of each location;

$$H = -\sum_{i=1}^{s} (p_i \log_2 \, p_i) \quad (2)$$

where $s$ is the number of species IDs and $p_i$ is the proportion of the community represented by species i. These calculations were conducted using the scikit-bio 0.5.6 (http://scikit-bio.org/) package in Python. Min-max normalization of all metrics provided all values scaled between 0 and 1.

### 3.2.5. Statistical analysis

The structure of our data complicated a straightforward application of single goodness-of-fit measures such as $R^2$ or Pearson's r correlation (Khamis, 2008; Schober and Schwarte, 2018). Therefore, we evaluated the relationship between satellite estimates and the corresponding in-situ measurements by different metrics of association, error and correlation (Lee's L statistic, Spatial Error Models, Spearman's rho (ρ) and Root Mean Square Error (RMSE)).

The plots/pixels (N=97) were non-randomly distributed, which might inflate the correlation and lead to biases. An ordinary least squares linear regression model and Moran's I statistics on the residuals indeed confirmed the presence of spatial autocorrelation in our data (Suppl. Mat. Table S. 10). To account for autocorrelation, we ran Lee's L test (instead of Pearson's r). Lee's L statistic captures the spatial co-patterning by integrating a univariate spatial autocorrelation of each variable (Moran's I) and their bivariate point-to-point association (Pearson's r) (Kim et al., 2018; Lee, 2001). In addition, we ran a spatial error regression model implemented with the "spdep" package of R (Bivand et al., 2011), which controls for the bias of spatially autocorrelated errors. We evaluated the model's performance for spatial autocorrelation by reassessing the residuals with Moran's I, which showed that spatial autocorrelation was no longer significant (Suppl. Mat. Table S. 11).

In addition, we evaluated the correspondence of satellite and in-situ observations at the location-level. The means and standard deviations at the location-level gave insight in local variability of estimates and potential robustness of aggregation against noise and misregistration. Moreover, location-wise trait means eliminate the effects of spatial auto-correlation resulting from multiple plots/pixels per locations. The locations are randomly distributed over our study area. However, the small sample size of locations (N=12) makes it difficult to warrant for normality. In precaution of non-normality, we implemented Spearman's rho, as the non-parametric and rank-based alternative to Pearson's r (Fowler, 1987; Khamis, 2008; Schober and Schwarte, 2018). In addition, we calculated the Root-Mean-Square Error (RMSE) to quantify absolute biases for both plot-/pixel-level and location-level analyses.

The functional diversity metrics (CHV, Rao's Q) derived from satellite observations were compared against in-situ functional diversity observations. In addition, the satellite-based functional diversity metrics were compared against in-situ taxonomic diversity to evaluate the ecological relevance of the selected RTM-based traits for assessing species-based biodiversity and conservation planning. For the analyses of functional diversity patterns, we used Spearman's rho to warrant for possible non-normality in the small sample size (N=12).

## 3.3. Results

### 3.3.1. Trait estimates

Table 3.2 shows the performance of the three retrievals against in-situ trait measurements, both at pixel-level and location-level aggregation. All three methods estimated the distribution of trait values from Sentinel-2's spectral reflectance reasonably well. LAI was estimated with relatively high precision across all three methods (Table 3.2). Across approaches, forest locations generally exhibited higher LAI values compared to shrublands in line with field observations.

LMA estimates corresponded well with the variation in in-situ measurements, with SVR and ARTMO performing better than SNAP. Despite relative correspondence with the field data, ARTMO exhibited a strong bias, overestimating absolute in-situ LMA observations. SVR produced accurate estimators for LMA both in a relative and absolute sense. All three approaches consistently identified generally higher LMA values in shrublands as compared to forested locations.

CAB retrievals were still significantly correlated to the in-situ measurements at plot-level, but with weaker relationships and stronger deviations from the 1:1 line compared to the other traits for all three retrieval methods (Table 3.2).

Spatial error (regression) models (Table S. 11) accounting for spatial autocorrelations at the plot level indicated a strong significance of the satellite-based estimates and high overall predictive power of the models (Pseudo-$R^2$: 0.76-0.93, depending on trait and inversion method) with the exception of ARTMO's CAB estimation (Not significant, Pseudo-$R^2$: 0.35).

Despite the smaller sample size, the location-level aggregation of trait means retained a strong association between in-situ measurements and the satellite-based estimates for LMA and LAI, while CAB estimation by SVR's hybrid inversion and SNAP's biophysical processor were no longer significant (>0.05) (Table 3.2).

The retrieval of within-location standard deviation was less convincing overall compared to mean estimates, although LAI variability correlated significantly for all three inversion methods (Table 3.2). Only ARTMO's LUT-based inversion performed was significantly correlated to the in-situ variability of LMA (Fig. 3.3). Retrieval for SVR and ARTMO is illustrated in Fig. 3.2 and Fig. 3.3, respectively, while figures for retrieval based on SNAP's biophysical processor can be found in Fig. S. 12. The patterns of location-wise standard deviations did not differ evidently between forested and shrubland locations.

*Table 3.2: An overview of satellite-based single trait estimation of the three RTM inversion algorithms (SVR, ARTMO, and SNAP) compared against in-situ field measurements. Validation was done both at the individual pixel-level (in-situ: plot) and the location-level aggregation. Measures of association indicate the strength of correlation between in-situ measured and satellite estimated trait values. At the pixel/plot-level, Lee's L statistic was implemented as an alternative to Pearson's r to account for spatial autocorrelation within spatially neighbouring plot/pixel observations. At the location-level, Spearman's rho (ρ) was implemented to warrant for the possible non-normality in small sample sizes (N=12). RMSE and nRMSE are indicative of the absolute and relative error found in trait means.*

| Algorithm | Trait | Pixel-level trait estimates | | | Location-level trait means | | Location-level trait standard deviations | |
|---|---|---|---|---|---|---|---|---|
| | | Lee's L | RMSE | nRMSE (%) | Spearman's ρ | RMSE | Spearman's ρ | RMSE |
| SVR (Hybrid) | Leaf Area Index (m2/m2) | $0.70^{**}$ | 0.49 | 15.71 | $0.73^{**}$ | 0.43 | $0.67^{**}$ | 0.18 |
| | Leaf Mass per Area (mg/cm$^2$) | $0.96^{**}$ | 6.36 | 17.78 | $0.77^{**}$ | 5.77 | 0.46 | 1.20 |
| | Leaf Chlorophyll (μg/cm$^2$) | $0.52^{**}$ | 7.07 | 17.35 | 0.53 | 5.80 | 0.04 | 1.87 |
| ARTMO (LUT) | Leaf Area Index (m2/m2) | $0.72^{**}$ | 0.51 | 16.24 | $0.81^{**}$ | 0.44 | $0.66^{*}$ | 0.13 |
| | Leaf Mass per Area (mg/cm$^2$) | $0.79^{**}$ | 31.06 | 34.43 | $0.83^{**}$ | 30.25 | $0.73^{**}$ | 4.70 |
| | Leaf Chlorophyll (μg/cm$^2$) | $0.29^{**}$ | 12.03 | 28.45 | $0.71^{**}$ | 9.62 | 0.49 | 2.63 |
| SNAP | Leaf Area Index (m2/m2) | $0.68^{**}$ | 0.62 | 19.84 | $0.73^{**}$ | 0.58 | $0.76^{**}$ | 0.16 |
| | Leaf Mass per Area (mg/cm$^2$) | $0.71^{**}$ | 5.94 | 23.46 | $0.71^{**}$ | 5.50 | 0.24 | 1.62 |
| | Leaf Chlorophyll (μg/cm$^2$) | $0.41^{**}$ | 13.79 | 28.54 | 0.39 | 13.23 | -0.24 | 2.61 |

$^{**}$: Significant correlation (p <0.01), $^{*}$: Significant correlation (p <0.05), $^{ns}$: Not significant (p>0.05)

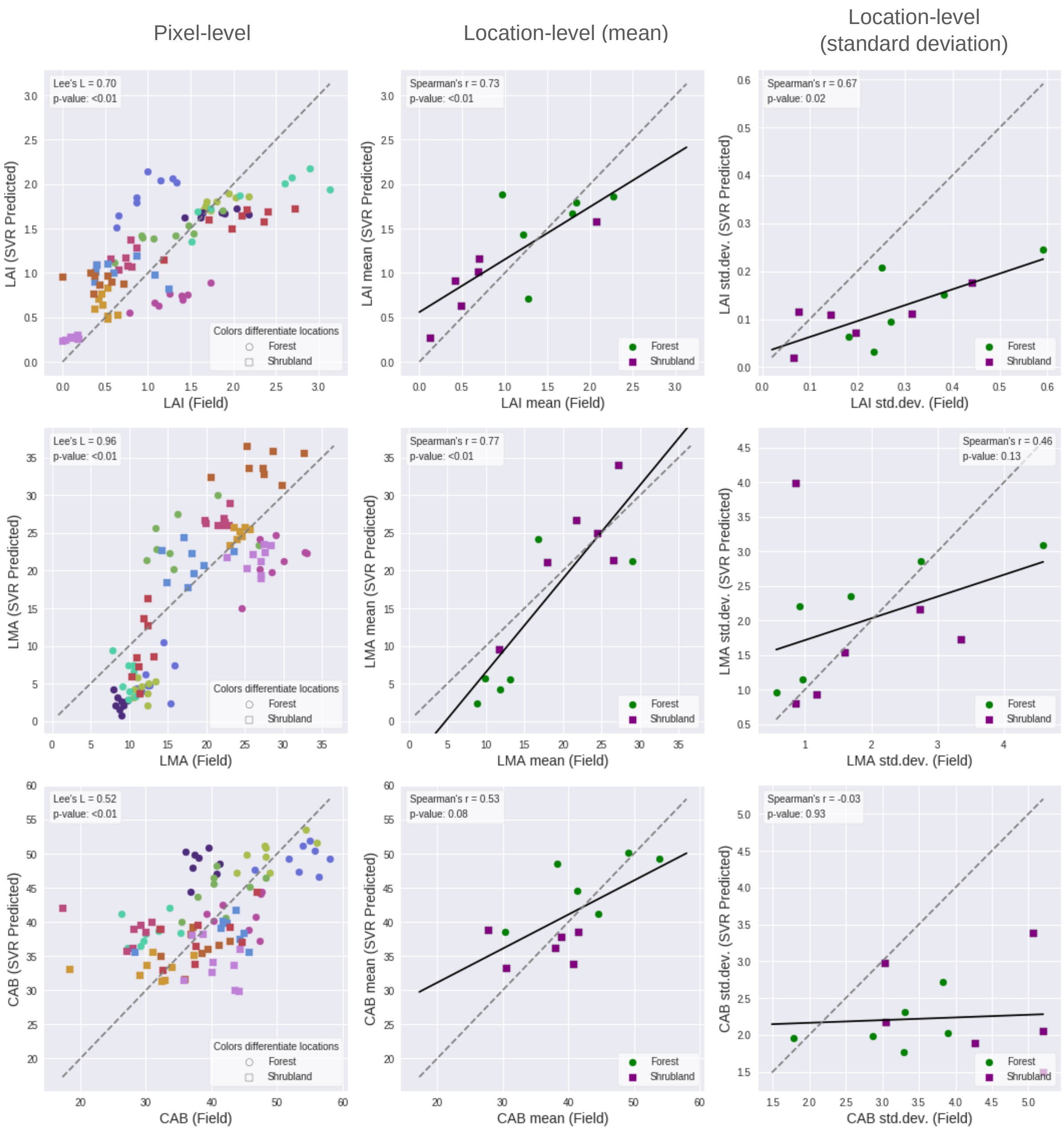


*Fig. 3.2: Comparison of Sentinel-2-based trait estimates (y-axis) retrieved using a Support Vector Regression (SVR) hybrid inversion algorithm against in-situ field measurements (x-axis). The left column shows pixel-level (in-situ: plot) comparisons of traits, where different colors indicate plots of respective locations. The middle column depicts trait means per location and the right column presents trait standard deviations per location. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the fitted linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

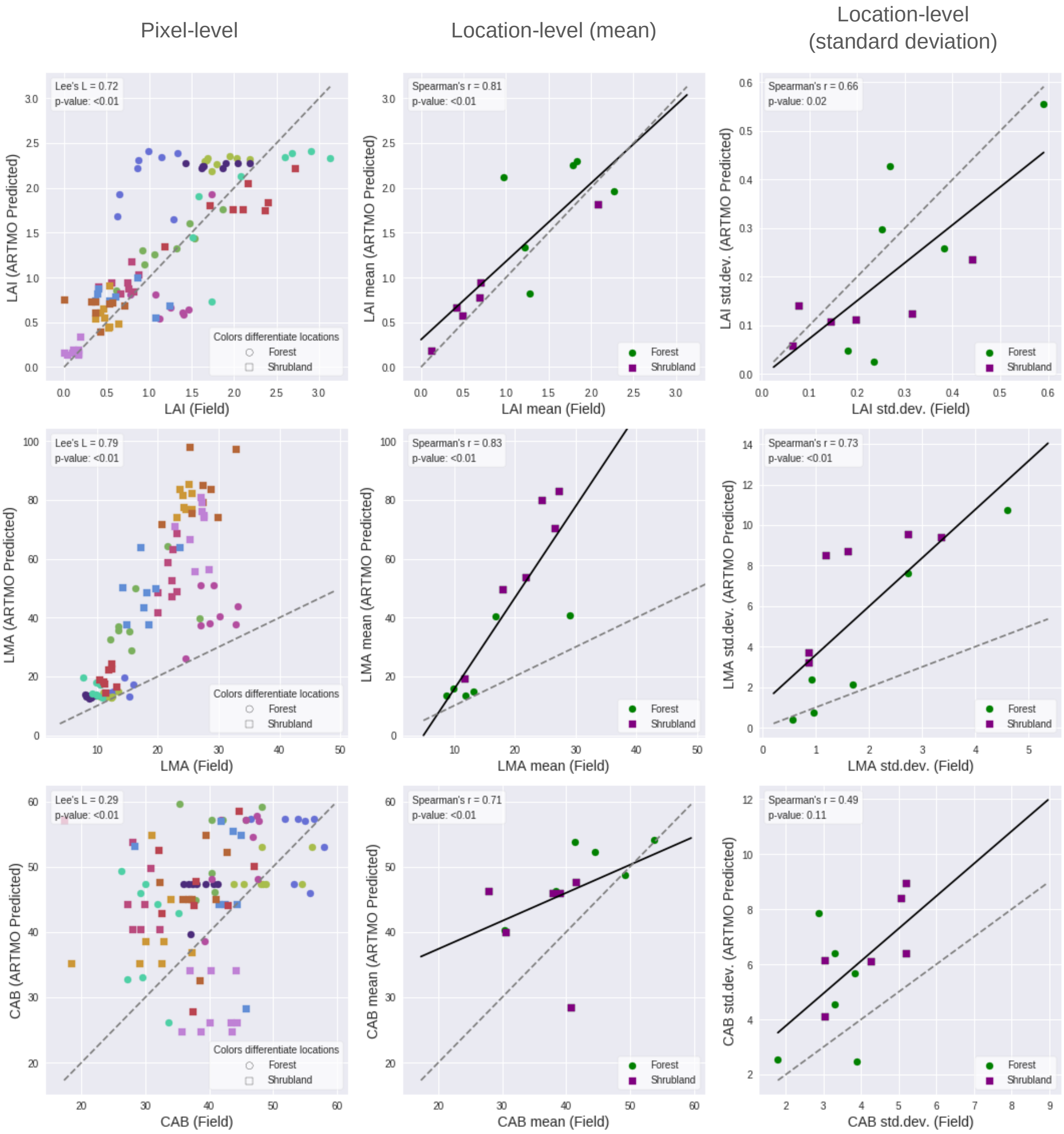


*Fig. 3.3: Comparison of Sentinel-2-based trait estimates (y-axis) retrieved using ARTMO LUT-based inversion against in-situ field measurements (x-axis). The left column shows pixel-level (in-situ: plot) comparisons of traits, where different colors indicate plots of respective locations. The middle column depicts trait means per location and the right column presents trait standard deviations per location. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the fitted linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

### 3.3.2. Functional diversity estimates

Despite the small sample size (N= 12) and availability of only 8-9 trait observations per location to calculate functional diversity, functional diversity exhibited a significant relationship between in-situ and satellite-based estimates in most cases. The CHV metric was significantly associated with in-situ functional diversity across all three inversion algorithms. For Rao's Q, this significant relationship only holds for SVR and LUT-based ARTMO trait retrieval. Yet, in general, the three approaches indicate feasibility in predicting in-situ plant functional diversity through satellite-based estimates (Table 3). Fig. 3.4 shows the results of the SVR and ARTMO inversion approaches. The results of the SNAP inversion can be found in Fig. S. 13.

*Table 3.3: Rank-based correlation between in-situ observed plant functional diversity (CHV and Rao's Q) and satellite remote sensing observed functional diversity. Calculations of functional diversity combine canopy trait (LAI) and leaf-level traits (LMA and CAB). Significant correlations (α < 0.05) are highlighted in bold. RMSE and nRMSE are indicative of the absolute and relative error found in functional diversity estimates.*

| | Algorithm | Spearman's ρ | Sig. | RMSE | nRMSE (%) |
|---|---|---|---|---|---|
| Convex Hull Volume (CHV) | SVR (Hybrid) | 0.80 | <0.01 | 0.11 | 20.48 |
| | ARTMO (LUT) | 0.76 | <0.01 | 0.09 | 20.94 |
| | SNAP | 0.67 | 0.02 | 0.11 | 25.74 |
| | | | | | |
| Rao's quadratic entropy | SVR (Hybrid) | 0.75 | 0.01 | 0.13 | 22.08 |
| | ARTMO (LUT) | 0.80 | <0.01 | 0.08 | 19.28 |
| | SNAP | 0.19 | 0.56 | 0.19 | 43.06 |

Remotely sensed functional diversity metrics were also significantly tied to in-situ community taxonomic diversity (Fig. 3.4, rightmost column). This significant relationship indicates that the selected traits are relevant for both trait and species diversity and serves as cross-validation of the capability of RTM inversion of Sentinel-2 spectral information to predict ecologically relevant in-situ plant biodiversity, either directly or through surrogacy. Functional diversity and taxonomic diversity were also related in-situ (Fig. S. 14).

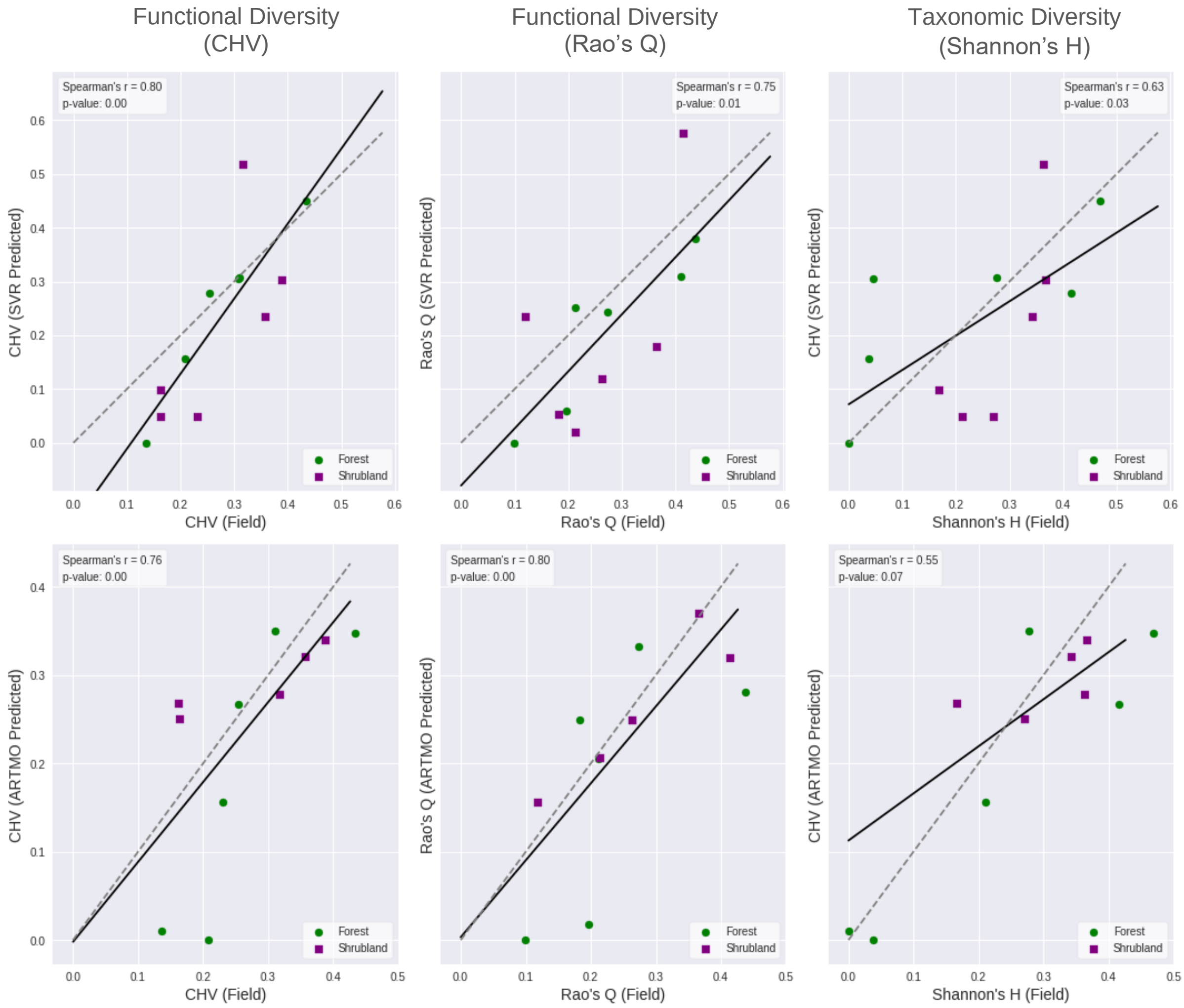


*Fig. 3.4: Remotely sensed functional diversity estimates (CHV and Rao’s Q) calculated from Sentinel-2 derived traits through the SVR hybrid inversion (top row) and ARTMO LUT-based inversion (bottom row) compared against in-situ functional diversity measurements (left and center columns). The rightmost column compares the remotely sensed functional diversity (CHV) against in-situ taxonomic diversity (Shannon’s H). The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

## 3.4. Discussion

### 3.4.1. Estimating canopy and leaf traits

The capability to estimate spatial plant canopy trait patterns from currently operational optical satellite remote sensing, both in terms of mean and variability, serves as an important starting point towards the assessment of satellite-based functional diversity estimates. Estimation of individual plant traits from Sentinel-2 inference using RTM inversion has been shown to be viable in numerous previous studies conducted in relatively homogeneous (semi-)natural environments (Ali et al., 2020a, 2020b; 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). Similarly, in our study, we demonstrated the potential of remote sensing to estimate the relative spatial distribution of multiple individual vegetation traits simultaneously, yet in a relatively heterogeneous landscape using a comparatively simple RTM. Unique to this study, we assessed a multivariate retrieval of three traits (LAI, LMA and CAB) in twelve separate locations consisting of multiple adjacent pixels (N=97) in a set-up designed for further assessment of plant community patterns of functional diversity (Fig. 3.1). The georeferenced and carefully scaled in-situ field measurements allowed us to validate satellite remote sensing directly without relying upon interpolation of point data and/or temporally and/or spatially transposed secondary trait data (e.g. Ma et al. 2019; Butler et al. 2017; Moreno-Martínez et al. 2018).

In light of the multitude of existing inversion methods, we ran three different algorithms to invert PROSAIL on Sentinel-2 reflectance data (Verrelst, Malenovský, et al. 2019; Rivera et al. 2013; Verrelst et al. 2015). Despite the heterogeneity of the canopies and the landscape, all three retrieval approaches (SVR, ARTMO (LUT-based) and SNAP) showed significant correlations between the estimates of the various traits and the actual in-situ measurements (Table, 2, Fig. 3.2 and Fig. 3.3). Significant relations were found for pixel-wise trait estimates as well as aggregated trait means at the location level. The good performance of the latter is noteworthy as aggregation potentially attenuates the influence of noise. The Sentinel-2 retrieval performed specifically well for estimating the relative distribution of LAI and LMA despite biases (RMSE), whereas CAB exhibits a considerably less association with field measurements (Table 3.2). Differences in the performance of CAB may be attributed to its parameterization in different versions of PROSPECT, as well as strong absorption of radiation in the visible range and associated low signal-to-noise ratios.

Differences in performance between the three algorithms is in part due to parameterization and the mathematical intrinsic properties of the individual inversion methods. However, also the role of ‘a priori’ information deserves further attention (Verrelst et al. 2015; Verrelst, Malenovský, et al. 2019). In this study, the ARTMO LUT-based and SVR hybrid approaches both rely on PROSAIL simulations that are generated from the minimum and maximum trait ranges found in the field, while the SNAP biophysical processor runs completely independently of ancillary data (Weiss and Baret 2016). Databases like TRY (Kattge et al. 2020) can aid future analyses to generate locally optimized trait ranges based on species occurrences without the need for dedicated field campaigns. The optimized LUTs, taking into account the trait ranges of the ecosystem under study, enhanced performance in terms of the relative prediction of in-situ trait and the absolute bias.

For an accurate assessment of functional diversity, proper estimation of local trait variability is important, which has received little attention in the body of research on the retrieval of plant traits from satellite remote sensing thus far. In comparison to location-level trait means, our ability to retrieve trait variability is relatively inconsistent (Table 3.2). The observed inconsistencies might require additional accounting of adjacency effects, noise/inconsistencies in field measurements, noise from atmospheric correction (5-10%) and reported multispectral misregistration of Sentinel-2 that complicate the process of deciphering subtle differences at a local scale (Brede et al., 2020; Skakun et al., 2017).

Atmospheric scattering causes light reflected from adjacent landscapes to be observed by the sensor. Without adequate correction of possible adjacency effects (being only an option within the Sen2Cor processor, with a low resolution of 1km), scattering leads to minor biases or spectral convergence (Louis et al., 2016). While the local mean traits would be affected little, spectral convergence could result in a lower sensitivity to capture the variation between neighboring pixels and thereby affect functional diversity estimates.

As an exception, the results for LAI still indicate high sensitivity across the three retrieval algorithms to accurately depict local variability in LAI between adjacent pixels and plots (Table 3.2) despite a general underestimation. LAI is known to exhibit a relatively strong spectral response across large part of Sentinel-2's spectrum, which could favor the capability in detecting small changes and an improved signal-to-noise ratios as opposed to other traits (Asner 1998).

This validation of multivariate single plant traits demonstrates how an RTM approach can present us with a semi-mechanistic way to retrieve plant traits based on the physical principles of radiative transfer, even if limited field data is available. For now, field data remains critical for validation. More specifically, further independent testing will be needed to examine the scalability of the approach across multiple diverse ecosystems, canopy types and even biomes. Accuracies of simultaneous retrieval of multiple traits can be further improved with RTMs optimized for the specific vegetation types under study. However, RTM selection and configuration needs to be done under consideration of the trade-offs between local optimization and generality across heterogeneous landscapes, as well as the ill-posedness induced by heavy parameterization of complex optimized models in inversion applied to limited spectral information (Huang et al., 2011). In the future, data assimilation developments (Lewis et al. 2012) and the prospective launch of hyperspectral satellite imagers (e.g. EnMAP, SBG, CHIME; Cavender-Bares, Gamon, and Townsend 2020; Lahoz and Schneider 2014) will likely enable more detailed spectral information for inversion to accurately derive more traits for functional diversity assessments.

### 3.4.2. Estimating multivariate functional diversity

The retrieval and validation of single trait estimates and the relative spatial variability thereof serves our study's core objective of estimating plant functional diversity from satellite remote sensing. The study demonstrates a methodology for one-to-one scaled ground-truthing of functional diversity based on satellite observed mean trait estimates for aggregate canopies. We tested two different metrics (CHV and Rao's Q) to calculate functional diversity. Functional diversity was calculated over three traits combining canopy structure through LAI, and foliar morphology through LMA, and leaf chemistry (pigments) through CAB as key functional traits (Croft et al., 2017; Díaz et al., 2016; Rossi et al., 2020; Serbin et al., 2019).

Across different setups, the majority of satellite-based functional diversity metrics corresponded significantly with in-situ measurements. The convex hull volume (CHV) operationalization of functional diversity showed strong *concordance* with in-situ observations across all three inversion methods (Spearman's ρ: 0.67-0.80). For the interpretation of these results, we highlight the implications of the distance-based nature of the functional diversity metrics and the statistical power of the study in the following paragraphs.

The functional diversity metrics used here, and many of the multivariate alternative metrics (e.g. Schleuter et al. (2010), Mouchet et al. (2010), Aiba et al. (2013)), rely on the quantification of "diversity" or "entropy", based on relative distances or volume between trait observations set in a n-dimensional space in which each axis represents a specific trait. Accordingly, the accurate prediction of functional diversity is determined predominantly by the normalized relative position of trait combinations rather than the absolute trait value deviation itself. As such, the functional diversity metrics presented here have shown a degree of robustness against biases in RMSE, specifically for CHV calculations. For instance, the SVR hybrid inversion reveals better RMSE for LAI, LMA and CAB (Fig. 3.2), especially compared to the overestimation of LAI by ARTMO (LUT-based) and the inferior accuracy of SNAP, yet the functional diversity estimates show a level of robustness to these errors given the reasonable performance across retrieval algorithms (See Table 3.3, Fig. 3.4, and Fig. S. 13).

The interpretation of the results needs to be done in consideration of the sample size which is dictated by the laboriousness of validating functional diversity at the scale of satellite pixels. Our field campaign involved comprehensive efforts to representatively sample the composition of the dominant canopies, based on an average of 17 sampled sunlit leaves from individual branches, within each of the eight to nine plots across each of the twelve semi-natural shrubland/forested locations. Despite these efforts, the statistical power of the twelve points for functional diversity estimation imposes limitations on the confidence and our ability to attest the patterns found between remotely sensed estimates and in-situ observations. In addition, each functional diversity calculation only relies on eight to nine individual observations. Statistically, we know that a larger number of individual observations allows us to better characterize functional diversity and result in higher robustness against noise, misregistration, and random artifacts (Frank, 2009; Hubbell, 2001; Steinbauer et al., 2012). This robustness is relevant considering that convex hull volumes are particularly sensitive to outliers and that satellite remote sensing, including atmospheric correction, remains susceptible to unfavorable signal-to-noise ratios (Blonder et al. 2014; Lewis et al. 2012; Brede et al. 2020; Verrelst, Vicent, et al. 2019; Skakun et al. 2017).

### 3.4.3. Ecological implications

The validation results show the potential of using satellite remote sensing to estimate spatial patterns of plant functional diversity. However, for ecological implementation, we need to go beyond validation and delve into the ecological relevance and usefulness of satellite remote sensing products quantifying functional diversity (Feilhauer et al., 2018). Here, we highlight three aspects - the selection, scale, and number of traits, the spatial resolution of the functional diversity metrics, and the need for further validation – as considerations for interpreting and improving the ecological relevance of remotely sensed metrics.

The selection of which and the number of traits to include in functional diversity measurements is a critical step that will impact the patterns ultimately observed (Legras et al., 2020; Petchey and Gaston, 2006; Tsianou and Kallimanis, 2016). The majority of studies render functional diversity using traits largely determined by data availability despite that ideally such decisions are driven by the specific function of interest (Petchey and Gaston, 2006; Tsianou and Kallimanis, 2016). Likewise, in direct retrieval through (optical) remote sensing, we are limited to traits that are spectrally obtainable (Homolová et al., 2013). Exemplar prioritized lists of key functional plant traits that are remotely observable from space have been compiled by e.g. Jetz et al. (2016) and the National Academies of Sciences Engineering and Medicine (2019) among others.

LMA and CAB implemented in this study feature among those prioritized lists (Jetz et al., 2016; National Academies of Sciences Engineering and Medicine, 2018) and are part of the PROSAIL input parameters. These traits allow us to characterize part of the foliar morphology through LMA and leaf chemistry (pigments) through CAB. These capture the tradeoffs of a plant's investment in leaf structure, robustness, versus leaf surface area and per area capacity for photosynthesis (Croft et al., 2017; Díaz et al., 2016; Rossi et al., 2020; Serbin et al., 2019). Functional diversity can both be driven by intra- and interspecific variation. Our field observations indicate that higher taxonomic diversity (Shannon's H) in the study area does translate to higher functional diversity (Fig. S. 14), implying that the observed species exhibit distinct functional profiles shaping trait space. While the implemented traits might not fully capture all aspects of functional importance, the selection does significantly resonate with the taxonomic composition. This relationship is relevant, as species diversity is still the most commonly used indicator by decision-makers in conservation planning and biodiversity monitoring (Gaston, 2010; Petchey and Gaston, 2002).

In agreement with this, functional diversity (based on LAI, LMA, and CAB) captured from satellite remote sensing indeed also showed a relationship to in-situ community taxonomic diversity (Fig. 3.4). Fig. S. 15-Fig. S. 18 indicate that the inclusion of LAI as a key trait of functional diversity actually weakens the relationship between trait diversity and taxonomic diversity both in in-situ and satellite-derived observations. Diversity in LAI seems to be relatively orthogonal to the taxonomic diversity in the dataset of our study area. As such, functional diversity measures only involving the leaf traits (LMA and CAB) resulted in stronger significant relationships to taxonomic diversity, both for in-situ and satellite-based observations (See Fig. S. 15-Fig. S. 18). Given the dominance of LAI on the canopy reflectance signal, proper estimation of LAI and diversity thereof is still highly important to accurately obtain canopy-level traits and structural diversity (Asner et al. 2015; Roelofsen et al. 2013).

These findings illustrate the importance of trait selection considerations in functional diversity assessments and decisions to be made regarding the scale at which we look at traits; at a leaf-level or at the canopy-level. The incorporation or multiplication with LAI facilitates a relatively straightforward approach to upscale leaf traits to the canopy scale (Bacour et al., 2006; Kattenborn et al., 2019; Musavi et al., 2015). The retrieval of canopy traits for functional diversity, either through incorporation (see Fig. 3.4) or multiplication with LAI, resulted in higher accuracies as compared to solely through leaf-level traits as illustrated here by SVR and SNAP inversions (see Fig. Fig. S. 15 and Fig. S. 17). The improved retrieval accuracy of canopy traits compared to leaf traits has also been noted by e.g. Bacour et al., 2006; Homolová et al., 2013; Roelofsen et al., 2013. However, for our study area, this better retrieval seems to come at the cost of lesser relationship to taxonomic diversity.

Sentinel-2's pixel size, with most bands scaled at a 20m spatial resolution, thus resulting in plots of 400m$^2$, is significantly larger than most plant canopies. This mismatch between ecology's sampling units and the homogeneous coarse raster offered by satellite remote sensing complicates ecological interpretation (Wang and Gamon, 2019). The calculation of functional diversity requires multiple observations embodied in pixel-scaled plots. The calculations provided a characterization of functional diversity in ecological communities captured through multiple pixels covering around 3200 m$^2$. As such, for ecological interpretation, the remotely sensed functional diversity metrics likely capture both elements of alpha and beta-diversity indicative of the local turnover of functional diversity in arbitrary ecological communities (Barton et al., 2013; Rocchini et al., 2015).

Besides ecological interpretation, this scale mismatch also challenges validation efforts. Our field campaign carefully followed Sentinel-2's spatial scaling resulting in comprehensive but laborious sampling efforts of large plots. Our spatial scaling enabled a unique one-to-one validation of remotely sensed estimates against in-situ community functional diversity patterns. The results are indicative of current capabilities in mapping functional diversity from space through RTM inversion approaches (Table 3.3 and Fig. 3.4), yet remain ambiguous in terms of sample size and the number of observations on which functional diversity is calculated. An injection of finer scaled remote sensing approaches, such as a two-tier validation between field, UAV and satellite remote sensing may provide a better characterization of the spatial scaling of functional diversity patterns observed from space, and potentially facilitate feasible validation campaigns that include a larger number of observations. Complementary, wall-to-wall (i.e. spatially explicit) landscape retrieval approaches of functional diversity from remote sensing would allow further assessment of the validity of remotely sensed functional diversity metrics along well-studied ecological gradients (Durán et al., 2019). Finally, interpolation of species-mean trait estimates based on carefully curated trait and species occurrence databases may complement the extensive sampling of field observations presented here to build a more complete validation dataset, possibly covering multiple ecosystem types, regions and or biomes (e.g. Aguirre-gutiérrez et al., 2021; Ma et al., 2019; Serbin et al., 2019).

## 3.5. Conclusions

We demonstrated the potential of RTM inversion of Sentinel-2 to simultaneously derive multiple relevant traits to calculate satellite remotely sensed functional diversity estimates in a (semi-)natural heterogeneous landscape. The implementation of our study design allowed for a unique direct one-to-one validation of individual traits and community patterns of functional diversity based on in-situ measurements that are precisely scaled and georeferenced to the satellite observed pixels. The implemented general RTM approach is relevant for wider application in ecosystem and biodiversity research as it allows for the retrieval of in-situ measurable multivariate trait estimations from reflectance without heavy reliance on field data for input. The approach is semi-mechanistic and the universal principles behind its physics are in theory scalable, although further research across ecosystems and canopy types is necessary. Across a representative selection of different inversion approaches, the functional diversity metrics (CHV in particular) appear relatively robust against errors in trait retrievals. Taken together, the study provides an important step towards maturation of operational, scalable, spatially and temporally explicit methods and, hopefully, inspires further validation and assessment of satellite-based functional diversity metrics across ecological gradients and larger datasets. A validated assessment will allow monitoring large-scale patterns of plant functional diversity to better understand the dynamics of functioning of our ecosystems.

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

**Based on**:

Hauser, L. T., Timmermans, J., Soudzilovskaia, N. A., & P.M. van Bodegom (2022). Linking Land Use and Plant Functional Diversity Patterns in Sabah, Borneo, through Large-Scale Spatially Continuous Sentinel-2 Inference. Land, 11(4), 572. https://doi.org/10.3390/land11040572. (Impact Factor: 3.4)

**Abstract:**

Global biodiversity losses erode the functioning of our vital ecosystems. Functional diversity is increasingly recognized as a critical link between biodiversity and ecosystem functioning. Satellite earth observation has been proposed to address the current absence of information on large-scale continuous patterns of plant functional diversity. This study demonstrates the inference and spatial mapping of functional diversity metrics through satellite remote sensing over a large key biodiversity region (Sabah, Malaysian Borneo of ~53,000 km$^2$) and compares the derived estimates across a land use gradient as an initial qualitative assessment to test the potential merits of the approach.

Functional traits (Leaf Water Content, Chlorophyll a-b, and Leaf Area Index) were estimated from Sentinel-2 spectral reflectance using a pre-trained neural network on radiative transfer modelling simulations. Multivariate functional diversity metrics were calculated, including functional richness, divergence, and evenness. Spatial patterns of functional diversity were related to land use data distinguishing intact forest, logged forest, and oil-palm plantations.

Spatial patterns of satellite remotely sensed functional diversity are significantly related to differences in land use. Intact forests, as well as logged forests, feature consistently higher functional diversity compared to oil-palm plantations. Differences are profound for functional divergence, whereas functional richness exhibits relatively large variances within land use classes.

By linking large-scale patterns of functional diversity as derived from satellite remote sensing to land use information, this study indicates initial responsiveness to broad human disturbance gradients over large geographical and spatially continuous extents. Despite uncertainties about the accuracy of the spatial patterns, this study provides a coherent early application of satellite-derived functional diversity towards further validation of its responsiveness across ecological gradients.

## 4.1. Introduction

The rampant decline of global biodiversity over the last decades has become a major threat to the ecosystems on which humans depend (IPBES, 2019). Land use change fuelled by agricultural expansion has been a particularly salient direct driver of biodiversity losses in terrestrial ecosystems as forests, wetlands, and grasslands have been converted (IPBES, 2019). Current estimates suggest that land use-related pressures have reduced local biodiversity intactness beyond the planetary boundaries for biosphere integrity as a safe operating space for humanity (Newbold, 2016).

In many tropical species-rich regions, the conversion of forests by land use change has led to stark contrasts in the spatial distribution of biodiversity (UNDP, 2012; Wilcove et al., 2013). Global demands for food, biofuel, and other commodities have driven the rapid expansion of oil-palm and paper-and-pulp industries at the expense of lowland rainforests jeopardizing forest biota (Sodhi et al., 2010, 2004). For instance, in Sabah, northern Borneo, records show that over 39.5% of the forest has been cleared and just 19.1% of the land surface of Sabah remained as intact primary forest in the period between 1973 and 2010 (Bryan et al., 2013; Gaveau et al., 2016, 2014). These trends have resulted in high rates of biodiversity loss and degradation of the forest landscape, threatening more than 1000 taxa of endemic plants present including iconic Dipterocarpaceae species as well as the unique variety of fauna dependent on these habitats (Maycock et al., 2012; UNDP, 2012; Wilcove et al., 2013). Small-scale field studies indicate that oil-palm plantations support substantially fewer plant species (Fitzherbert et al., 2008; Koh and Wilcove, 2008), non-volant small mammals (Bernard et al., 2009), butterflies (Benedick et al., 2006), and have lower arthropod and multi-trophic functional diversity in comparison to natural and logged forests (Barnes et al., 2014; Edwards et al., 2014).

The threats associated with land use pressure are likely to further disrupt the remaining intact primary lowland rainforests in the region and decrease biodiversity (Neo et al., 2021). One of the biggest challenges to combat these threats is that the monitoring the effects of land use in the region is subject to the relative paucity of data on basic ecology (Jetz et al., 2016). In order to effectively preserve and monitor plant biodiversity, it is necessary to quantify diversity patterns and understand the behaviors and ecologies governing the distribution and abundance of species, communities and ecosystems. In particular, the accurate characterization of plant functional diversity over large spatial and temporal scales would greatly improve our ability to track the status and resilience of key biodiversity areas, such as the entire biodiversity hotspot of Borneo, and understand the effects of human intervention (Hortal et al., 2015).

Functional diversity is associated with taxonomic and phylogenetichttps://www.nature.com/articles/nplants201624 - ref-CR14 biodiversity measures, yet tends to respond more consistently to environmental drivers (de Souza et al., 2013; Flynn et al., 2009; Petchey and Gaston, 2002). It captures the ranges and abundances of the combined functional traits of the organisms present in an ecosystem and is strongly indicative of the way these ecosystems operate (Cadotte et al., 2011; Diaz and Cabido, 2001). To maintain crucial ecosystem functions, a growing body of research highlights the importance of preserving plant functional diversity as the fundament of ecosystem functioning (Fukami et al., 2005; Hooper, 2002; Violle et al., 2014). Thus, large-scale functional diversity maps, currently absent, would provide essential information for biodiversity conservation.

Mapping plant functional diversity requires extensive, consistent, and repeated data on traits over (continuous) regional and global scales which we currently still lack (Jetz et al., 2016). Most field measurements of plant traits in terrestrial ecosystems have been rather small-scale and limited in spatial extent due to their laboriousness and related costs (Asner, Martin, Anderson, & Knapp, 2015; Chiarucci, Bacaro, & Scheiner, 2011; Götzenberger et al., 2012). Attempts to combine disparate in-situ research activities in global traits databases tend to be temporally and geographically constrained, suffer from sampling inhomogeneities, largely exclude remote areas and are bound by the limitations of interpolation (Granger et al., 2015; Jetz et al., 2016; Takashina and Economo, 2021). Moreover, existing field sampling efforts have been most sparse in the high-biodiversity tropics leading to a strong underrepresentation (Schimel et al., 2015).

Satellite remote sensing techniques are increasingly used to monitor and study large-scale temporal and spatial landscape changes across many parts of the world (Jensen, 2013). These observations are uniquely valuable because they can provide complete repeated spatial sampling even when the measurements reveal only part of the complex reality. With ongoing technological advances, satellite remote sensing observations are poised to move beyond the monitoring of land cover change and quantify plant functional diversity across regional landscapes (Butler, 2014; Schimel et al., 2015). Indeed, a growing number of studies is demonstrating the retrieval and analysis of individual canopy and leaf traits in discrete plots and locations through satellite remote sensing (e.g.: Aguirre-gutiérrez et al., 2021; Ali, Darvishzadeh, Skidmore, Gara, et al., 2020; Ali, Darvishzadeh, Skidmore, Heurich, et al., 2020; Brown, Ogutu, & Dash, 2019; Hauser, Féret, et al., 2021; Serbin et al., 2019; Verrelst et al., 2021). Yet, the step from using internally consistent trait estimates to derive functional diversity patterns from satellite remote sensing is undertaken less often and remains limited to spatially discrete observations as opposed to the potential to facilitate spatially continuous 'wall-to-wall' inference (e.g.: Hauser, Féret, et al., 2021; Hauser, Timmermans, et al., 2021; Ma et al., 2019; Rossi et al., 2020).

Satellite remote sensing of plant functional diversity, however, presents a paradox: the difficulties in acquiring temporally and spatially consistent ground data over large areas highlight the clear added value of satellite remote sensing to achieve such. At the same time, the scarcity and mismatch of present data provides significant challenges to train data models for retrieving plant diversity estimates and to validate the outcomes of satellite earth observation inferences (Jetz et al., 2016). Moreover, the coarse (multiple canopies aggregated), spectrally derived, timely, and pixel-wise observations from satellite remote sensing challenge a direct coupling of traditional, static, leaf-level trait measurements done in the field (Abelleira Martínez et al., 2016; Anderson, 2018). Instead, the evaluation of functional diversity patterns across well-studied ecological gradients can provide a means to qualitatively assess the responsiveness of satellite-based plant functional diversity estimates (Chaurasia et al., 2020; Durán et al., 2019).

In this study, we present spatially continuous ('wall-to-wall') inference of functional diversity estimates from satellite remote sensing retrieved over the biodiverse and heterogenous region of Sabah, Malaysian Borneo. The region's vastness, complexity, inaccessibility, and regulatory constraints (private ownership) are exemplary of the use of remote sensing to overcome the difficulties to conduct large-scale field campaigns. We apply the ESA's SNAP biophysical processor to retrieve spectral trait indicators - Leaf Area Index, Leaf Water Content, and Leaf Chlorophyll Content – from the spectral bands of Sentinel-2 imagery at 20m resolution.

Through multivariate diversity metrics (Villéger et al., 2008), an analysis of the functional diversity found in these combined traits is conducted and the large spatially continuous retrieval of functional diversity estimates is held against a land use gradient with a large number of observations (N=5626) comprising of large (40ha) remotely sensed single land use plots. Linking space-borne functional diversity to land use provides an initial step for the explorative assessment of the potential merits and challenges of large-scale spatially explicit inference of functional diversity metrics from spaceborne inference.

## 4.2. Methods

### 4.2.1. Study area

This study focuses on the Malaysian province of Sabah located in the northern tip of Borneo (115°12'27.317"E-117°59'5.608"E, 4°26'3.612"N - 7°13'51.89"N). The region represents a crucial global biodiversity hotspot (UNDP, 2012) with well-studied gradients of elevation (Aiba & Kitayama, 2010; Grytnes & Beaman, 2006; Kitayama, 1992) and validated maps of relevant land use types (Gaveau et al., 2016, 2014) (Fig. S. 19). Sabah consists of lowlands as well as mountainous forested territories with elevations ranging from sea level to over 4000m on Mt. Kinabalu's peak. Sabah records an average annual rainfall of 2890 mm and a mean annual temperature of 27.8 °C (Döbert et al., 2015). Over the past decades, widespread forest conversion for oil-palm and timber/pulp production has significantly altered and threatened biodiversity, including over 1000 taxa of endemic plants as well as the unique variety of fauna dependent on these habitats (Bryan et al., 2013; Maycock et al., 2012; UNDP, 2012). The study area is characterized by strong contrasts in human disturbance, from intact forests to intensively managed plantations, and elevational gradients that affect plant functional diversity and are expected to reflect in satellite remote sensing estimates of these patterns (Aiba & Kitayama, 2010; Barnes et al., 2014).

### 4.2.2. Retrieval of functional traits

Sentinel-2 L1c data were acquired through ESA's Copernicus Scientific Hub over the extent of our study area. The Multi-Spectral Imager (MSI) offers observations over 13 spectral bands; the majority of which are at a 20m spatial resolution (ESA, 2015). Optical remote sensing acquisition above Sabah, Malaysia, is challenged by its year-round high average cloud cover. For this study, we acquired the Sentinel-2 observations for the 9th of July 2017 covering the study area (Fig. S. 19a). The cloud cover on this date was one of the lowest since the launch of Sentinel-2 in 2014. Mosaicking multi-temporal images together would have introduced temporal deviances which could lead to diversity artefacts based on inference date rather than vegetation characteristics. After acquisition, the data were atmospherically corrected using the Sen2Cor processor (Gascon et al., 2014; Louis et al., 2016). Stringent quality flags stemming from both the atmospheric correction and the biophysical processor (see below) were applied to mask all areas affected by cloud contamination, poor atmospheric correction, poor trait retrievals (outside the physical range of variation), and shadows (Louis et al., 2016; Weiss and Baret, 2016). Additional cautionary buffers of 100m radius were applied around the quality flags to further limit the influence of clouds and cloud shadows on the spectral properties of the imagery. Non-vegetated areas with a fractional cover (FC) below 30% were masked out to remove non-/marginally vegetated areas.

Estimation of canopy traits from the Sentinel-2 imagery was conducted using the biophysical processor of the ESA's Sentinel Application Platform (SNAP) Sentinel-2 toolbox (Weiss and Baret, 2016). SNAP uses an artificial neural network (ANN) inversion pre-trained on a PROSAIL simulated database including canopy reflectance and the corresponding set of input parameters. SNAP includes an unreleased version of PROSPECT prior to PROSPECT-4 (Feret et al., 2008), coupled with the SAIL model (Fourty and Baret, 1997; Verhoef, 1984). The value, range, and distribution followed for each input parameter of the models are described in Weiss and Baret (2016) and aim to provide general global applicability without the ingestion of ecosystem-specific ancillary data, although that comes at the cost of precision (Weiss and Baret, 2016). PROSAIL is bound by strong simplification of canopies assuming a homogenous turbid medium where absorption is defined by leaf, canopy, soil, and angular properties (Jacquemoud et al., 2006). Therefore, the interpretation needs to be done in consideration of the underlying assumptions and application of a 1-D model (Jacquemoud et al., 2009). Despite its limitations, earlier validation studies have reported reasonable performance of SNAP retrievals in forested regions (Brown et al., 2019; Hauser et al., 2021) and are further addressed in the discussion section.

Traits in SNAP are derived at canopy-level and include Leaf Area Index (LAI), canopy chlorophyll (CAB*LAI), and canopy water (EWT*LAI). We reversed the multiplication by LAI to arrive at leaf level estimates: leaf chlorophyll (CAB) and leaf equivalent water thickness (EWT). LAI specifies the leaf surface area per unit ground surface area. The retrieval conducted here produces a measure of 'effective LAI' which does not account for clumping factors and therefore differs from a 'true LAI' measure (Asner et al., 2003; Hadi et al., 2017). LAI ($m^2/m^2$) determines how much light can be captured influencing primary production, but also transpiration and energy exchange (Asner et al., 2003; Castillo et al., 2017; Zheng and Moskal, 2009). Complementary to LAI, CAB and EWT influence processes occurring at the leaf level (Poorter and Bongers, 2006). CAB ($\mu g/cm^2$) corresponds to a surface-based leaf content of chlorophyll-a and -b. Chlorophyll has an important role in determining the photosynthetic capacity and resource strategy of plants (Cao, 2000; Croft et al., 2017). EWT (in $g/cm^2$) refers to the water mass stored in leaves per leaf surface area. EWT is important for the physiological plant performance and regulatory mechanisms playing a role in drought and stress tolerance (Asbjornsen et al., 2011; Damm et al., 2018; Lawlor and Cornic, 2002; Nieuwstadt and Sheil, 2005; Saura-Mas. S, 2007; Weiher et al., 1999). Taken together, the traits retrievable through SNAP are ecologically meaningful.

### 4.2.3. Estimating functional diversity

The spatially continuously retrieved traits from Sentinel-2 spectral reflectance were used to further estimate functional diversity. Functional diversity is commonly partitioned into three complementary aspects of functional diversity: richness, evenness, and divergence (Mason et al., 2005; Mouillot et al., 2005; Villéger et al., 2008). Functional richness is a measure of the functional space occupied by a community, and was calculated based on the convex hull volume (Cornwell et al., 2006). Functional divergence and evenness metrics describe how trait combinations are distributed within the community's trait space, indicative of niche differentiation and niche space optimization respectively (Aiba et al., 2013; Kraft, Valencia, & Ackerly, 2008; Mason et al., 2005; Mouchet, Villéger, Mason, & Mouillot, 2010). Functional divergence was calculated with Euclidian distances applied to a centroid-based approach (Villéger et al., 2008) adapted by Schneider et al. (2017) for a pixel-based approach. Functional evenness was determined through branch length variation of the Minimum Spanning Tree of Trait Distance Matrix signalling the regularity of the distribution across trait space (Villéger et al., 2008). The functional diversity metrics were calculated over the 95% centermost data points, determined by kernel density estimates, to limit the influence of extreme values, noise, and possible retrieval artifacts.

We opted for large plots, sized equally at 40ha. (1000-pixel observations) to calculate the functional diversity metrics. This allows showcasing the capability of satellite remote sensing to map large spatially continuous plots capturing a large share of the variability in canopy compositions to base functional diversity calculations on. With 1000-pixel observations, this design potentially harnesses robustness against noise in the observations. Despite the patchiness of the data due to the masks applied and the mosaic of land use patterns, the 40ha plots still offered a large number of data plots per land use type (N=5626). The plots are drawn by an algorithm based on minimal Euclidian distances to the starting pixel of the plot while solving the condition of meeting a single land-use continuous area of 40ha (Fornberg and Flyer, 2015).

#### 4.2.4. Land use data

Land use was derived from CIFOR's open-access and validated 'Atlas of deforestation and industrial plantations in Borneo' (https://www.cifor.org/map/atlas/)(Gaveau et al., 2016, 2014). Their validated maps are based on longitudinal, up to 30m spatial resolution, LandSat satellite imagery (1973-2016) with additional visual, expert-based interpretation methods and maps of oil-palm and pulpwood concessions. Here, we assessed the three largest vegetated land use types; (1) 'Intact Forest' which are old-growth forests. The overstory of these forest ecosystems is generally characterized by old closed-canopy emergent trees. Dipterocarpaceae are the dominant tree species in primary forest accounting for 25% of the tree population and 60% of the standing volume (Sist and Saridan, 1999). (2) 'Logged Forest' are intact forests that have been impacted by industrial-scale mechanized selective logging at some point since 1973. (3) 'Industrial Oil-Palm Plantations' which are production systems mainly revolving around monoculture planting of Elaeis guineensis jacq.. Small-holder oil-palm cannot be consistently distinguished in the land use maps. An overview of the spatial distribution of these three dominant land use types can be found in Fig. S. 19b. Oil-palm plantations were found to only occur in the lowlands (<500m ASL) (Table S. 20). Shuttle Radar Topography Mission (30m spatial resolution) was used to map elevation. Elevation may affect differences in functional diversity within and between land use types.

#### 4.2.5. Data analysis

To assess the plausibility of the trait values on which we based functional diversity estimates, the performance of the inversion of SNAP's biophysical processor retrieval from spectra to traits was examined. Firstly, we conducted a sensitivity analysis to assess the spectral layout of Sentinel-2 bands in terms of receptiveness to retrieve these traits. The analysis is based on repeated PROSAIL simulations with random variations of the trait values while mapping the spectral responses and the correlation between Sentinel-2's spectral bands and trait variation.

Secondly, we re-modeled spectra based on PROSAIL in forward-mode from estimated trait values. The simulated spectra were compared against the observed Sentinel-2 spectra to assess the performance across different land use types. This was done for 20,000 randomly drawn pixels over the study area. Search ranges for the remaining PROSAIL traits were constrained to the distribution of input variables described by Weiss & Baret (2016). We used Spectral Angle Mapper (SAM), Mean Absolute Error (MAE), and Root Mean Squared Error (RMSE) to assess the deviation between the simulated and actual spectra. We evaluated differences in errors across land use types to examine whether differential performance across land use types could have affected our results.

Thirdly, we compared retrieved trait distributions against in-situ measured traits of common species in the different studied land use types (Apichatmeta et al., 2017; Kattge et al., 2020; Martin et al., 2018). For LAI, the study by Hadi et al. (2017) provides measurements of effective LAI across sampling sites in Sabah consisting of unlogged forest, logged forest, and oil-palm plantations although the plantations sampled were relatively young (planted <10 years ago). CAB of forests and oil-palm plantations was available for top-of-canopy chlorophyll for adult oil-palms (Elaeis guineensis) by Apichatmeta et al. (2017), and of intact forests in Danum Valley (Martin et al., 2018). Relevant field measurements on EWT relevant to our study area were difficult to acquire. However, we were able to model EWT based on data on LMA available from the 'Traits of Bornean Trees Database' (Kurokawa & Nakashizuka, 2008) – part of the global TRY plant trait database (Kattge et al., 2011) - and from top-of-the-canopy LMA samples taken by Martin et al. (2018) in the Danum Valley. For the 'Traits of Bornean Trees Database', we focussed on Dipterocarpaceae specifically, considering their dominant role in primary forest in Sabah accounting for 25% of the tree population and 60% of the standing volume (Sist and Saridan, 1999). To model EWT, we assumed a leaf water content of 63%, following findings by Wu et al. (2017) for tropical evergreen forests. We simulated the range of EWT values based on these data through the following equation:

$$EWT = \left(\frac{LWC_{\%}}{1 - LWC_{\%}}\right) * \ (LMA\,)$$

Differences in functional diversity metrics between land use types were assessed by ANOVAs. The assumptions of the ANOVAs were evaluated and a log transformation of Functional Richness was conducted to ensure normality of residuals in an otherwise strongly skewed distribution. The explained variance was expressed through Eta$^2$ values which is a measure of effect size for use in ANOVA, analogous to R$^2$ in multiple linear regression. Significant differences between individual land use types were further analyzed using a post-hoc Tukey's HSD test.

## 4.3. Results

### 4.3.1. From mapping spatially explicit spectral trait indicators to functional diversity estimates

The trait maps present a high degree of patchiness due to the applied masks (incl. clouds, quality flags, vegetation cover, and land use) (Fig. 4.1a). The plausibility of the spectral trait indicators was assessed through three analyses to test the validity of the spectral trait indicators. Firstly, the sensitivity analysis of Sentinel-2's bands to the spectral trait indicators (LAI, CAB & EWT) retrieved in this study showed promising responsiveness (Fig. S. 21a). Secondly, the reversely estimated spectra modelled by PROSAIL – simulated from the SNAP-retrieved trait estimates as input - had an RMSE of 0.012 which is a 7.6 percent mean deviation from the actual observed spectra. No profound differences in errors were observed between the individual land use types which suggest there is no structural bias in the inversion performance for approximation of the vegetation present in different land uses (Table S. 21b).

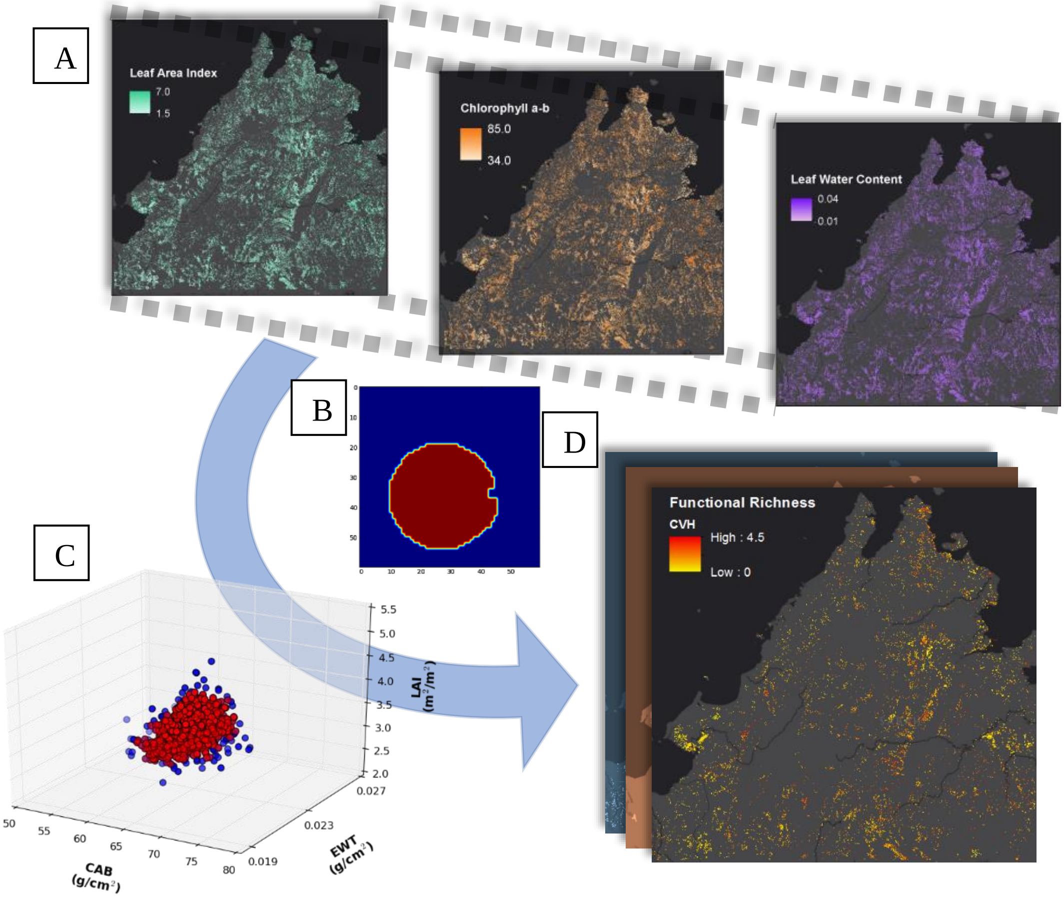
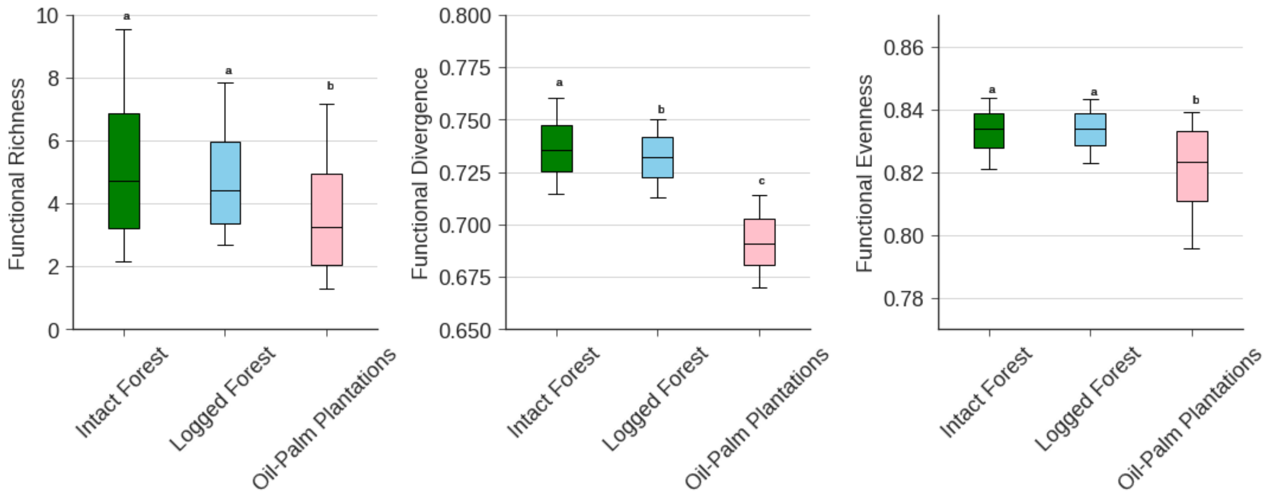


*Fig. 4.1: The data pipeline from satellite remotely sensed traits to functional diversity metrics maps; (A) maps of Leaf Area Index ($m^2/m^2$) (LAI), leaf Chlorophyll-a-b Content ($\mu g/cm^2$) (CAB), and leaf Equivalent Water Thickness ($g/cm^2$) (EWT). Masks are portrayed in dark grey. (B) Zoom-in on the pixel-wise selection of 40ha plots, 1000 pixels, based on a minimal Euclidian distance drawing new pixels relative to the starting pixel of the plot while remaining within land use and quality masks. (C) Functional diversity metrics calculated over 40ha plots, 1000 pixels, as illustrated in the 3D plot example with axes representative of different functional traits. (D) Maps of functional diversity over the study area of Sabah, Malaysia, exemplified here by functional richness as one of the three functional diversity metrics.*

Finally, the comparison of retrieved trait values to those presented in literature suggests that the trait estimate ranges retrieved are to a large degree in line with the range of trait values measured in Borneo previously (Fig. S. 21c). The most notable deviance is an overestimation in oil-palm plantations of LAI compared to Hadi et al. (2017)'s effective LAI measurements. Differences in LAI between young plantations versus older plantations might be responsible for this discrepancy. In our study, observed LAI values –were the highest in plantations rather than tropical evergreen broadleaf forests (Fig. S. 21c). This was also reported by Asner et al. (2003). Intensive management regimes -through planting schemes, fertilizer, and pest management- aim to maximize production in these plantations and both resonate with relatively high chlorophyll and LAI ranges. Industrial oil-palm plantations are often located on more favorable lands for high productivity in terms of elevation and slope. In terms of EWT and CAB, we find much larger variation in field-based estimates. These estimates separate individual species whereas our observations are based on a pixel-based aggregation of multiple species, possibly levelling out some of the variation. In consideration of this convergence, the range of spectral trait indicators is reasonable with the exception of an overestimation of EWT compared to Martin et al. (2018)'s in-situ measurements.

### 4.3.2. Land use patterns of plant functional diversity

The spatially continuous maps of functional diversity estimates are exemplified by functional richness in Fig. 4.1d. All functional diversity metrics appeared to differ significantly across land use types, with all p-values well below 0.001 (Fig. 4.2). The post-hoc analysis revealed that logged forest and intact forest are statistically similar in terms of functional richness and functional evenness. For all functional diversity metrics, intact and logged forests were significantly different from oil-palm plantations (Fig. 4.2).



**Functional Richness (CVH)**
F: 276.0
Eta$^2$: 0.09
p: 0.000

**Functional Divergence (MNND)**
F: 3729.1
Eta$^2$: 0.57
p: 0.000

**Functional Evenness (FE)**
F: 628.2
Eta$^2$: 0.18
p: 0.000

*Fig. 4.2: Differences in functional diversity metrics across land use types (below 500m ASL) in boxplots and ANOVA results. Boxplots' box represents 25, 50 and 75 percentiles and the whiskers depict the 10, 90 percentiles. Differences in retrieved trait estimates between land use types according to a post-hoc Tukey's HSD test are indicated with different letters.*

*Table 4.1: Descriptive statistics per functional diversity metric across land use types in Sabah.*

| | | Functional Richness | | Functional Divergence | | Functional Evenness | |
|---|---|---|---|---|---|---|---|
| | N | Mean | St. Dev. | Mean | St. Dev. | Mean | St. Dev. |
| 🟩 Intact Forest | 1192 | 5.474 | 3.354 | 0.737 | 0.020 | 0.833 | 0.010 |
| 🟦 Logged Forest | 3018 | 4.971 | 2.331 | 0.732 | 0.015 | 0.833 | 0.008 |
| 🟥 Oil-Palm Plantations | 1416 | 3.974 | 2.876 | 0.692 | 0.018 | 0.820 | 0.018 |

## 4.4. Discussion

Our case study in Sabah is illustrative of a biodiversity hotspot at risk of commodity-driven land use changes (Bryan et al., 2013; Gaveau et al., 2016; UNDP, 2012). The impact of land use on functional biodiversity has been widely studied in ecology, generally through small-scale local field studies (de Souza et al., 2013; Flynn et al., 2009). We have re-projected these ecological expectations to scale up considerably from traditional field assessments to the potential to study large-scale landscapes, whole regions, and terrestrial ecosystems instantaneously and with spatial continuity. Despite still being an early adoption, the results indicate initial correspondence of satellite remote sensing derived functional diversity metrics to broad human disturbance gradients shaped by land use. These insights may be further developed when in-situ validation data and relevant ancillary ecosystem-specific information would become available. In this discussion, we address the current workflow and results in light of the limitations of the methodology applied and the value of qualitative assessments against historic trait measurements and land use gradients.

### 4.4.1. Functional diversity retrieval

This paper applies a workflow (Fig. 4.1) to map functional diversity using Sentinel-2 over a large continuous region without a heavy reliance on a priori in-situ canopy trait measurements. The latter is relevant as matched field samples are hard to obtain across large geographic extents and pixel-based scales. The validity of such large-scale functional diversity estimates depends on the accuracy and representation of traits. Trait selection is constrained by the specifications of the sensor and the parameters of the radiative transfer models applied. Here, the selected traits relate to relevant carbon and water fluxes and offer three axes of functional differentiation (Asner et al., 2003; Croft et al., 2017; Damm et al., 2018; de Bello et al., 2010). The current selection of traits was pragmatic, a larger number of traits might increase the ability to detect functional differences between observations (Cadotte et al., 2011). In practice, however, model inversion becomes increasingly challenged by ill-posedness with a larger number of traits to be retrieved with the same amount of input data, especially in multi-spectral broadband inference.

For the current trait selection (LAI, CAB & EWT), the sensitivity analysis of Sentinel-2's bands showed promising responsiveness (Fig. S. 21a). This analysis serves as a precursor of the performance of PROSAIL within SNAP when applied to Sentinel-2. Due to its ease of use, genericity, and most importantly the functionality without hard to obtain ancillary data, the SNAP biophysical processor is currently a likely first port of call for many users (Brown et al., 2019), although it clearly also has limitations.

The artificial neural network in SNAP has been meant to provide generic global applicability without the ingestion of ecosystem-specific ancillary data (Weiss and Baret, 2016). However, it has been shown that local optimization of the trait ranges under study for inversion can improve retrieval performance (Combal et al., 2002; Dorigo et al., 2009; Hauser et al., 2021; Verrelst et al., 2019a). SNAP's biophysical processor does not facilitate a re-training of the ANN on PROSAIL simulations specific to the ecosystems studied here. Such functionality could theoretically improve the accuracy of spectral trait indicators. Additionally, the implementation of active learning heuristics can prove helpful to add constraints to inversion space and facilitate intelligent sampling for the training of retrieval algorithms to overcome some of the ill-posedness and optimize a simulation subset to the ecosystem under study (Berger et al., 2021; Verrelst et al., 2021).

Similarly, it may be argued that there are radiative transfer models that are better suited for heterogeneous forest canopies as compared to PROSAIL which is bound by 1-D simplification of canopies (Berger et al., 2018a). Alternative radiative transfer models, e.g. INFORM (Schlerf and Atzberger, 2006) and FRT (Kuusk and Nilson, 2000), are, however, complex and require a larger number of biophysical parameters. Without a priori information, the heavy parameterization in inversion may further induce ill-posedness and therefore, in fact, hamper retrieval performance and feasibility, especially in multi-spectral settings (Brown et al., 2019; Huang et al., 2011).

Despite its limitations, the suitability of SNAP for agricultural applications was confirmed in several studies (Danner et al., 2021; Pasqualotto et al., 2019; Vanino et al., 2018; Vinué et al., 2018; Xie et al., 2019). For forests, Brown et al. (2019), Hauser et al. (2021) and Nguyen et al. (2022) report reasonable performance of the SNAP retrieval algorithm in a deciduous broadleaf forest site in Southern England, a heterogenous shrub-forest landscape in Portugal and mangrove forests, respectively. Moreover, the performance of SNAP in a heterogeneous mixed mountain forest in Bavaria, Germany was similar to that of the input parameter heavy INFORM inversion (Ali et al. 2020). While none of these studies applied SNAP in rainforest ecosystems relevant to our study area, these quantitative findings suggests that our pipeline is reasonable for large-scale applications.

Consistent with that assessment is our finding that there was no indication of structural biases in inversion between the land use types (Table S. 21b) or deviation from regionally relevant trait ranges presented in literature and the TRY database (Fig. S. 21c). Nonetheless, the comparison against historic trait measurements should be considered carefully. Firstly, there are temporal mismatches between the data of Sentinel-2 acquisition and the in-situ trait measurements used for comparison. This likely results in inconsistencies in the comparisons made, especially given the cyclical nature and phenology of ecosystem processes (Noormets, 2013; Schimel et al., 2015). Secondly, the used in-situ data was sampled at the level of individual canopies/branches/leaves, whereas the Sentinel-2 inference results in an aggregation of multiple canopies in pixels scaled in a 20m resolution raster (Abelleira Martínez et al., 2016). Thirdly, the aggregation of canopies in Sentinel-2 pixels results in a dominant signal of the overstory vegetation and in particular the top-of-the-canopy. Accurate correspondence of field measurements to top-of-the-canopy sunlit overstory samples is not necessarily warranted in trait databases (Gara et al., 2019). Lastly, in contrast to species-mean trait estimates, the large-scale continuous inference through remote sensing will likely include the local representation of intra-specific variation (Schimel et al., 2015).

### 4.4.2. Land use gradient as qualitative assessment

The scale and extent of satellite remote sensing in comparison to common field observations seriously challenges quantitative validation efforts for plant diversity assessments. In light of the scarcity of relevant ground measurements, this study aimed to exploit the spatial continuity and synoptic inference of satellite remote sensing observations by testing qualitatively against well-studied and large-scale ecological gradients. Airborne studies, e.g. Asner et al. (2017); Chaurasia et al. (2020); Durán et al. (2019), examined remotely sensed trait diversity against hypothesized linkages between functional diversity and ecosystem productivity, spatial scales, elevation, and climatic gradients. Here, we have scaled up to Sentinel-2 to compare functional diversity against a different land use types, given that land use is known to strongly impact functional diversity (de Souza et al., 2013; Duraiappah et al., 2005). The ability of satellite-derived functional diversity metrics to detect such differences at regional spatial extents offers an initial evaluation of its potential to study broad ecological phenomena from space.

The results indicate significant differences between land use classes across functional diversity metrics. Although different spatial scales and even taxa challenge quantitative comparison, our findings correspond qualitatively with conclusions from field studies using ground measurements; intact forests and logged forests harbor significantly more functional diversity than oil-palm plantations (Barnes et al., 2014; Edwards et al., 2014; Lin et al., 2011; Maeshiro et al., 2013). The significance of differences in functional diversity did vary strongly across the metrics applied. Land use explains approximately 9% of the variance in functional richness (Fig. 4.2). Functional divergence and evenness patterns differed more strongly across the land use gradient - explaining 57% and 17% of the observed variance, respectively.

The low explained variance for functional richness corresponds with its high variation within the different land use types (Fig. 4.2). Part of this variation could be related to a variation in landscape properties over the large geographic extent. Variation in terms of soil, elevation, slope, landscape heterogeneity (geodiversity), and microclimates may all affect functional richness (Wang, Rahbek, & Fang, 2012; Zarnetske et al., 2019). Additional analysis (Fig. S. 22) indeed confirms a strong decrease in functional richness with increasing elevation for the different land use types. By reducing the spatial extent of analysis to a smaller subset within the study area, the explanatory power of land use types increased substantially. The findings from the subset reveal a significant increase in the explained variance of land use for functional richness (~15%) while still signalling large variance within land use classes. Importantly, the convex hull volume - on which the calculation of functional richness is based - is relatively sensitive to anomalous observations (Blonder et al., 2014). Our analysis is somewhat conservative by looking only at the 95% centermost observations through kernel density estimates. Nevertheless, the large landscape heterogeneity combined with noise and inconsistencies in the surface reflectance and spectral trait indicator retrieval can introduce variations that strongly affect overall functional richness.

Despite large within-group variation in functional richness, the distinction between forested and oil-palm plantation land use types remained significant and prevailing across a large spatial extent and number of plots. The highest mean functional richness was found in intact forests, closely followed by logged forests. Previous studies pointed out that functional richness can peak in sites that are exposed to moderate disturbance, creating heterogeneity in ontogenetic stages and landscape characteristics which could play a role in the comparable functional richness between intact and logged forests (Biswas and Mallik, 2010; Bongers et al., 2009; Cadotte et al., 2011).

Functional divergence showed more profound differences across land use types. Intact forest recorded the highest levels of functional divergence in our analysis, followed by logged forests and oil-palm plantations. The interpretation of functional divergence is tied to niche differentiation within ecological communities (Aiba et al., 2013; Kraft, Valencia, & Ackerly, 2008; Mouchet et al., 2010; Mason, Mouillot, Lee, & Bastow Wilson, 2005). Niche differentiation contributes to the maintenance of functional diversity in natural tropical systems

(Kraft et al., 2008). More intensively managed land use regimes, characterized by monoculture, planting schemes, and pest management, diminish natural processes that allow for niche differentiation (Huston and Huston, 1994; Shipley, 2010; Suárez-Castro et al., 2022). This resonates with the main differences found in our results with oil-palm plantations scoring significantly lower on functional divergence (Fig. 4.2).

Functional evenness relates to how evenly trait space is filled (Mouchet et al., 2010; Mouillot et al., 2005; Villéger et al., 2008). Even distribution can be tied to a degree of optimization of trait space in response to resource availability, as well as to less functional redundancy. In man-made landscapes, such drivers are suppressed by monoculture planting, pest management, and homogenous ontogenetic stages/tree sizes. Oil-palm plantations exhibit significantly lower divergence and evenness within the trait space observed (Fig. 4.2). Both functional divergence and evenness are relatively unchanged across elevation (Fig. S. 22). This coincides with findings by Durán et al. (2019) in tropical forests across an Amazon-to-Andes elevation gradient.

### 4.4.3. Outlook

Beyond shortcomings, the study provides a new platform and geographic extent (spatial scale) that indicate that oil-palm plantations exhibit significantly lower functional diversity than intact or logged forests which can contribute to the debate on oil-palm's impact on tropical biodiversity and further build a case against controversial proposals to reclassify oil-palm as a forest cover type (Hinkes, 2020; Jong, 2022; Koh and Wilcove, 2008). Our exploration builds a case for further investment in quantitative validation through dedicated field campaigns. From this point, investing in and overcoming the challenges of representative in-situ validation of pixel-based functional diversity is the next stride to further assess its accuracy and more subtle differences, as well as the robustness of these metrics against uncertainties in trait estimates. Moreover, in terms of retrieval, further maturation of the current approach towards full spatio-temporal continuity will be needed. This will include multi-temporal as well as data assimilation of multi-sensor, multi-scale remote sensing observations, and ancillary ecological datasets to i) study change in functional diversity over time (important to study the impact of human disturbances; Jetz et al., 2016; Pakeman, 2011), ii) include a wider range of consistent traits and deal with the ill-posedness of such retrieval, iii) allow for cross-validation with spatial, temporal and spectral consistency across instruments, iv) study the effects of scale and grain, and v) overcome data gaps caused by clouds (highly relevant for humid tropical rainforests such as those found in Sabah) and other interferences (Belda et al., 2020; Hauser et al., 2020; Lahoz and Schneider, 2014; Lewis et al., 2012).

## 4.5. Conclusion

By linking the functional diversity estimates derived from remote sensing to land use information, this study showed the potential merits to study broad ecological patterns over large geographical extents using satellite earth observation. The study provides a new platform and geographic extent (spatial scale) that strongly indicate that oil-palm plantations exhibit significantly lower functional diversity as compared to intact and logged forests coinciding with results from earlier field studies. Specifically, we find that the observed differences in functional diversity across the land use gradient were significant. Notably, profound differences between metrics were observed: large variance within land use types was observed for functional richness while functional divergence exhibits particularly strong responsiveness to land use. With that in mind, this study acts as an exemplar for satellite-derived monitoring of functional diversity for a key biodiversity area for which traditionally little information is available. The study provides an early application towards the maturation of a spatially and temporally explicit method that hopefully fuels further validation efforts and assessment of its responsiveness across ecological gradients.

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

**Based on**:

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**Abstract:**

The dependency of biodiversity patterns on the spatial scale, at which we observe them, is widely acknowledged. This scale dependency is particularly important for satellite remote sensing applications of biodiversity patterns. With potential measurements at continuous and multiple scales, satellite remote sensing has a high potential to contribute to filling data gaps in large-scale plant functional diversity monitoring. However, apparent disparities of scale exist between the spatially continuous, and pixel-based modes of remote sensing observation versus the individual-plot and abstract conceptualisation of community diversity concepts of scale in ecology.

In this study, we looked at the scale dependency of functional diversity estimates derived from satellite remote sensing. Hereto, we apply the concept of functional diversity-area relationships (FARs) based on indicators of plant functional diversity over the vast, biodiverse, and heterogeneous region of Sabah, Malaysian Borneo. The satellite-derived FARs derived from Sentinel-2 observations allow us to empirically study these relationships at new unprecedented continuous spatial extents and examine how ecological concepts of community diversity reoccur in spatially explicit pixel-based observations.

The functional diversity-area relationships observed resonated with ecological theory and previous empirical field and airborne studies conducted at much smaller scales. The results also demonstrate a metric-dependent scale dependency of functional diversity estimates. Strong consistent trait convergence, compared to expectations from random spatial processes, was observed for functional richness with significant differences across a land use gradient. Landscape morphology, as an indicator of environmental heterogeneity, becomes increasingly important as plot area increases, suggesting a continuously increasing importance of beta diversity.

The spatial continuity of the Sentinel-2 imagery allowed for easy-to-conduct multi-scale analysis and stratification of functional diversity estimates across land use. Such analyses can contribute to unveiling the role and continuous transition of different drivers at different spatial scales and across large spatial extents while omitting the need for arbitrary decisions of a fixed

optimal plot area. This prompts a reconsideration of whether the traditional ecological focus of discrete ‘within’ versus ‘between’ community diversity (i.e. alpha vs beta diversity) should be maintained or whether we need new more continuous concepts.

## 5.1. Introduction

The rampant decline of global biodiversity over the last decades has become a major threat to the ecosystems on which humans depend (IPBES, 2019). To further our 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). 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 (Wang and Gamon 2019). Orbiting satellite remote sensing provides a unique perspective on Earth’s biodiversity with frequent and spatially continuous observations over large areas. However, with the increased usage, a full understanding of how exactly the configuration of these monitoring tools affects the observation of biodiversity patterns is crucial. This paper focuses on how spatial scaling, in particular the plot area over which we calculate diversity metrics, shape community patterns observed in functional diversity estimates derived from satellite remote sensing.

Our perception of biodiversity patterns is affected by the conceptual scale as well as the spatial scale of observation. Conceptually, biodiversity complexity can be considered through different dimensions following the central organizing principles of modern biology (Anderson, 2018; Gaston, 2010), from genetic to species, communities and ecosystems. Historically, studying large-scale spatio-temporal biodiversity patterns has been strongly rooted in (taxonomic) species concepts and led to global models of species’ ranges and species diversity patterns to develop and test ecological theories (Kreft and Jetz, 2007). Increasingly, a call to go beyond taxonomic identities and incorporate intra- and interspecific traits in an attempt to quantify community’s functional diversity (Mason et al., 2005; Violle et al., 2014). This is founded in the increased acknowledgment that the functional components of biodiversity, i.e., the diversity of forms and functions, are a principal link between biodiversity and ecosystem functioning (Funk et al., 2016; Violle et al., 2014)- affecting the productivity, adaptability, vulnerability to disturbances of ecosystems (Cadotte et al., 2011; Cardinale et al., 2011; Duncan et al., 2015; Grime, 1998; Hooper, 2002; Isbell et al., 2011; Mori et al., 2013; Ruiz-jaen and Potvin, 2010). These insights predicate the need for a better representation of functional diversity over large biogeographical scales to further validate ecological theories (Musavi et al., 2015; Reichstein et al., 2014) – a void that satellite remote sensing could potentially fill (Jetz et al., 2016).

Optical remote sensing and the evolution of plants come together through the importance of solar radiation for both. The way plants interact with sunlight provides a window into plant strategies for resource allocation manifested through biophysical, biochemical, and structural plant properties which, in turn, result in distinct spectral responses measurable through remote sensing (Ollinger, 2011; Schweiger et al., 2018). Recently, the functional diversity of plant traits has been successfully mapped from spectral reflectance through hyperspectral airborne instruments (Durán et al., 2019; Schneider et al., 2017; Zheng et al., 2021), and multi-spectral satellite remote sensing (Hauser et al., 2021; Ma et al., 2019). The latter is particularly interesting as it holds potential for studying large-scale plant trait patterns at regional and continental extents (e.g. Aguirre-gutiérrez et al., 2021; Campos-Taberner et al., 2018; Serbin et al., 2019). An undertaking that would virtually be impossible through laborious ground measurements (Májeková et al., 2016).

The influence of scale on spatial patterns is a central theme both in biodiversity research as well as in remote sensing (Anderson, 2018; Field et al., 2009; Marceau and Hay, 1999). Spatial scales (i.e. the scale dependency of observations) affect the way we observe spatial patterns of plant diversity. Yet, clear discrepancies exist between how spatial diversity is calculated in ecology and remote sensing, namely at individual/community level (using spatially irregular and discrete observations) versus between pixels (using spatially continuous rasterized observations). To advance remote sensing for ecological applications and mapping spatial plant diversity patterns in particular, a translation between these concepts is necessary. This requires us to overcome, or at least understand the effects of, spatial scaling discrepancies found between ecology and remote sensing.

In ecology, the concept of scale generally refers to the sampling scale shaped by the units of observation, including the geographic extent of field sampling design, and the plot area (grain size) of the ecological community for which to determine diversity (Field et al., 2009; Smith et al., 2013). In this perspective, ecological communities are abstractly defined as *"a group of organisms representing multiple species living in a specified place and time"* (Vellend, 2010) and serve as the window through which we measure diversity separated in 'within' (alpha) and 'between' (beta) diversity of community plots (Jurasinski et al., 2009; Whittaker, 1972). Application of these concepts in field studies generally results in discrete plots scattered across the study area, where alpha diversity is characterised characterized by differences between individuals within a plot, while beta diversity is calculated as the differences between plots (Chase et al., 2019).

The pixel-based spatially continuous mode of observation of satellite remote sensing differs strongly from these (relatively fluid) ecological concepts (Jurasinski et al., 2009; Whittaker, 1972). In general, most satellite remote sensing sensors offer spatial resolutions that are too coarse for the delineation of individual plant canopies (Anderson, 2018). This mismatch becomes further amplified when aiming to grasp the ecological community concept in a set of pixels. In contrast, some studies have simply assumed that every single pixel (e.g. 10-20m of Sentinel-2) equals an ecological community (Hoffmann et al., 2019; Khare et al., 2021, 2019; Rossi et al., 2020). While such assumptions might be defendable for specific grasslands, they are likely inadequate for larger tree and shrub canopies.

In theory, diversity of ecological 'communities' may be grasped through remote sensing by applying diversity metrics to clusters of pixels ranging from two single pixels to an entire scene of pixels. Different terms have been used for describing such pixel-based 'communities', e.g. spectral plot extents (Végh and Tsuyuzaki, 2021), (moving/sliding) window size (Barton et al., 2013; Schneider et al., 2017), and area (Durán et al., 2019; Zheng et al., 2021). However, community diversity metrics calculated over such pixel clusters raise questions whether we looking at alpha or beta-diversity, or a mix of both (Laliberté et al., 2019). Not all individual differences will be captured given the coarseness of individual satellite-based pixels while the community concept is arbitrarily captured through a cluster of pixels (Hauser et al., 2021; Rocchini et al., 2015). Given these challenges, a meaningful evaluation of the pixel-based integration of ecological spatial scaling concepts and the scale dependency of observed spatial patterns will be essential to conduct, interpret and advance with large-scale plant diversity assessments using satellite remote sensing (Wang et al., 2018).

The scale-dependency of biodiversity metrics is perhaps most demonstrated and widely studied through the concept of the species-area relationship (SAR), fundamental to spatial ecology and biogeography (Lomolino, 2000; Preston, 1960). The principle of SARs suggests that species richness ($S$) is proportional to the area ($A$) raised to some exponent ($z$) (Plotkin et al., 2000), often described as the power law relationship $S \propto A^z$(Rosindell and Cornell, 2007). Similarly, yet less widely studied, the functional diversity-area relationship (FAR) is the trait-based counterpart of SAR (Karadimou et al., 2016; Smith et al., 2013). Importantly, FAR/SARs can be linked to the community diversity concepts (Whittaker, 1973) in which 'area' is representative for (landscape) gamma diversity: the species/trait space pool of a certain (increasingly large) area. Gamma diversity, in turn, is affected by alpha and beta diversity drivers that together determine the increases in diversity as a function of area (Chase et al., 2019).

A few airborne remote sensing studies have been conducted to research the effect of different spatial scales on functional or spectral diversity (Dahlin, 2016; Durán et al., 2019; Schneider et al., 2017). Given the spatial resolution of the airborne observations used in these studies, the impact of mixing alpha and beta diversity within plots might be less relevant as compared to satellite remote sensing. Furthermore, given the limited spatial extent of airborne observations, these studies have remained limited in geographical extent. To our knowledge, so far, no studies have attempted to study the scale dependency of functional diversity in general or the FAR concept in particular using satellite remote sensing.

Here, we apply the concept of FAR to diversity metrics (Villéger et al., 2008) calculated from spectral trait indicators derived from the Sentinel-2 over the vast, biodiverse, and heterogeneous region of Sabah, Malaysian Borneo. Based on this, we construct FARs to study the scale dependency of satellite remote sensing observations of functional diversity estimates. We use a comparison against null-models, a land use gradient, and environmental drivers to assess the scale-dependent influence of assembly processes on satellite remotely sensed FARs. A land use gradient, from oil-palm plantations to intact forests, is used to indicate how different species pool (from monoculture to species-rich) environments affect the curvature of FAR, while landscape morphology as a driver of habitat heterogeneity can be indicative of the beta composition of functional diversity patterns (Grytnes and Beaman, 2006; Tello et al., 2015). The findings of this analysis open discussion on the role of satellite remote sensing for studying traditional ecological concepts of scale including FARs, and (drivers of) alpha and beta-diversity.

## 5.2. Methods

### 5.2.1. Study area

We opted for a study area in the Malaysian province of Sabah as it represents a crucial global biodiversity hotspot (UNDP, 2012) with well-studied gradients of elevation (Aiba and Kitayama, 2010; Grytnes and Beaman, 2006; Kitayama, 1992) and validated maps of relevant land use types (Gaveau et al., 2016, 2014). The study area is located in the northern tip of Borneo (115°12'27.317"E-117°59'5.608"E, 4°26'3.612"N - 7°13'51.89"N) and covers a rectangular tile of 14400 $km^2$ square (120*120km, 6000 by 6000 pixels) surrounding the Danum Conservation Area (Marsh et al., 1992). Over the past decades, widespread forest conversion for oil-palm and timber/pulp production has significantly altered the landscape threatening more than 1000 taxa of endemic plants present in Sabah including iconic Dipterocarpaceae species and a unique variety of fauna dependent on these habitats (Bryan et al., 2013; Maycock et al., 2012; Wilcove et al., 2013). We implemented a land use classification representative of the historic forest conversion developments and related plant diversity implications. The gradient consists of three different land use types; intact forests within and surrounding the protected Danum Valley Conservation area and nearby logged forests and oil-palm plantations (Fig. 5.1c). These three dominant land use types (Fig. 5.1b) are defined as (Gaveau et al., 2016, 2014); (1) 'Intact Forest' which are old-growth forests. These forest ecosystems usually include old closed-canopy emergent trees. (2) 'Logged Forest' are intact forests that have been impacted by mechanized selective logging at some point since 1973, and (3) 'Industrial Oil-Palm Plantations' which are production systems mainly revolving around monoculture planting of Elaeis guineensis jacq..

### 5.2.2. Datasets

Optical remote sensing acquisition above Sabah, Malaysia, is challenged by its year-round high average cloud cover. For this study, we focused on the Sentinel-2 observations for the 9th of July 2017 (illustrated by a RGB composite in Fig. 5.1a) covering the study area, as the cloud cover was the lowest since the launch of Sentinel-2 in 2014.

After the acquisition, the data were atmospherically corrected using the Sen2Cor processor (Gascon et al., 2014; Louis et al., 2016) within ESA's Sentinel Application Platform (SNAP) toolbox. Stringent quality flags stemming from both the atmospheric correction and the biophysical processor (see below) were applied to mask all areas affected by cloud contamination, poor atmospheric correction, poor trait retrievals (outside the physical range of variation), and shadows (Louis et al., 2016; Weiss and Baret, 2016). Additional cautionary buffers of 100m radius were applied around the quality flags to further limit the influence of clouds and cloud shadows on the spectral properties of the imagery. Non-vegetated areas with a fractional cover (FC) below 30% were masked out to remove non-/marginally vegetated areas.

Finally, functional trait estimates were obtained using the biophysical processor through spectral trait indicators (Weiss and Baret, 2016) within SNAP. The biophysical processor is based on a hybrid approach combining physical modeling and machine learning (Weiss and Baret 2016). Specifically, SNAP uses an artificial neural network (ANN) inversion pre-trained on a spectral database including canopy reflectance (simulated using an unreleased version of

PROSPECT prior to PROSPECT-4 (Feret et al., 2008), coupled with the SAIL model (Verhoef, 2002, 1984)). The value, range, and distribution for each input parameter aim to provide general global applicability without the ingestion of ecosystem-specific ancillary data (Weiss and Baret, 2016).

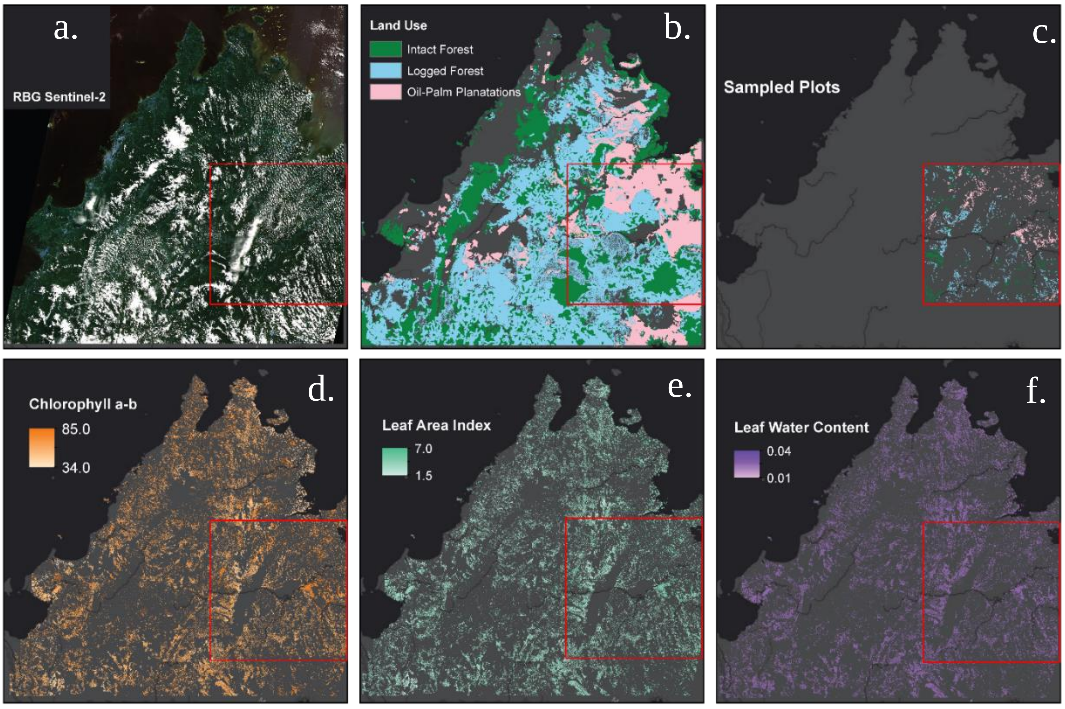


*Fig. 5.1: a) Map of the Sentinel-2 observation, as seen through a true visible range composite image, over the study area in Sabah, Malaysia on the 9th of July 2017 after atmospheric corrections. b) Map of the three land use classes within the Sabah study area used for analysis. c) Map of study area consisting of sampled plots that have been used to scale the functional diversity metrics from 0.4 to 60 ha uninterruptedly. d-f) Canopy trait estimate maps derived of Sabah through imaging spectroscopy that represent Leaf Chlorophyll Content (µg/cm$^2$) (d), Leaf Area Index (m$^2$/m$^2$) (e), and Leaf Water Content (g/cm$^2$) (f), respectively.*

From the complete set of spectral trait indicators that SNAP can retrieve, we focused on Leaf Area Index (LAI), Leaf Chlorophyll-ab (CAB) and Leaf Water Content (LWC), as shown in Fig. 5.1d,e,f. These retrievable traits are both spectrally and ecologically relevant: LAI (m$^2$/m$^2$) relates directly to primary productivity and to competitive and complementary light use, transpiration and energy exchange (Asner et al., 2003; Castillo et al., 2017; Zheng & Moskal, 2009). Through PROSAIL, effective LAI captures the canopy structure simplified in a 1-D simplified representation (Jacquemoud et al., 2009). Complementary to LAI describing resource use at the canopy level, CAB and LWC relate to processes occurring at the leaf level (Poorter and Bongers, 2006). CAB (µg/cm$^2$) directly plays a functionally important role in the photosynthetic capacity and resource strategy of plants (Cao, 2000; Croft et al., 2017). LWC (g/cm$^2$) is important for physiological plant performance and regulatory mechanisms such as photosynthetic carbon assimilation, electron transport rate, and isohydric behavior (Damm et al., 2018; Lawlor and Cornic, 2002). Furthermore, it plays a role in plant responses to drought and stress tolerance (Nieuwstadt and Sheil 2005; Saura-Mas 2007; Weiher et al. 1999), and plant-water relations and water uptake (Asbjornsen et al., 2011; Damm et al., 2018).

We assessed the plausibility of the retrieved estimates of spectral trait indicators using; 1) a sensitivity analysis, 2) reverse inversion to assess possible biases between canopy types, and 3) detailed comparison to field measurements conducted in previous studies in Sabah, Borneo, of plant traits of regionally common tree species and the dominant oil-palm species. Further details on the retrieval of traits using SNAP and qualitative assessment of retrievals are found in Suppl. Mat. Fig. S. 21.

Land use data were derived from CIFOR's open-access 'Atlas of deforestation and industrial plantations in Borneo' (https://www.cifor.org/map/atlas/). The data is based on longitudinal LandSat satellite imagery (1973-2016) with additional visual, expert-based interpretation methods and maps of oil-palm and pulpwood concessions. The maps have been validated (Gaveau et al., 2016, 2014). Fig. 5.1b presents a map of the land use types of interest in the study area.

In addition to land use, elevation and slope are considered as environmental drivers in shaping functional diversity patterns (Sanders and Rahbek, 2012; Stein et al., 2014; Zarnetske et al., 2017). The Shuttle Radar Topography Mission (30m spatial resolution) was used to map elevation and slope across the study area.

### 5.2.3. Functional diversity

The spectral trait indicator maps retrieved over the study area were used to calculate functional diversity. Specifically, we focus on two multi-trait functional diversity indices; 1) functional richness (FRich) and 2) functional divergence (FDiv). FRich (calculated using Quickhull Algorith, http://www.qhull.org, within the Scipy.spatial package in Python) represents the amount of niche space occupied by the community and is calculated as the convex hull volume (CHV) of the three pixel-based spectral trait indicators (Cornwell et al., 2006). FDiv (calculated using EQ1 and EQ2 equations by Villéger et al. (2008) as implemented by Schneider et al. (2017)), quantifies how combinations of spectral trait indicators diverge in their distances from the centre of gravity in multi-dimensional trait space based on Euclidian distances (Villéger et al., 2008):

$$\Delta|d| = \sum_{i=1}^{S} \frac{1}{S} \cdot \left| dG_i - \overline{dG} \right| \qquad \text{EQ1}$$

$$\text{FDiv} = \frac{\overline{dG}}{\Delta|d| + \overline{dG}} \qquad \text{EQ2}$$

where S is the number of pixels mapped in the multidimensional space, $dG_i$ is the Euclidean distance between the $i^{th}$ pixel and the center of gravity, and $\overline{dG}$ is the average distance of all pixels to the center of gravity. Functional divergence is scaled from 0 to 1, with 1 indicating all pixels lying on a sphere with equal distance to the centre of gravity and large trait differences within a community.

The functional diversity metrics were calculated for pixel-based 'communities'. Within these, higher FRich values represent a larger volume in trait space caused by richer diversities of trait combinations, while higher FDiv values represent broader distributions of trait space niches relative to trait space. The multi-variate diversity calculations considered only the 90% centermost data points, as determined by kernel density estimates, to limit the influence of extreme values, noise, and possible retrieval artifacts. We based this on estimated signal-noise ratios (5-10%) found in atmospherically corrected Sentinel-2 spectral reflectance (Brede et al., 2020).

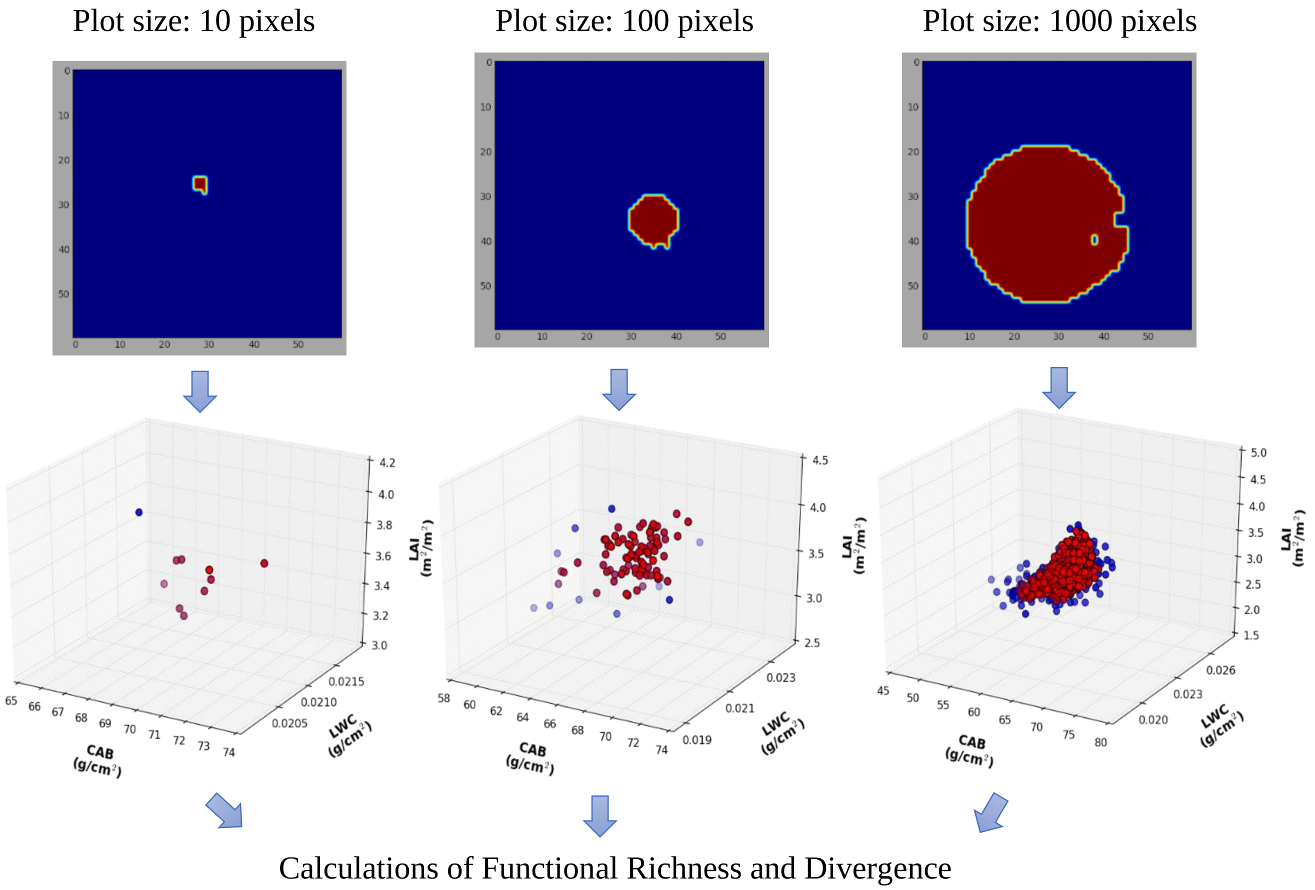


*Fig. 5.2: Three different plot sizes are exemplified for functional diversity calculations. All plots (N = 1713) are grown based on a nest radial nearest neighbour search and plot locations are chosen in which plot sizes van be varied from 0.4ha to 60ha continuously without masks transecting the plots.*

### 5.2.4. Scaling of plots

To assess the changes across different scaling of the functional diversity metrics, we calculated the functional diversity metrics over pixel ‘communities’ with increasing window sizes, i.e. plots with an increasing area and inherently an increasing number of pixels. The range of spatial scaling in this study consisted of plot areas with extents analysed from 0.4 ha to 60 ha which translates to ‘communities’ comprised of 10 to 1500 Sentinel-2 pixels at 20m spatial resolution. Plot sizes of 60 hectares were considered the largest possible window size considering data patchiness (due to cloud cover, quality masks, vegetation masks, and the mosaic of land use types) while still obtaining a large number of observations across all land use types (N>300). Hereafter, we will refer to plot area to indicate the changing spatial scale over which we calculated functional diversity metrics (i.e. FARs).

Across the entire study area, we found 1713 plots consisting of a single uninterrupted land use type (Intact Forest or Logged Forest and Oil-Palm plantations), with an area of at least 60ha. For each of the 1713 60ha-plots, functional diversity was calculated repeatedly while increasing the area (i.e., number of pixels) of the same plot up to 60ha within a single uninterrupted land use type. The set-up ensures consistency in functional diversity metrics across all scales as the exact same 60ha plots are analysed from smallest to largest extents. This implies that the same areas are sampled consistently and the sample size (N) remains constant across scales and land use types.

Increments were made by steps of 10 pixels in the repeated calculations. The approach adopted for increasing plot areas followed a nested radial nearest neighbour search where pixels were selected adjacent to the previously selected pixels (Fornberg and Flyer, 2015). Search decisions were based on the minimal spatial distance to the starting point of the pixel-based ‘community’. All starting points and pixels selected lay within the maximum plot extent (60 ha) and were of the same single land use type. To assure representativeness for the entire plot, we conducted repeated random drawings (ten times) of different starting points and radial nearest neighbour search approach to ensure a representative sample of the entire 60ha single land use plots at smaller spatial extents. Fig. 5.2 illustrates the nested radial nearest neighbour search for three exemplar scales; 0.4 ha (10 pixels), 4 ha (100 pixels) and 40 ha (1000 pixels).

### 5.2.5. Data analysis

The satellite remote sensing estimates of the functional diversity-area relationship were evaluated against null-models and stratified across land use types. Our analysis involved three main parts.

Firstly, we developed null-models to compare our observed FARs against expectations from random spatial trait distributions. Null-models allow testing of the passive sampling hypothesis (Rosenzweig, 1995) which suggests that larger areas passively sample more individuals and thus statistically will incorporate more trait diversity from the regional pool. Deviance from such probabilistic artifacts and purely random processes in the Sentinel-2 observed data can signal trait convergence/divergence, i.e. functional under-/over-dispersion, through environmental filtering and/or biotic sorting (Smith et al., 2013; Zheng et al., 2021). These null-models give a random, spatially blind account of the mathematical effect of having more data points (pixels) available as the plot area increases from 0.4 to 60ha plots. Two kinds of null-models were applied. Both draw from the pool of existing trait combinations as observed through our remote sensing estimates. The ‘random null-model’ contained trait combinations that were randomly drawn without consideration of land use, whereas for the ‘land use null-model’ trait combinations were drawn within the matching land use type to which the null-model is compared. In other words, both null-models draw from trait combinations found in the observed data trait distribution, but one with consideration of the specific trait pools of different land use types and the other from the total trait pool of the study area without consideration of land use. The comparison between observed patterns and the null-models allowed for insights in the shape of FAR curvature, passive sampling hypothesis, di-/convergence as opposed to random processes, and possible trait pool saturation.

Secondly, we stratified the functional diversity-area relationships between the distinct land use types of the study area; intact forests, logged forests, and oil-palm plantations. Functional diversity-area curvatures were expected to differ significantly across land use types. The distinct land use types were expected to underpin different community assembly processes that translate into different FAR curvatures (Barnes et al. 2014; Edwards et al. 2014; Fitzherbert et al. 2008; Koh and Wilcove 2008; Varsha et al. 2016; Wang and Foster 2015). Differences in functional diversity metrics between land use types and across scales were assessed by ANOVAs and post-hoc analyses executed across the full range of different plot areas (0.4 to 60ha). Notably, all plot areas were selected to consist of a single land use with no plots of mixed land use. The assumptions of the ANOVAs were evaluated and a log transformation of Functional Richness was applied to ensure normality of residuals.

Thirdly, the predictive power of environmental drivers of spatial patterns in functional diversity was assessed. In addition to land use, we looked at the explanatory role of landscape morphology – as captured by the variation in elevation and slope - on patterns of functional diversity. Variation in landscape morphology can introduce heterogeneity within and between habitat patches which, in turn, drives beta-diversity by introducing opportunities for different communities and environmental niches (Barton et al., 2013). Statistical analysis was based on regression models run for each plot area from 0.4ha to 60ha separately. Ordinary least squares (OLS) regression models were used to quantify the extent to which studied environmental drivers explained the functional diversity patterns at different spatial scales dictated by the plot area. We ran two sets of regression models; one to focus only on the effect of land use, and one set of models that incorporates both land use and variation in elevation and slope as predictors.

## 5.3. Results

### 5.3.1. FAR against null-model predictions

Fig. 5.3 shows how functional diversity metrics, from both satellite observations and null-models, change as a function of plot area (for non-log transposed representations see (Fig. S. 23a). Functional richness is highly scale-dependent, with the curvature appearing to be biphasic; initially depicting fast increases in richness which phases out to a more linear pattern from 10ha and beyond. At the largest plot area (60ha), no full saturation in increases of functional richness is observed yet. This implies that trait variation at 60ha is not yet exhausted. In comparison to the null-models, the observed clustering of functional traits was much stronger, as indicated by the significantly lower functional richness. This comparison suggests a spatial convergence of traits as opposed to a random distribution. Observed functional richness is 3-5 times more converged than what would be expected from a random distribution. With increasing plot area sizes, the convergence gap becomes smaller.

The patterns in functional divergence (FDiv) are relatively scale-independent. At plot area <5ha, functional divergence decreases with plot area until it ultimately stabilizes. We observe a close resemblance between the actual observed data and the land use null-model, while the fully random null-model deviates more strongly from the actual observed patterns. This suggests that land use plays an important role in shaping actual functional divergence patterns while there is a higher divergence between trait combinations in the observed data than would be expected based on fully random processes.

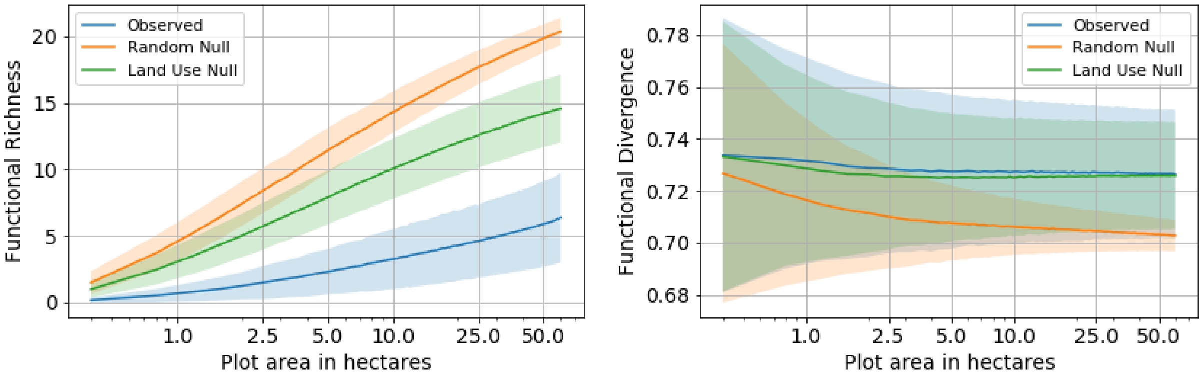


*Fig. 5.3: Scale dependency of the functional richness (left) and divergence (right) metrics comparing observed remotely sensed diversity in Sabah, Borneo, versus null-models based on randomly drawn trait combinations from observed trait values. The 'Random Null' model (orange) draws random trait combinations irrespective of land use type, whereas the 'Land Use Null' model draws random trait combinations in consideration of land use. Dark lines represent the mean and standard deviations are represented by the respective shaded areas. Note the Log-transformed x-axis.*

### 5.3.2. FAR across land use types

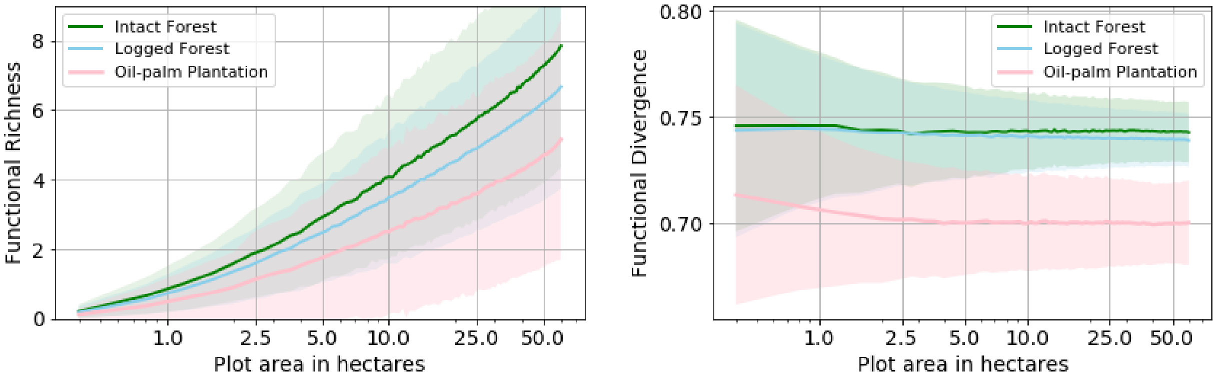


*Fig. 5.4: Scale dependency of the functional richness (left) and divergence (right) metrics stratified across land use types. Functional diversity calculations were done over continuous plots of one land use type over a range from 0.4 to 60 ha. Dark lines represent the mean and standard deviations are represented by the respective shaded areas. Note the log-transformed x-axis.*

Fig. 5.4 shows the FAR curvatures for the different land use types studied. Functional richness is largest in intact forests, followed by logged forests, whereas oil-palm plantations structurally host the lowest mean functional richness across all plot area sizes (for non-log transposed representations see Fig. S. 23b). Standard deviations for all three land use types are relatively large and could relate to the large variation in environment and landscapes across the vast study area and/or the relative sensitivity of convex hull volumes to anomalous observations. Despite large standard deviations, differences between the land use types are found to be statistically significant across all plot areas. Post-hoc analysis further revealed that differences in functional richness between logged forests and intact forests become significant from around 4 ha onwards while oil-palm plantations significantly deviated from the forested land use types across all plot areas (Fig. S. 24). In addition to a lower functional richness, oil-palm plantations are characterized by significantly lower functional divergence compared to the forested land use types while logged forests and intact forests exhibit comparable mean functional divergence across the range of plot areas considered (For post-hoc analyses results; see Fig. S. 24).

### 5.3.3. The scale dependency of environmental predictors

Fig. 5.5 depicts the explained variance of two sets of linear regression models that were run over the same 1713 plots at area size varying from 0.4. to 60ha. For functional richness, we find a significant contribution of the environmental drivers as plot area increases. Like the universal principle behind SAR, abiotic heterogeneity likely increases when larger areas are considered for analysis. As a response to the more diverse environment, a higher richness of trait combinations and a corresponding larger trait space volume is a logical response of ecological communities. As plot area increases, the role of landscape morphology as a driver of environmental heterogeneity becomes an increasingly important explanatory predictor in comparison to the model only accounting for land use as a predictor. Land use steadily explains around 15 % of the variance in functional richness across all plot areas which is relatively low in part due to the large standard deviations in functional richness found within land use types.

Elevation and slope as indicators of landscape morphology contribute relatively little to explaining functional divergence patterns. The processes driving the distribution of traits within relative trait space appear to be for a large part determined by land use. Land use becomes an increasingly important predictor with increasing plot area.

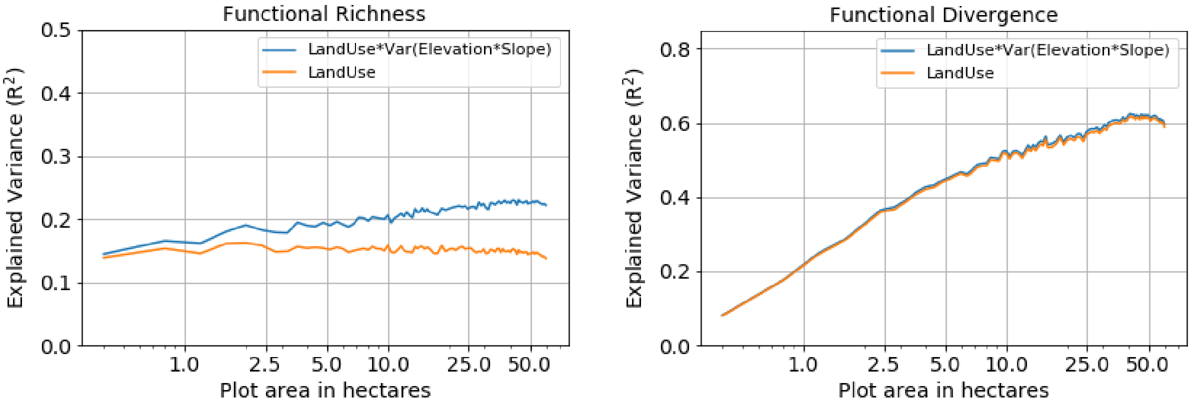


*Fig. 5.5: Explained variance of two sets of linear regression models as predictors of spatial functional richness (left) and divergence (right) patterns across plot area size. The first set of models (orange) includes land use as a predictor of functional diversity. The second set of models (blue) expands with elevation and slope as environmental drivers in predicting spatial functional diversity patterns. All models were found to be significant (p<0.01) across the entire range of plot areas.*

## 5.4. Discussion

The dependency of biodiversity patterns on spatial processes has been widely acknowledged (Kunin et al., 2018; Marceau & Hay, 1999; Smith et al., 2013; Steinbauer, Dolos, Reineking, & Beierkuhnlein, 2012; Wang, Rahbek, & Fang, 2012). With ongoing advances in sensor technologies and processing methodologies, satellite remote sensing is widely expected to contribute to current data gaps in large-scale biodiversity monitoring (Almeida et al., 2021a;

Jetz et al., 2016). As such, future attempts to estimate plant diversity patterns over large spatial extents using satellite remote sensing are similarly subject to spatial scaling decisions that will affect the patterns we observe. In this study, we looked at the scale dependency of functional diversity estimates derived from satellite remote sensing, specifically at how the ‘community’ concept translates into a pixel-based plot area affects spatial functional diversity patterns. The results demonstrate a metric-dependent scale dependency of functional diversity estimates across an unprecedented range of scales. Here, we further discuss the shape of the presented satellite-based FARs in relation to previously conducted studies at smaller scales, the passive sampling hypothesis, trait convergence, land use, and alpha/beta diversity concepts.

### 5.4.1. Comparison against field and airborne studies

The results show that functional diversity holds a consistent relationship with plot area, with different degrees of scale dependency between functional richness and functional divergence metrics. At smaller plot areas, curvatures were similar to those found by Karadimou et al. (2016) and Smith (2013) using traditional field sampling approaches applied to vascular plant diversity. Although the range over which the grain and extent varied, was much lower than ours (Karadimou et al. (2016) had plots ranging from 1 to 128 $m^2$ and Smith et al. (2013) 0.02 $m^2$ to 4 $m^2$), both studies found that functional richness increases consistently with area. In addition, Karadimou et al. (2016) observed, similar to our study, that functional divergence exhibited a nearly flat curve with plot area.

The application of (airborne) remote sensing generally allows increasing the range of study. Schneider et al. (2017) looked at functional diversity derived through imaging spectroscopy using airborne optical and LiDAR remote sensing over a Swiss mountain ridge- across radii from 60m radius to 1020m with 6m spatial resolution. Durán et al. (2019) used hyperspectral sensors to retrieve foliar trait indicators to estimate functional diversity in tropical forests across an Amazon-to-Andes elevation gradient (215 to 3537 m). Durán et al. (2019) ranged plot areas between 20 $m^2$ and 0.5-5.3 ha stratified across different segments of elevation. Again, both studies demonstrated functional richness curves similar to patterns observed in our study. These curvatures are characterized by initial steep increases attenuating as area sizes increase. Although functional divergence patterns differed across elevation according to Duran et al. (2019), in general, both studies (Durán et al., 2019; Schneider et al., 2017) revealed relatively scale-invariant patterns of divergence that are similar to those found here.

Dahlin (2016) evaluated the effects of land use on the FARs, using spectra(l diversity) instead of using spectral trait indicators as proxies for functional diversity. In a mixed landscape of forest and agriculture in Northern US with plots ranging from 8 to 12 $m^2$, Dahlin (2016) showed the typical biphasic curvature for functional richness with fast increases at smaller scales and slowed down increases at large scales as seen in our and other studies. The data of Dahlin (2016) showed trait convergence compared to random null-models. In addition, forest plots were characterized by a higher diversity and amplitude of the curvature as compared to agricultural plots.

Through satellite earth observations, we were able to extend the range of scale far beyond the spatial extents studied in previous empirical studies. The general curvature among scales and approaches seems to correspond. The previous in-situ, airborne, and our presented satellite observations all demonstrate a steep increase in functional richness at smaller scales and relatively scale-invariant patterns for functional divergence. At larger scales, we show that the increase in functional richness flattens as plot area increases while functional divergence stabilizes and becomes relatively scale-independent at the larger plot areas.

These observations are in line with ecological theory. The scale dependency of functional richness relates to the amount of available resources present in an area, a relationship that follows those seen in the species richness - area relationship (Karadimou et al., 2016; Plotkin et al., 2000). The cumulative amount of available resources rises with increasing area. This leads to communities supporting a larger number of species and corresponding trait combinations (Karadimou et al., 2016). Initially, each added area adds new trait combinations that may be due to compositional changes, stochastic species occupancy patterns, and intra-specific trait variation. As the area increases, the convergence of traits to its surrounding environment results in fewer new inter-/intra-specific trait combinations relative to the trait space of the sampled community (see also Barton et al., 2013). This causes the relationship of increasing functional richness with scale to attenuate. However, no full saturation is observed as the surrounding environment of plots also tends to change with increasingly larger scales (Zarnetske et al., 2019, 2017). At 60 ha plots, we notice no saturation has yet occurred, suggesting that either the total trait pool is expressed at even larger scales or that we might need to abandon the concept of one clear-cut trait pool from which selection occurs but rather rely on a continuum that hardly saturates at these scales.

### 5.4.2. Passive sampling hypothesis

Increases in plot area also result in an increase in sample size, caused by the larger number of pixels to cover a larger area. In line with the passive sampling hypothesis, plot areas with a larger number of sampled individuals will statistically be more likely to exhibit higher richness. Our datasets are fixed by the 20m spatial resolution of Sentinel-2. Given the fixed spatial resolution, an increase in areas is automatically tied to an increase in the number observations/pixels. An area of 0.4 ha requires 10 pixel-based observations, whereas a plot of 60ha would require 1500 similar observations. With substantial increases in the number of observations as the area expands, the probabilistic likelihood of encountering new trait combinations distinct to the already observed trait space increases too. This effect diminishes as the area continues to increase as the probability of encountering new trait combinations becomes smaller given the presumably finite possible trait ranges. Our null-models, based on randomization, with and without consideration of land use, mimic this probabilistic effect and are indicative of the passive sampling hypothesis for FARs. The shape of curvatures calculated based on satellite-derived functional diversity estimates did not differ from the null-models (Fig. 5.3), even when stratified across different land use types (Fig. 5.4). Nonetheless, importantly, the amplitude of the different FARs was found to be crucially different for the observed data, and for different land use types. Specifically, the observed functional richness reveals much smaller increases in functional richness with plot area as would be expected based on the null-models. Functional richness increases are converged beyond what could be expected solely on random effects. The role of the passive sampling hypothesis is not dismissed; however, the observed patterns are shaped by other non-random factors as indicated by the deviance from the random null-models.

### 5.4.3. Trait convergence

At any given plot area, we observed strong trait convergence of the observed functional richness estimates as compared to the randomization-based null-models (Fig. 5.3). The spatial distribution of functional traits appears to be confined geographically, but is also further bound by land use patterns. A confined subset of trait combinations is expressed at each plot area and for each land use type which results in significantly smaller trait spaces, i.e. functional richness, in the observed data as compared to the null-models.

From an ecological perspective, these trait convergence patterns signal the role of environmental filtering and biotic sorting, creating an underdispersion of trait combinations in space (Schneider et al., 2017; Smith et al., 2013; Tello et al., 2015; Weiher and Keddy, 1995; Zarnetske et al., 2017). When we stratify FARs by land use, intact forests - followed by logged forests - exhibit the largest functional richness whereas oil-palm plantations host structurally lower mean functional richness across all scales (Fig. 5.4). These results are in line with findings of earlier field studies in Borneo and (sub-)tropical ecosystems comparing functional diversity in oil-palm plantations with intact and logged forests (Barnes et al., 2014; Edwards et al., 2014; Maeshiro et al., 2013), albeit that previous studies analysed different taxa and did not investigate the scale-dependence of land use impacts. The land use gradient represents how different species pool (from monoculture to species-rich) environments affect the curvature of FAR. The lower functional richness of oil-palm plantations can readily be explained by the intensive management selecting for monocultures. Given that intra-specific trait variability is commonly lower than inter-specific trait variability (Baraloto et al., 2010; Hulshof and Swenson, 2010; Messier et al., 2010; Swenson, 2013), this translates into lower functional richness.

In contrast to the richness metric, functional divergence between trait combinations observed from satellite data was higher than what would be expected based on random processes. The land use null-model fares particularly well in modelling the observed data, which highlights the role of land use in driving functional divergence patterns. The distinct patterns of lower functional divergence in oil-palm plantations likely relate to the intensively managed nature of this monocultural land use type as its management suppresses community assembly processes, e.g. competition and niche partitioning (Smith et al., 2013). The comparisons against random null-models and across land use types suggest that a degree of non-random niche differentiation and/or competitive adversity is taking place, resulting in more relative divergence than would be expected from purely random spatial trait selection (Weiher and Keddy, 1995). Notably, processes of competitive adversity are assumed to be prominent at fine scales as organisms compete for resources within each other's vicinity (Smith et al., 2013).

From a remote sensing perspective, two considerations are important in relation to the observed trait convergence in functional richness estimates as opposed to the random and land use null models. Firstly, the 20m spatial resolution of Sentinel-2 is too coarse to support the delineation of individual canopies, rather pixels are aggregates of multiple canopies. Pixel aggregation of functional traits of multiple canopies can mediate and converge the extremes otherwise found between individual canopies leading to a degree of trait convergence. Secondly, atmospheric scattering causes light reflected from adjacent landscapes to be observed by the sensor. Without adequate correction of possible adjacency effects, scattering leads to minor biases or possible spectral convergence with effects for the convergence of functional richness estimates (Hauser et al., 2021; Louis et al., 2016).

### 5.4.4. Environmental drivers

Beyond the general shape of FARs themselves, we looked into environmental drivers to assess the scale-dependent influence of assembly processes on satellite remotely sensed FARs. For functional divergence, land use seems to be dominant as an explanatory variable of the spatial patterns observed (Fig. 5.5). With increasing plot area, the effect of land use becomes increasingly profound as standard deviations of functional divergence become increasingly smaller in proportion. This might be attributable to a crystallization of within-trait space relationships and a waning effect of noise on diversity metrics when based on larger sets of observations (Brede et al., 2020; Skakun et al., 2017). Land use, and correspondingly its management intensity, is an important driver shaping natural community assembly processes that influence the divergence between trait combinations within multidimensional trait space. Intensive management and monoculture practices are likely to undermine processes of competition naturally occurring in forests which resonates with the higher functional divergence found in the latter (Fig. 5.4). In contrast, the role of landscape morphology appeared virtually absent in the models explaining spatial differences in our estimates of functional divergence.

In the case of functional richness, our findings highlight that the importance of land use remains rather constant across plot area sizes (Fig. 5.5). On the other hand, slope and elevation, i.e. landscape morphology, as an indicator of environmental heterogeneity, manifests itself as a predictor of functional richness only with increasing plot area (Fig. 5.5). In other words, the importance of landscape morphology (slope and elevation) appears to be a function of plot area. The latter could relate to the larger probability to contain a more heterogeneous environment at larger plot areas. In most ecosystems, the environment can act as a selective filter on plant species along abiotic gradients (Read et al., 2014). As a result, the observed functional diversity in a plot could become increasingly shaped by environmental heterogeneity and the diverse adaptations of individuals thereupon. Slope and elevation are limited indicators of the real complexity of factors shaping the environment. For future studies, including soil data or water availability could be important environmental drivers to consider (Chave, 2008; John et al., 2007).

### 5.4.5. Alpha and beta diversity components

Alpha and beta concepts make a distinction between within- and between-community diversity dynamics (Whittaker, 1972). In this study, the plot area through which ‘community’ diversity was conceptualized was assessed from 0.4ha to 60ha. The functional richness estimates showed a monotonous change in increases as a function of plot area. The fast increases observed at small scales may be attributable to high variation in stochastic species occupancy patterns among sampling units, and variation in species responses to competition and niche occupancy. Such shapers of variation are commonly attributable to alpha diversity drivers (Field et al., 2009).

At larger plot areas (> 5ha), increases of richness per area slow down leading to saturation in variation. Particularly at larger plot areas, an increasingly large share of the variance of functional richness could be explained by landscape heterogeneity, for which we used morphology (slope and elevation) as an indicator (Fig. 5.5). The increasing explanatory role of landscape morphology at bigger (intermediate) scales (Fig. 5.5) suggests the increasing importance of beta diversity drivers that capture distinct ecological communities that are present adapting to different environmental conditions (Barton et al., 2013; Weiher and Keddy, 1995). As a mechanism for the FAR, larger areas are expected to have higher levels of habitat heterogeneity compared to smaller areas. Habitat heterogeneity leads to new environments that require trait adaptation following the niche theory (Weiher and Keddy, 1995). Distinct heterogenous environmental conditions are linked to hosting distinct ecological communities to thrive resulting in higher ‘between’ community diversity (i.e. beta diversity) (Barton et al., 2013).

### 5.4.6. Recommendations

In combination, our findings show how discrete concepts of alpha and beta diversity translate to a continuous transition when observed from spatially explicit satellite remote sensing. This challenges the applicability of discrete alpha and beta concepts and raises the question of whether we need new more continuous concepts. It may even be questioned whether the strong ecological focus of within vs. between communities (alpha vs beta) may be maintained given that the spatially explicit continuity of remote sensing allows for multi-scale analyses of diversity patterns across communities of different sizes.

Conceptually, the concepts of alpha and beta diversity are of value to make sense of spatial functional diversity patterns. Alpha and beta diversity concepts allow coupling biodiversity assessments to distinguish the relative importance of different processes, mechanisms, and drivers underlying diversity patterns (Socolar et al., 2016; Wang et al., 2015). The distinction between alpha and beta diversity allows for a full understanding of biodiversity patterns as high local diversity and distinctiveness in composition (alpha) versus habitat heterogeneity and species/trait turnover (beta) are both key criteria used to determine the ecological value of ecosystems (Laliberté et al., 2019).

Whittaker’s (1972) conceptualization of alpha and beta diversity stems from field study sampling schemes. While it is still possible to create discrete clusters of pixels to represent communities following a similar approach to traditional field studies, remote sensing offers a powerful tool to spatially explicitly assess multi-scale analyses to be calculated and mapped at potentially continuous scales. This allows us to omit arbitrary decisions to decide upon fixed community sizes in terms of area/ number of pixels. Additionally, a consistent optimal plot area in terms of pixels to calculate functional diversity estimates for an entire region might not exist. Different plot area sizes exhibit different patterns and relationships to environmental drivers as shown in Fig. 5.5. Moreover, in a heterogenous landscape, scale dependence of functional diversity estimates is also vegetation (canopy size) dependent (Magurran, 2003; Zheng et al., 2021). Fig. 5.4 demonstrated distinct amplitudes of FAR curvatures for different land use types representing different species pools and vegetation compositions. Together, these findings highlight the value of multi-scale and stratified approaches to assess the scale dependence of the patterns observed.

While satellite remote sensing of functional diversity is still in its infancy, the link between field studies for validation and calibration is still very important for validation and calibration

(Hauser et al., 2021). Therefore, alpha and beta-diversity concepts as imposed in most field designs will remain equally relevant. However, further along the line, the availability of spatially explicit and continuous data through remote sensing allows the development of theories that underpins a continuum of gradual community dynamics that go beyond a discrete scaling of alpha and beta diversity. Alternatively, there are methods available (e.g. Laliberté et al. 2019) that can help partition spectrally derived plant diversity into alpha and beta components.

### 5.4.7. Limitations

In our analyses using Sentinel-2, the pixel size remained invariant at 20m spatial resolution. At 20m spatial resolution, already part of the local diversity is occurring at a sub-pixel level which challenges the interpretation of traditional ecological diversity concepts. For future development and application of satellite remote sensing, it is important to increase understanding of how both grain (spatial resolution) and the number of pixels (this study: plot area to capture a 'community') affect the patterns observed in functional diversity assessments done from space-borne instruments. This requires expanding our current analysis to include both variant pixel sizes (e.g. Rocchini, 2007 has compared different sensors). A continuum of various combinations of changing grain and extent (change grain maintain extent, change extent maintain grain, change grain and extent) could be examined to explore scaling relationships like theorized by Barton et al. 2013. Integration of in-situ measurements, hyperspectral airborne measurements, and large-scale repeated satellite remote sensing approaches combined with the ongoing advances in these instruments will be necessary to assess the totality of scaling effects of both spatial grain size, plot sizes, and spatial extent on patterns observed (Gholizadeh et al., 2019; Jetz et al., 2016; Rocchini, 2007; Wang et al., 2018). Furthermore, data assimilation of multi-temporal and multi-sensor images may help overcome the patchiness of optical remote sensing data in tropical regions to study even wider range of spatial extents (>60ha), possibly even beyond biogeographic regions with distinct geological barriers and evolutionary histories to observe the changes and turnover in functional diversity patterns.

Lastly, we relied on the performance of the SNAP toolbox for retrieving spectral trait indicators to estimate functional diversity patterns. Future studies will require further in-depth validation against in-situ estimates (e.g. Ali et al., 2020; Hauser et al., 2021). Moreover, spectral and spatial resolutions of satellite missions will continue to advance and facilitate improvements in the range and number of ecologically relevant -yet accurately retrieved- trait estimates (Wang & Gamon, 2019). The accuracy of functional trait retrieval can be further improved by optimizing retrieval methodologies, for instance through more realistic radiative transfer models (Huang et al., 2011), alternative hybrid inversion techniques (Verrelst et al., 2019a), assimilation of ancillary data (Hakkenberg et al., 2018; Moreno-Martínez et al., 2018), data-driven deep learning (Reichstein et al., 2019), and active learning heuristics (Berger et al., 2021).

## 5.5. Conclusions

How much biological diversity occurs within a given area is a fundamental question in spatial ecology. At the same time, the magnitude of diversity is a function of area too. We showed how satellite remote sensing estimates of functional diversity hold a consistent relationship with plot area, with different degrees of scale dependency between functional richness and functional divergence. The shape of functional diversity-area relationships observed was found to correspond with ecological theory while satellite remote sensing allowed us to extend the range of area considered far beyond the spatial extent of previous empirical field and air-borne studies. Strong consistent trait convergence was observed through our estimates of functional richness compared to the random spatial processes of the null-models. Moreover, trait convergence differed significantly between different land use types.

The fluidity of ecological concepts of community diversity bears challenges when attempting to fit these into the spatially continuous pixel raster of satellite remote sensing observations. Nonetheless, the spatial continuity of this data allows for easy-to-conduct multi-scale analysis of functional diversity while omitting the shortcomings for arbitrary scaling decisions of a discrete sampling design. This challenges the applicability of discrete alpha and beta concepts and raises the question of whether the strong ecological focus of within versus between communities (alpha vs beta) is sufficiently justified or whether we need new more continuous concepts. For now, stratified multi-scale analyses through remote sensing instruments help unveil the role of different drivers at different spatial scales and across larger spatial extents while illustrating the continuity of assembly processes driving the functional diversity-area relationship.

# Chapter 6.: General discussion

The central challenges presented in this thesis revolve around how we can use currently operational satellite remote sensing for observational monitoring of terrestrial plant biodiversity at large regional geographic extents without heavy reliance on field measurements for training. Fundamentally, these challenges relate to: i) scale disparities we observe between ecology and remote sensing at conceptual, spatial, spectral, and temporal scales, and ii) the lack of qualitative and quantitative validation of the capabilities of currently operational multispectral satellite remote sensing (Sentinel-2) to estimate spatial patterns of in-situ plant diversity.

Through four research chapters, the capabilities of multispectral satellite remote sensing to map plant functional diversity using Sentinel-2 were examined using different approaches, conditions, scales, and means for validation. The approaches were applied to two different regions with diverse land use and ecosystem types but also with different spatial extents geographically and conceptually from discrete (sampled locations) to continuous ('wall-to-wall') modes of inference of plant functional diversity. These analyses build on two different observational approaches linking spectra to plant diversity; i) spectral diversity versus ii) RTM-based functional diversity from optical trait estimates. Means of validation to assess the performance were provided directly through precisely scaled plot-based trait measurements as well as multi-plot functional and taxonomic diversity estimates measured in-situ. In addition, I demonstrated the use of trait databases and literature as well as land use gradients to check the plausibility of spatial plant functional diversity patterns in a qualitative approach. Lastly, I assessed different spatial scales in relation to functional diversity and how scale impacts the diversity patterns observed. All in all, the multitude of possible ways to implement Sentinel-2 observations for studying plant functional and taxonomic diversity is exemplified in the individual chapters, highlighting how the decisions in our workflow influence how we perceive spatial plant diversity patterns from satellite remote sensing. In this chapter, I highlight and review some of the main findings of this thesis:

The spectral variability hypothesis based on Sentinel-2 observations is able to predict taxonomic diversity in our Portugal case study. No evidence was found for a role for environmental or leaf trait heterogeneity as intermediate variables explaining the workings of the spectral variability hypothesis. Instead, the spectral diversity metrics appeared to be dominated by vegetation cover (density, canopy architecture, background signals). To overcome the spectral dominance of vegetation cover, I explored approaches based on (hybrid) RTM inversion to disentangle some of the soil and canopy signals to isolate actual functional plant diversity elements within spectral diversity.

For this, I provided an elaborate validation effort based on in-situ measurements in Northern Portugal to precisely match the scale of Sentinel-2 (clusters of) pixels to assess both individual plant trait estimates as well as the estimated combined community plant functional diversity. This validation was inspired by the discrepancy between scientific acknowledgment on the role of satellite remote sensing for mapping plant biodiversity, yet a lack of validation and performance assessment of viable satellite remote sensing to retrieve plant functional and taxonomic diversity. We advocate the importance of such studies to gain recognition and application among ecologists. Moreover, I examined the responsiveness of plant functional diversity estimates based on spectral trait indicators qualitatively against explicit patterns of land use, historic trait measurements, and across spatial scales in Northern Borneo.

This thesis demonstrates the role Sentinel-2's spectral sensitivity can play in estimating plant functional and taxonomic diversity, retrieving multiple traits simultaneously, and successfully applying the spectral variability hypothesis. Nevertheless, we found that the spatial resolution (20m) challenged validation efforts (laborious at these scales) and interpretation. The latter highlights the spatial mismatch between ecological concepts of scale and that of remote sensing while considerations of scale are critical in the way we perceive patterns of biodiversity. Sentinel-2 pixels were unable to delineate individual canopies but rather present aggregated patterns. Functional diversity estimates based on (clusters of) pixels were hard to translate to discrete alpha and/or beta diversity community concepts. Yet, spatially explicit remote sensing facilitated multi-scale analyses that illustrate how beta diversity drivers become increasingly influential as a predictor of plant diversity at larger spatial community scales.

## 6.1. Lessons learned

### 6.1.1. Disentangling spectral diversity

Spectral diversity has increasingly been adopted and studied as a biodiversity metric that captures plant diversity through the reflectance of electromagnetic radiation from plant canopies (Wang and Gamon, 2019). Conceptualization of the mechanisms behind the spectral diversity-plant diversity relationship is either founded by environmental heterogeneity ('surrogacy') driving taxonomic and functional diversity indirectly or through the physical relationship between spectral properties and the (dis)similarity of plant characteristics.

At the leaf level, spectral dissimilarity has been shown to reflect functional and phylogenetic dissimilarities between individuals (Schweiger et al., 2018). Yet, this does not directly translate to the scale of satellite remote sensing where signals are complex and leaves are aggregated to (multiple) canopies that can include a soil signal and additional environmental and angular influences. Despite the unfavorable spatial resolutions of satellite remote sensing, studies have shown a promising positive relationship between spectral diversity and in-situ plant diversity, e.g. Torresani et al. (2019), Madonsela et al., (2017), and Rocchini et al. (2004; 2007). However, empirical validation and characterization of what is measured within spectral diversity and what mechanisms relate it to plant diversity remain limited and untransparent in the current body of research.

Chapter two looked into the use of spectral diversity derived from Sentinel-2 applied over a heterogeneous landscape encompassing shrub- and forested land. RTM simulations based on the collected trait dataset indicated that spectral diversity indeed has a strong correlation with leaf trait diversity at the leaf level (Fig. 2.2). When scaling up from the leaf to the canopy scale, this relationship becomes considerably weaker (Fig. 2.2). Logically, within the canopy reflectance signal, structural, canopy, and soil characteristics become influential on the overall spectral signal and can obscure spectral signals present at the leaf level, especially at lower vegetation cover densities (Asner, 1998). Optimization of canopy RTM simulations revealed a trade-off in describing either the in-situ trait diversity or the actual Sentinel-2 spectral diversity highlighting the importance of canopy and soil characteristics (Fig. 2.2).

The combination of a coordinated field data campaign georeferenced to Sentinel-2 information allowed for direct comparisons between community spectral, taxonomic, and trait diversity, as well as confounding factors to further assess the workings of spectral diversity when applied at large scales using satellite remote sensing. The empirical observations of the study area showed that spectral diversity indeed relates to taxonomic diversity (Fig. 2.3, Spearman's $\rho = 0.61$) in line with the 'spectral variability hypothesis'. I further examined the mechanisms behind this positive relationship, both through environmental factors as well as functional traits. Despite the relationship between spectral diversity and taxonomic diversity (Fig. 2.3), spectral diversity observed from Sentinel-2 revealed no clear correlation with in-situ measurements of leaf trait diversity. In addition, neither landscape morphology nor vegetation cover served as environmental 'surrogates' linking spectral diversity and taxonomic diversity. In other words, although the 'spectral variability hypothesis' appeared to hold for taxonomic diversity using Sentinel-2 observations in our case study, the exact drivers of the relationship remained concealed despite consideration of functional properties, landscape morphology, and vegetation cover. Future studies can elaborate on this relationship by integrating and exploring the spectral species concept (Féret and Asner, 2014), unmeasured canopy traits, structural diversity (Schneider et al., 2020), fire regimes, plant phenology, grazing, dead biomass, and soil types for further consideration (Pausas and Vallejo, 1999; Rossi et al., 2021; Schneider et al., 2017; Vivian and Cary, 2012; Zarnetske et al., 2019).

By breaking down the spectral diversity signal in different contributing components, chapter two highlighted the importance of vegetation cover as a driver of spectral diversity patterns. Vegetation cover, measured through the Plant Area Index (PAI), influences the extent to which soil, litter, and understory appear in the spectral reflectance signal of a Sentinel-2 pixel. Additionally, vegetation cover is tied to the present canopy architecture dictated by morphological traits. Canopy traits tend to have a profound impact on the spectral signal of vegetation across a broad range of the electromagnetic spectrum (Asner, 1998; Gu et al., 2016). Within our heterogenous study site, the variation in vegetation cover dominates the spectral diversity signal observed from Sentinel-2 (53-84% of the explained variance by fixed effects, Fig. 2.4). This shows that, while spectral diversity is relatively straightforward to deploy, caution is required to characterize what exactly is measured within spectral diversity. Vegetation cover, structural diversity and soil characteristics do not necessarily covary with functional or taxonomic plant diversity. Across different ecosystems, variation in vegetation density might align more strongly with leaf trait diversity (Sheil and Bongers, 2020; Walter et al., 2020), while in other ecosystems vegetation cover density could mask or be ordinal or even negatively related (e.g. fertilized monocultures) to plant diversity (Rossi et al., 2021; Villoslada et al., 2020).

Thus, our findings indicated that direct application of spectral diversity metrics circumvents the challenges and difficulties in isolating direct plant diversity signals, however, at the same time, the approach risks overemphasizing spectrally dominant characteristics that can overshadow the elements of plant diversity that we are actually interested in. While the 'spectral variability hypothesis' based on Sentinel-2 observations was able to predict taxonomic diversity, chapter two also exemplified the risks that the spectral diversity signal to be dominated by other factors. At the time of writing, several studies came to similar conclusions regarding a range of factors that may confound the spectral diversity-biodiversity relationship using airborne remote sensing, including the fraction of bare soil (Gholizadeh et al., 2018), biomass/vegetation density (Villoslada et al., 2020; Wang et al., 2016), and litter and dead biomass (Rossi et al., 2021). Given that these studies use hyperspectral airborne observations, chapter two is unique at this point in providing a characterization of the spectral diversity derived from Sentinel-2 multispectral satellite observations highlighting the dominance of vegetation cover in the spectral diversity patterns.

Our ability to account for spectrally dominant confounding factors, such as vegetation cover and soil, could improve the robustness and relationship of spectral diversity approaches to in-situ plant diversity across spatial, spectral, geographic, and temporal resolutions. Several approaches are already in place to assist in further dissection of the spectral signal to isolate plant diversity (Musavi et al., 2015). Chapter three explored the application of a physics-based RTM inversion to dissect the spectral signal and derive multiple relevant plant traits to quantify community patterns of functional diversity across a heterogeneous and biodiverse (semi-)natural landscape. The approach presented in chapter three could help to account for the canopy and vegetation cover dominance that can confound the spectral diversity-plant diversity relationship.

### 6.1.2. Physics-based estimation of functional diversity

Physics-based approaches are appealing given its theoretical universal applicability as opposed to statistical learning approaches and/or spectral indices that 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). Physics-based approaches using RTMs have two major advantages over spectral diversity applications (as applied in chapter two); 1) RTM inversion allows to break down the spectral signal into multiple relevant canopy and leaf traits while accounting for soil, canopy, angular and other parameters, and 2) the spectrally derived traits relate directly to measurable, and thus verifiable, in-situ ecological field data. While for spectral diversity the link to plant diversity remains relatively abstract, a physics-based remotely sensed functional diversity links spectra to verifiable optical traits before quantifying diversity estimates. The downside is that these physics-based approaches require an additional and challenging step compared to direct use of spectral diversity metrics; the inversion of spectra through Look-up Tables (LUTs) or hybrid emulation of RTMs. Such inversion is challenging as RTMs are subject to strong assumptions, heavy parameterization, and ill-posedness (Combal et al., 2003; Koetz et al., 2007; Musavi et al., 2015), especially for multispectral observations (Brede et al., 2020; de Sá et al., 2021). Likewise, the choice of RTM holds implications of what biophysical parameters can be retrieved and its underlying assumptions, inversion complexity, and ill-posedness.

In addition, active decisions need to made on a set of spectrally derived traits retrievable through RTM emulation/inversion that hold ecological relevance to study plant biodiversity. Trade-offs between the number and selection of traits is difficult considering spectral limitations, ill-posedness, and ensuring relevant functional differentiation in plant community. Yet, these choices are highly influential to the patterns observed. In the end, functional diversity patterns are dictated by the functional traits selected that make up the diversity metrics (Legras et al., 2020).

Using the physics-based approach, chapter three examined our ability to retrieve multiple traits simultaneously to estimate community plant functional diversity in heterogeneous (semi-)natural landscapes from Sentinel-2 observations. At the time of writing, the presented two-fold multivariate validation of plant traits as well as community functional diversity at the scale of satellite remote sensing was completely novel. Strong performance is demonstrated in characterizing leaf area index (LAI; $R^2$= 0.58 - 0.63, RMSE= 0.49 - 0.51 $m^2/m^2$), a key biophysical parameter that relates to the canopy architecture and vegetation cover density. Beyond the canopy, leaf biophysical and biochemical traits were estimated focusing on leaf mass per area (LMA) and leaf chlorophyll (CAB). Chapter three demonstrates the utility of RTM-based retrieval of LMA ($R^2$ = 0.66 - 0.68, RMSE = 6.36 - 31.06 $mg/cm^2$) in a forest and shrubland ecosystem at canopy scale. Notably, very few studies have evaluated the RTM-based retrieval of LMA, particularly at the canopy level in forest ecosystems using satellite remote sensing (Gara et al., 2021). Besides trait means, the analysis included an assessment of our ability to estimate trait variability within the 20m adjacent plots which is rarely seen in validation studies and highlighted the challenges to predict local trait variability.

Combining the retrieved traits in diversity metrics, the implemented inversion approaches demonstrated a general performance and applicability of RTM-based functional diversity estimates when compared against in-situ estimates of functional diversity. The remotely sensed functional diversity estimates exhibited a degree of robustness against biases in individual mean trait retrievals and the variability thereof. Despite biases, relatively robust estimates of functional diversity from Sentinel-2 were predicted especially when using convex hull volume calculations to quantify the diversity. This robustness is largely attributable to the distance-based (relative) nature of the metrics applied. Our results showed that relatively simplistic and assumption-bound RTMs and general inversion algorithms (e.g. SNAP) can already produce maps indicative of coarse relative spatial patterns of plant diversity (Table 3.3).

The functional diversity estimates captured from satellite remote sensing were also in agreement with in-situ community taxonomic diversity (Fig. 6.1). In particular, I found that leaf-level traits, biophysical (e.g. LMA) and biochemical (chlorophyll) properties, were effective in estimating both taxonomic and functional plant diversity, whereas the inclusion of canopy trait LAI somewhat weakened the former relation (Fig. 6.1). Further testing across different ecosystem types and larger sample sizes will be necessary.

Chapter three demonstrates that different inversion methods produce acceptable results. However, optimized look-up tables, and predefined trait ranges enhanced performance noticeably which is in line with earlier studies showing that *a priori* information can reduce ill-posedness of retrievals (Combal et al., 2002; Dorigo et al., 2009). When such *a priori* knowledge is absent, trait databases (e.g. TRY of s-Plot) and active learning approaches can prove helpful to add constraints to inversion space and facilitate intelligent sampling for the training of retrieval algorithms to overcome some of the ill-posedness (Berger et al., 2021; Bruelheide et al., 2019; Kattge et al., 2020).

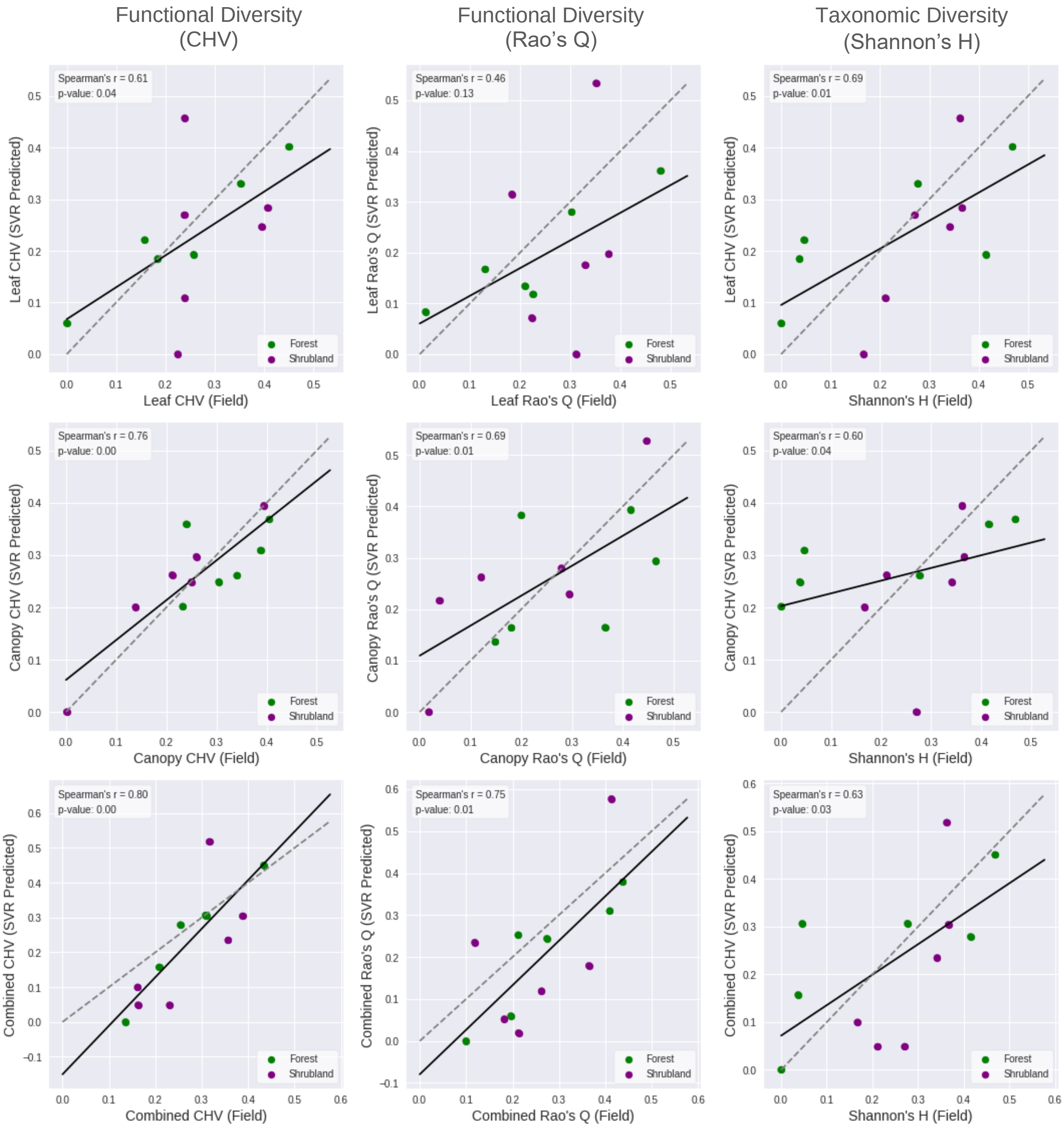


*Fig. 6.1: Remotely sensed functional diversity estimates (CHV and Rao's Q) calculated from Sentinel-2 derived traits through the Support Vector Regression (SVR) hybrid inversion compared against in-situ functional diversity measurements (left and center columns). The rightmost column compares SVR-derived remotely sensed functional diversity (CHV) against in-situ taxonomic diversity (Shannon's H). Comparisons are made across different scales; Leaf-level traits (leaf LMA and leaf CAB), Canopy-scaled trait (LAI*LMA, LAI*CAB), and combined canopy and leaf traits (LAI, leaf LMA, and leaf CAB). The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green points represent shrubland and forested locations, respectively.*

Hybrid modeling approaches, such as the PROSAIL-D Support Vector Regression approach (SVR) presented in chapter three amongst others, are potentially superior to lookup-table (LUT) based inversion strategies through the hybrid combination of the generic capabilities of physics-based methods (theoretical foundations, interpretable compartments) and the versatility of machine learning (data-adaptiveness and computationally efficient) (Reichstein et al., 2014; Verrelst et al., 2015). An added benefit of hybrid models is the ability to propagate uncertainties and estimate confidence intervals through Bayesian/probabilistic inference (Reichstein et al., 2014; Verrelst et al., 2015). Moreover, the next generation of hybrid retrieval algorithms can integrate active learning (AL) heuristics to optimize training datasets (Berger et al., 2021). The key idea behind AL is that the hybrid model can obtain higher accuracy with fewer training data if it is allowed to choose the data from which it learns through an iterative procedure (Settles, 2009). The extension of AL approaches in hybrid retrieval methods offers adaptive solutions to overcome the genericity and assumptions of RTM models when held against noisy satellite-inferred spectra and the trait-based particularities of the real-world ecosystems under study.

Chapters two and three present two complementary approaches. Our analyses suggest that RTM-based approaches are more robust to predict in-situ plant functional and taxonomic diversity as compared to using spectral diversity directly based on Sentinel-2 observations. Yet, the latter has the advantage that less technical and methodological steps are needed. To further understand the pros and cons, comparative studies are needed. Such studies would implement different approaches to quantify plant diversity from satellite remote sensing to compare performances to assess plant diversity in reproducible and transferable workflows. Future work on this should also compare the presumed transferability of spectral diversity and RTM-based approaches against the use of vegetation indices (Schneider et al., 2017), fully data-driven approaches, and could include alternative approaches such as the spectral species concept (Féret and Asner, 2014). Improved sensors (e.g. PRISM, CHIME; Cavender-Bares et al., 2020; Ustin and Middleton, 2021), optimized state-of-the-art RTMs, advanced inversion techniques (e.g. deep learning and AL) (Berger et al., 2021; Reichstein et al., 2014), and multi-source data assimilation can further enhance the performance of the presented RTM approach across ecosystems (Lahoz and Schneider, 2014; Lewis et al., 2012).

### 6.1.3. Validation of satellite remotely sensed plant diversity

Maturation and the widespread application of remote sensing approaches for biodiversity and conservation studies are still in dire of proper and in-depth validation (O'Connor et al., 2015). Validation campaigns help to understand the accuracy and uncertainties tied to remotely sensed plant diversity products, and to gain acceptance of remote sensing products in the field of ecology and among practitioners and relevant decision-makers. So far, most validation studies focused on agricultural applications rather than natural areas (Berger et al., 2018a; Djamai et al., 2018; Jacquemoud et al., 2009; Lu et al., 2019). And, if done in natural areas, validation is mostly done for remotely sensed estimates of single trait mean values in relatively homogeneous (semi-)natural environments set in relatively small study areas (e.g. 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). Combined validation studies on plant diversity metrics and multiple underlying optical traits were not done thus far for scalable physics-based retrieval approaches of satellite remote sensing. Moreover, many of the large-scale remotely-sensed trait validation studies heavily depend on interpolation or extrapolation of spatially and temporally fragmented in-situ data points (Ma et al., 2019; Moreno-Martínez et al., 2018; Serbin et al., 2019). In many other cases, accuracy assessment is missing or unusual, often not having independent validation data.

Building upon these insights, chapter three provides a thorough validation study for functional diversity metrics derived from satellite remote sensing. It presents a validation exercise in its simplest form: pixel-wise comparison of presumably high accuracy in-situ data with the remotely sensed data (Richter and Hank, 2021). Despite its simplicity in theory, actual sampling proved to be a challenging undertaking to ensure representative areas of individual plants with individual leaf samples to align with the Sentinel-2 imagery and spatial scale (spatial resolution) and orientation (raster). The study presented validation both at the pixel level (N=115), aggregate average trait values of the representative canopy, and at the community-level of clusters of pixels in terms of functional and taxonomic diversity. Unique to this study and lacking in current validation literature was the validation of our ability to estimate individual trait means but also local trait variability between adjacent plots.

Chapters two and three rely on a relatively small yet carefully sampled and scaled dataset for validation that comprises a heterogeneous ecosystem in the Northern Mediterranean mountainous region surrounding the Montesinho national park. More studies and large sample sizes will be needed across different ecosystem types to study the transferability of physics-based satellite remotely-sensed derived functional diversity. At the same time, the small sample presented here speaks of the labour-intensiveness of validating functional diversity at the scale of satellite pixels.

### 6.1.4. Large-scale spatially continuous application

To investigate satellite remote sensing as an operational tool for monitoring biodiversity at large continuous spatial extents, chapter four and five presents wall-to-wall retrieval of spectral trait indicators over the vast and biodiverse Sabah region, Northern Borneo, Malaysia. Based on Sentinel-2 retrieved spectral trait indicators, the study mapped functional diversity estimates over the region's diverse landscape consisting of intact forests, logged forests, and oil-palm plantations. For qualitative assessment, the derived functional diversity maps were held against a human disturbance of land use, historic trait measurements, and across spatial scales. The remotely sensed functional diversity estimates based on Villeger’s (2008) metrics indeed reflected ecological expectations across land use (chapter 4), elevational gradients and spatial scale through functional richness-area relationships (Chapter 5). The qualitative assessment signalled a responsiveness of satellite remotely sensed functional diversity metrics to differences in land use and plot area size. However, the lack of quantitative error estimates limits our ability to draw conclusions beyond descriptive patterns. The spatially continuous nature of satellite remote sensing did lend itself particularly well for iterative multi-scale analyses of plant functional diversity estimates across increasingly large areas as representatives of differently sized functional communities which gives new insights in the role of spatial scaling in how we observe plant diversity patterns (section 6.2.1).

For future studies, a two-tier validation approach linking in-situ measurements with satellite remote sensing through airborne, unmanned aerial vehicles *(*UAV*)/*drone observations may facilitate validation campaigns that are more feasible in terms of spatial scales (Almeida et al., 2021b). Drones and other UAVs tend to present higher spatial resolutions, and therefore, may help serve as a bridge to scale up field observations to aggregated satellite remote sensing scales (Almeida et al., 2021b). In addition, the establishment of repeatedly sampled field laboratories such as the US National Ecological Observatory Network (NEON) (Kampe, 2010), the

Laegeren forest site in Switzerland (Morsdorf et al., 2020; Schneider et al., 2017), and the ‘Data pool initiative for the Bohemian Forest Ecosystem’ (Latifi et al., 2021). These sites can serve as natural biodiversity observatories presenting harmonized data pools for repeated detailed validation and training/calibration for optimizing retrieval algorithms.

## 6.2. Considerations of scale dimensions

Discussions of scale have a rich history in both ecology and remote sensing. Thus far, the majority of the literature on remote sensing of plant biodiversity relies on the use of 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). Rightfully so, higher spatial and spectral resolutions present more opportunities to assess plant canopies in detail. Nevertheless, this thesis has focused on the potential of currently available satellite remote sensing by a thorough examination of the use of Sentinel-2 for estimating functional and taxonomic diversity through spectral diversity and physics-based approaches. Integral to this is the examination of the spectral and spatial opportunities and limitations in capturing patterns of plant diversity. The derived findings hold new lessons on the effects of scale, relevant for its interpretation, and for guiding the future developments in satellite remote sensing for plant diversity observations.

### 6.2.1. Spatial scale and resolution

The spatial resolution of remote sensing instruments, i.e. pixel size, is shown to be highly influential but thus far mostly studied using airborne/drone remote sensing (Gholizadeh et al., 2019; Wang et al., 2018b). I encountered throughout the four research chapters that the coarse and geometric nature of pixel-based satellite remote sensing challenges traditional ecological interpretation. While Sentinel-2 provides improved spatial and spectral resolutions compared to most of its publicly available space-borne predecessors, its spatial resolution is still relatively coarse for ecological interpretations. With the majority of bands scaled at 10-20m spatial resolution, pixels observed from Sentinel-2 are too large for delineation of individual vegetation canopies. Even in the case of relatively large tree canopies, such pixels will aggregate several individual plants. Hence, individual trait observations such as those traditionally collected in the field are not easily compared to the satellite remote sensing spatial scale. Generally, each pixel will consist of multiple aggregated canopies inapt to delineate individual canopies, complicating straightforward interpretation of ecological measures of functional and/or taxonomic diversity that are traditionally based on diversity between individuals and/or discrete ‘communities’ of individuals (Laliberté et al., 2019; Schleuter et al., 2010). Additionally, pixel-wise aggregation of plant canopies does neither account for the effects of density of individual plants as an important variable related to diversity, nor for canopy size which affects the number of individuals aggregated within a pixel (Magurran, 2003; Zheng et al., 2021).

The challenges of scale become amplified when looking at diversity, given that a combination of multiple pixels is required to assess spectral or functional (information) entropy. Chapter three’s calculations were scaled at functional “communities” of 8 pixels covering pixel-based communities of 3200m$^2$. These geometric pixel-based clusters further raise challenges for ecological interpretation. In particular, what type of diversity are we looking at; alpha or beta-diversity? Clarifying and disentangling the combined and separate effects of α and β diversity on satellite-based observations is a remaining challenge. The disparity between remote sensing observations and the scale of individual organisms in field sampling muddles the separation of traditional additive α or β diversity. Not all individual differences will be captured given the coarseness of individual pixels while the community concept is arbitrarily captured through a cluster of pixels. Therefore, it remains unclear how much of the alpha diversity is captured through relatively coarse aggregations of multiple canopies. Some studies have simply assumed that every single pixel equals an ecological community (Hoffmann et al., 2019; Khare et al., 2021, 2019; Rossi et al., 2020). In the case of grasslands, for instance, such assumptions can be understood and/or justified given the small canopy crown size and a large number of canopies aggregated in a single pixel observation. However, for larger tree and shrub canopies, such assumptions are likely inadequate. Logically, the coarser the satellite spatial resolution compared to the grain and delineation of field data (i.e. in-situ canopies), the more spatial heterogeneity with sub-pixel plant diversity remains concealed (Khare et al., 2019; Rocchini, 2007). In other words, part of the alpha diversity is happening sub-pixel and is lost through pixel aggregation. At the same time, coarser resolutions and larger clusters of pixels are more likely to be composed of beta diversity.

Chapter five particularly looked into the role of area, i.e. the number of adjacent pixels, used to calculate functional diversity patterns over a large spatial extent covering Sabah, Malaysian Borneo. Firstly, the study confirms the common law that diversity increases with increasing area. Chapter five is novel in demonstrating this through satellite remote sensing observations, estimating functional diversity based on spectral trait indicators at large observational scales ranging from 0.4 to 60 ha single land use plots. The curvature of the functional richness-area relationship (FARs) reveals a pattern typically found in field and airborne studies conducted at much smaller scales (Durán et al., 2019; Karadimou et al., 2016; Schneider et al., 2017; Smith et al., 2013). The curvature follows exponential increases up to 5ha plots. From 10ha plots onwards, increases in diversity shift from exponentiality to linearity. The fast increases observed at small scales may be attributable to high variation in stochastic species occupancy patterns among sampling units, and variation through species responses to competition and niche occupancy. Such shapers of variation are commonly attributable to alpha diversity drivers (Field et al., 2009).

At larger sampled scales (> 5ha), increases of diversity per area attenuate leading to saturation in variation. Particularly at larger scales, a larger share of the explained variance could be explained by landscape heterogeneity, for which I used morphology (slope and elevation) as an indicator. The increasing explanatory role of landscape morphology at bigger (intermediate) scales suggests the increasing importance of beta diversity drivers that require communities to adapt to different environmental conditions (Barton et al., 2013; Weiher and Keddy, 1995). In combination, chapter five shows how discrete concepts of alpha and beta diversity are expressed in a continuous transition when observed from spatially explicit satellite remote sensing. This challenges the applicability of discrete alpha and beta concepts and raises the question of whether we need new more continuous concepts, and illustrates how multi-scale analyses can unveil the compound role of different drivers at different spatial scales.

In our analyses across the four research chapters, the pixel size remained invariant at 20m spatial resolution following the majority of Sentinel-2 bands. For future development and application of satellite remote sensing, it is important to increase understanding of how both grain (spatial resolution) and the number of pixels (spatial ‘window’, plot area to capture a ‘community’, chapter 5) in functional diversity assessments done from space-borne instruments affect the patterns observed. This requires expanding the analysis of chapter five by including both variant pixel sizes and the number of pixel observations for remotely sensed functional diversity estimates. Various combinations of changing grain and plot area (changing grain while maintaining plot area, changing plot area while maintaining grain, changing grain and plot area) could be examined to explore scaling relationships like discussed conceptually by Barton et al. 2013.

In terms of spatial extent, future attempts can be expanded to the scales of cross-biome and latitudinal gradients by mosaicking images and data assimilation principles to overcome cloud cover and temporal mismatches (Lahoz and Schneider, 2014; Lewis et al., 2012). Satellite remote sensing of plant diversity over large spatial extents (cross-biomes and continental) could help allow us to validate and calibrate large-scale ecological models of biodiversity with observational data.

In terms of grain, the integration of multi-platform remote sensing, most notably drones, can be valuable to inform on the sub-pixel heterogeneity not captured at satellite earth observation scales (Almeida et al., 2021b). Additionally, even within the capacity of Sentinel-2, recent developments relying on pan-sharpening, Bayesian frameworks and machine learning techniques have resulted in algorithms to enhance or resolve Sentinel-2’s spatial resolution (Brodu, 2017; Lanaras et al., 2018). Rather than resampling all bands to 20m for spatial consistency as done in our current analyses, future studies could explore either Sentinel-2’s original four 10m bands or a super-resolved spatial resolution of 10m across all bands (e.g. Brodu, 2017) to assess (artificially) enhanced spatial resolution to capture sub-pixel (20m) heterogeneity. Fig. 6.2 provides an example of such a potential analysis. In this preliminary analysis, 10m resolved bands did not significantly differ in terms of prediction of our in-situ measurements of taxonomic diversity. Still, resampling at 10m would offer advantages for validation as representative sampling campaigns become more manageable at 10m plots.

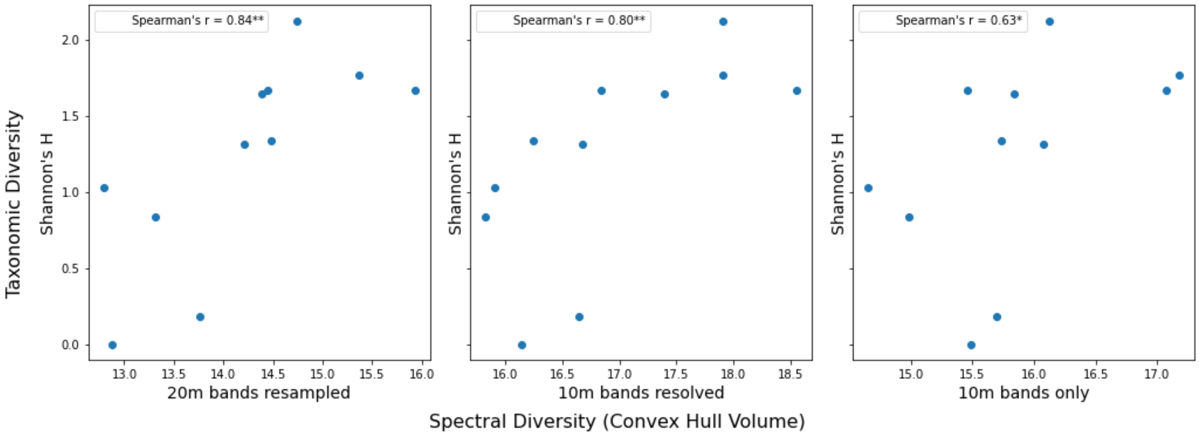


*Fig. 6.2: Preliminary analysis examining the relationship between spectra diversity calculated by convex hull volume to predict in-situ taxonomic diversity (Shannon’s H) measured in the Montesinho (PT) national*

*park region across three different spatial-spectral configurations derived from Sentinel-2 observations; i) nine resampled 20m bands (left), ii) nine resolved 10m bands (following Brodu et al., 2017) (middle), iii) and four original 10m bands.*

### 6.2.2. Spectral resolution

Approaches for optical detection of plant diversity, i.e. spectral diversity (chapter two), physics-based approaches (chapters 3-5), depend on the information content of the spectra themselves. The spectral layout of sensors can influence plant diversity detection in complex ways (Nagendra et al., 2010; Rocchini, 2007). Therefore, attention is required to how the spectral resolution and spectral range of the instruments influence the derived observations. Both chapters two and three suggest that the Sentinel-2 sensor's multispectral broadband setup may increase the dominance of canopy, soil, and biomass signals as opposed to expressions of biochemical and biophysical leaf traits found in narrower ranges of the electromagnetic spectrum that benefit from hyperspectral measurements (Durán et al., 2019; Schneider et al., 2017; Schweiger et al., 2018).

The forthcoming launch of hyperspectral satellite imagers (e.g. EnMAP, SBG, CHIME; Cavender-Bares et al., 2020) offers more spectral detail and versatility that can benefit plant diversity assessments. For instance, satellite-based imaging spectroscopy offers new potential to retrieve traits that are hard to detect from multi-spectral setups, such as leaf and canopy contents of nitrogen (Verrelst et al., 2021), anthocyanin, anthocyanin, carotenoid content, and carbon-based constituents (Féret et al., 2021). Additionally, hyperspectral observations potentially offer additional input information to improve the ill-posedness experienced in the inversion of RTMs using few multi-spectral bands. Hyperspectral imaging might offer benefits for spectral diversity approaches too; the few studies conducted on spectral resolution and plant biodiversity thus far state that more spectral information is generally better than less (e.g., Asner et al. 2012).

On the other hand, hyperspectral imagery is not always significantly better. Hyperspectral narrowbands tend to be highly correlated resulting in high redundancy in spectral information (Hakkenberg et al., 2018). Rocchini (2017) concluded that more bands are not necessarily better but the placing of bands is crucial as the study shows that ASTER images, having a better spectral resolution, yielded worse results than LandSAT images, in estimating species diversity. Using airborne remote sensing, Lu et al. (2019) concluded that the extra bands in the hyperspectral image did not substantially improve chlorophyll estimation in vegetation. Gholizadeh et al. (2019) showed that the standard deviation of NDVI (two bands) performs well among other spectral diversity metrics (multi- and hyperspectral derivatives). Wang et al. (2018b) found no additional benefit of using full-range spectrometer data in quantifying plant diversity versus dimension reduction techniques. Using UAV imagery, Rossi et al. (2021) stress the overriding importance of high spatial resolution in comparison to high spectral resolution in predicting plant diversity using spectral diversity metrics. Across these studies the spatial resolution appears the limiting factor. Spectral resolution does affect the spectral diversity-biodiversity relationship, yet higher spectral resolutions cannot replace or compensate for the lack of high spatial resolution (Gholizadeh et al., 2019; Rocchini, 2007; Rossi et al., 2021; R. Wang et al., 2018a).

Current momentum emphasizes the development of hyperspectral sensors and the need for satellite-based imaging spectroscopy (Ustin and Middleton, 2021). Due to technical constraints, a trade-off exists between spatial and spectral resolution to ensure adequate signal-to-noise ratios which determines the sensor design of space-borne instruments (Rossi et al., 2021). The planned hyperspectral satellite missions present sensors with 30m spatial resolution at best, slightly worse than Sentinel-2 (10-20m). With an eye on the application for biodiversity studies, the question arises whether a tradeoff to more spectral resolution and less spatial resolution is the most beneficial investment for mapping plant diversity.

Research chapters two to five reveal that Sentinel-2's relatively simple multi-spectral and 20m spatial resolution can predict coarse community plant diversity patterns, even despite strong assumptions in retrieval algorithms, and challenging interpretation of mixed alpha and beta diversity. While Sentinel-2's spectral capabilities allowed for an estimation of multivariate functional diversity and spectral covariates of taxonomic diversity, this thesis highlights that interpretation and validation of these diversity patterns is challenged by especially its spatial resolution. To advance the detection of plant diversity from space and advance beyond Sentinel-2's capabilities, smart trade-offs are needed to facilitate continuous improvements in both spectral resolution and spatial resolution (working towards <5-10m resolution). Therefore, with eyes on mapping plant biodiversity, an overemphasis on hyperspectral sensors may be unwanted. Rather, we should seek technical trade-offs that lead to spectral advances without compromising the spatial resolution. At the same time, data assimilation techniques and multi-sensor constellations will continue to advance and open new venues to combine the strengths of space-borne hyperspectral imagers to complement pre-existing multi-spectral sensors and future high spatial resolution sensors.

### 6.2.3. Temporal dimension

Satellites in orbit offer the advantage of frequent revisit times. In the case of the Sentinel-2a/b constellation, inferences of the same region of interest can be as frequent as every five days. These repeated measurements offer the potential to closely study changes and dynamics over time as well as the phenology of traits and the diversity thereof. Within the four research chapters of this thesis, the temporal element of mapping functional diversity has unfortunately not been analyzed. Yet, obviously, ecological processes are subject to microclimatic properties, phenology, management strategies, grazing, or nutrient availability that occur over the course of time and seasons. Ultimately, when working towards the maturation of approaches in mapping plant diversity through satellite remote sensing, we need to account not only for spatial patterns but also temporal spectral variation.

Plant diversity is shaped by temporal trends and dynamics. Single inferences in time are simply a snapshot and are inferior to more robust multi-temporal assessments and time series to capture spectrally-derived estimations of plant diversity patterns. Time series analysis will improve the confidence in patterns observed through temporal cross-validation and can overcome temporal fluctuations in noise and retrieval accuracies (Hauser et al., 2020). Moreover, combining temporal observations can help us overcome cloud, cloud shadow and atmospheric contamination often encountered in optical imagery. The assimilation of multi-temporal observations, potentially combined with ancillary ecological, and phenological datasets, will enable us to study changes in functional diversity over time while overcoming data gaps and inference intervals (e.g. gap-filling approaches such as implemented by Belda et al., 2020). Ultimately, temporal dynamics will be a key factor in understanding changes in plant (functional) biodiversity.

Temporal variability also influences our ability to capture relevant elements of plant diversity from spectral reflectance. For spectral trait indicators, Schiefer et al. (2021) show that accuracies vary during the growing season for both RTM-based and statistical (Partial Least Squares Regression) retrieval. The study concludes that for the application of PROSAIL, the highest accuracies are reached when canopy conditions are closest to the model assumptions. Therefore, the RTM traits were better estimated towards the middle or end of the growing season when plant canopies were fully developed and corresponded most to a turbid medium. The exception is LAI which is better retrieved at the beginning of the growing season as dense canopies suffer from saturation effects for LAI retrieval. These findings could be relevant for the retrieval accuracies presented in Chapter 3.: which marked superior retrieval of LAI compared to leaf chlorophyll conducted before the peak of the growing season (early-mid June). It remains to be seen how fluctuations in temporal accuracy will affect functional diversity metrics as distance-based calculations exhibit a degree of robustness against structural biases (Chapter 3.:).

These findings are also relevant for estimating plant diversity through the ‘spectral variability hypothesis’. Denser ecosystem types tend to allow for multiple-scattering, enhancing the contribution coming from leaf-level biochemical and biophysical information within canopy scale reflectance (Asner, 1998; Baret et al., 1994). Temporally, this could translate to a superior ability to pick up leaf traits and the diversity thereof during seasonal peak biomass. In line with this, in Torresani et al. (2019)’s temporal study in an alpine conifer forest, the highest correlations between spectral diversity and in-situ plant diversity were found at the peak of the growing season in June and July.

## 6.3. Future outlook

Crisis-level losses of biodiversity are requiring action right now. To protect the ecosystems on which our lives depend, public and private commitments have been voiced to halt current declines as evidenced by the establishment of the Aichi targets and the post-2020 Convention on Biological Diversity (CBD) (IPBES, 2019; Skidmore et al., 2021). Nevertheless, significant challenges currently remain to monitor progress towards commitments, and to quantify the impact of human actions and interventions from local to global scales (Pettorelli et al., 2016). For countries to deploy cost-effective systems to monitor the post-2020 goals and targets, the integration of satellite remote sensing with models will be essential. Satellite earth observation approaches can fill data gaps, facilitate transparency, open-source data access, and repeatable workflows (Latifi et al., 2021).

Plant functional and taxonomic diversity observations from space have the potential to provide a global context for biodiversity research, and link plant diversity at local scales to ecosystem functioning around the globe (Jetz et al., 2016; Rocchini et al., 2015). Moreover, such observations would help map spatio-temporal plant biodiversity dynamics in relation to human interventions. Despite the anticipation of future satellite missions, research on currently operational sensors cannot be overlooked, especially considering the urgency of current biodiversity declines, and the value of such research as a learning curve for the development of future sensors and methodologies. The quantitative and qualitative assessments of this thesis outline the capabilities and opportunities for assessing plant biodiversity from space using Sentinel-2, while acknowledging spectral and spatial limitations and implications for the ecological interpretation.

These limitations affect the patterns we can and cannot observe and the confidence margins that are realistically possible. A more detailed understanding of how spectral, temporal, and spatial resolutions affect our capability to monitor plant diversity from space is still needed and can be achieved through multi-sensor or multi-platform analyses. Furthermore, a wider range of validation campaigns is needed to assess the robustness of different spectral approaches across different ecosystem types and scales and to facilitate the propagation of uncertainties of plant diversity estimates. Quantitative approaches (Chapter 3.:) are more difficult to acquire, yet more valuable than qualitative assessments (Chapter 4).

The importance of data assimilation has been highlighted in this discussion chapter. To overcome shortcomings, data gaps, signal-to-noise ratios, and trade-offs between different sensors, we need to advance towards the assimilation of multi-sensor, multi-temporal, multi-scale remote sensing observations. Similarly, data assimilation and gap-filling will need to look beyond the horizon of earth observation datasets. The ingestion of in-situ trait/taxonomic measurements, innovative techniques (e.g. eDNA), and ancillary environmental and phenological datasets can help us to study changes in plant biodiversity across hierarchical levels and over space and time. Ultimately, temporal and spatial continuity is a key factor in understanding changes in plant biodiversity.

The thesis also highlights that different operationalization and workflow choices will impact the observed patterns of plant diversity. Academics have proposed 'Essential Biodiversity Variables (EBVs)' to help structure and harmonize biodiversity monitoring globally (Skidmore et al., 2021; Pereira et al., 2013). Satellite remote sensing has been designated as an important instrument for the derivation of a selection of EBVs. Indeed, satellite remote sensing EBVs (SRS-EBVs) have been conceptualized as the subset of EBVs whose monitoring relies largely or wholly on the use of satellite-based data (Jetz et al., 2016; Pettorelli et al., 2016). However, so far, there has been little agreement on what these SRS-EBVs should be and what reproducible workflows are needed (Skidmore, 2015).

For the metrics used in this thesis to be included within a suite of SRS-EBVs, agreement on reproducible workflows is important (Skidmore, 2015). Justified and well-understood decisions underlie the design of such workflows and metrics. This thesis exemplifies the importance of underlying decisions; what sensors to use, what scales to apply, what traits to consider, what inversion and retrieval algorithms to run. This thesis also reveals that a degree of robustness and 'surrogacy' occurs in terms of scale (taxonomic versus functional), metrics (spectral diversity versus functional diversity), and inversion algorithms. Extrapolation of the findings is still needed at a cross-ecosystem scale. In terms of scaling up current efforts to global observations, cloud computing infrastructures, e.g. Google Earth Engine and DIAS, will play a key role when combined with the aforementioned data assimilation principles into harmonized workflows (Campos-Taberner et al., 2018; Moreno-Martínez et al., 2018). Moreover, further test cases are necessary to assess the sensitivity and suitability of plant diversity metrics to study ecological phenomena and gradients, and including; community assembly (chapters 4-5), elevation (Durán et al., 2019, chapter 4), productivity (Durán et al., 2019), post-fire recovery (chapters two and three), invasive species (Khare et al., 2021, 2019), protected areas, rewilding and legislative efforts (Lausch et al., 2016).

To further understanding on the human impact on plant biodiversity, environmental footprints of human intervention and consumption are becoming increasingly relevant (Marques et al., 2017). Chapter four has shown distinct patterns between land use types (oil-palm plantations versus logged and intact forests) in terms of plant functional diversity observed from Sentinel-2 spectral reflectance. These findings are relevant given that land use change for agricultural expansion like oil-palm remains the most detrimental driver of biodiversity declines (IPBES, 2019). Agricultural expansion serves human consumption and is largely driven global commodity supply chains. A fundamental modelling technique to evaluate and quantify environmental impacts of products, processes or services across entire supply chains is Life Cycle Assessment (LCA; e.g. Guinée and Lindeijer, 2002). LCA models can help quantify the impact of human consumption on biodiversity, yet current methodologies are hampered by data gaps and quality relying on highly aggregated, limited, and static characterization factors (Ahmed et al., 2018; Chaudhary et al., 2015; Curran et al., 2016).

Current state-of-the-art LCA modelling approaches that seek to evaluate the biodiversity impacts of human consumption through commodities and sourcing regions tend to rely on (self-disclosed) national or regional characterization of species losses as model input through classification schemes based on land use (Jaroenkietkajorn et al., 2021) or ecoregions (Olson et al., 2001). The implemented datasets require spatio-temporal interpolation, use one or few key indicative taxa, and tend to rely on heavy assumptions for extrapolation across large spatial extents (Winter et al., 2017). Satellite-based estimates of plant diversity could complement current model input simplifications with considerably more spatial detail, overcome field inconsistencies among observers (Takashina and Economo, 2021), and provide global representativeness in observational data (Rocha et al., 2021). Local and spatially explicit estimates of plant diversity from satellite remote sensing would allow for local characterization of plant diversity impacts as opposed to regional or national aggregates. Moreover, local characterization can go beyond taxonomic indicators and include estimated plant functional diversity impacts which tend to respond more consistently to environmental drivers (Ahmed et al., 2018; de Souza et al., 2013; Scherer et al., 2020).

Similarly, accurate characterization of plant functional diversity for Earth system models would greatly improve our ability to model and understand the effects of global change on the cycling and storage of carbon, water, energy, and ecosystem functioning (Serbin et al., 2019). However, current analyses are hampered by data gaps and the use of aggregated, interpolated, and third-party data (e.g. IUCN threat categories or indicator species inventory data) which is overly coarse, taxonomy-dominated, high-level aggregated, and/or not spatially explicit. Over time, with growing validation and methodological improvements, satellite remote sensing estimates of plant functional diversity can address major data gaps, contribute to posterior models, and overcome the widespread lack of national biodiversity monitoring systems. Specifically, once spatially explicit and validated land use impacts on plant biodiversity can be mapped confidently, we can integrate these estimates in models to quantify the impacts of human intervention and consumption (de Souza et al., 2013).

## 6.4. Conclusions

This thesis addressed current knowledge gaps in remote sensing applications for studying large-scale terrestrial plant diversity patterns regarding the understudied role of currently operational satellite earth observation and physics-based methods to estimate plant functional diversity patterns. The analyses presented relied on Sentinel-2's multispectral imager and reveal a promising ability to estimate plant diversity from physics-based RTM inversion for functional diversity as well as based on spectral diversity metrics for taxonomic diversity.

Validity of both was tested empirically against in-situ field measurements on taxonomic and functional plant diversity derived from a dedicated field campaign scaled to Sentinel-2's pixel-based raster as well as against large-scale gradients of land use, elevation and spatial scaling. The approximation of the satellite-based estimates to actual in-situ plant diversity suggests a sufficient spectral differentiation in Sentinel-2's broadband multi-spectral lay-out supportive of estimating functional/taxonomic diversity across aggregate plant canopies and the traits studied. A degree of robustness was observed in the distance-based diversity metrics deployed, in particular the Convex Hull Volume, to quantify the information entropy found in the observations. These metrics were not impaired by the observed estimation errors and biases found in the different RTM inversion methods or the signal-to-noise ratios of remote sensing observations but remained relatively effective in estimating plant diversity patterns.

The 'spectral variability hypothesis' when tested with Sentinel-2 in the presented case study held its presumed validity in estimating coarse taxonomic plant diversity patterns. However, the application of spectral diversity metrics will require caution given the potentially strong (orthogonal) dominance of vegetation cover, i.e. canopy architecture and density, over functional and taxonomic diversity in spectral diversity signals. Therefore, methods that can isolate functional and taxonomic diversity in the spectral signal are preferred despite generally requiring a more complex data processing chain. Functional and taxonomic diversity based on RTM inversion of spectral observations allowed for a two-fold validation of both the estimated individual plant traits as well as the diversity thereof. Using three different inversion techniques, the findings suggest a promising performance in estimating plant functional and taxonomic diversity based on three RTM-derived plant traits (LAI, LMA, and CAB). Inversion techniques that allow for locally optimized trait ranges performed best in the analyses exhibiting a 20-21% (nRSME) deviation and a strong rank-based relationship (Spearman's ρ: 0.76-0.80) to plant functional richness (CHV) patterns.

The PROSAIL RTMs implemented in the retrieval techniques offer a simplified representation of heterogeneous canopies. Therefore, future improvements in the accuracy of plant functional diversity estimates may be achieved by RTMs better-equipped to the ecosystems under study, or the use of more versatile hybrid inversion methods such as the implementation of active learning heuristics and deep learning. A major advantage of the presented physics-based methods lies in its foundation in the universal principles of light-vegetation interaction which should theoretically be scalable and applicable across ecosystems types without a heavy reliance on a priori field measurements or ancillary data. However, its actual scalability across different study sites, ecosystems and vegetation types remains to be thoroughly tested, preferably at large continuous scales.

The spatial scaling of Sentinel-2 at 20m spatial resolution leads to challenges in how to apply and interpret plant diversity patterns observed. Its spatial resolution is ill-equipped to delineate individual canopies. Instead, it presents an aggregation of individual species and canopy traits at rasterized scales that are difficult to validate in the field given its size, geometry, and mixing of canopy and background signals. This aggregation leads to a mixing of both alpha and beta diversity scales that are traditionally instrumental to the ecological interpretation of spatial plant diversity patterns. Future studies that seek to overcome such challenges may want to rely on multi-sensors integration. For instance, two-tier validation using drones can aid field validation campaigns with spatial scales that are more feasible to match on the ground. Moreover, multi-sensor approaches can offer adaptability to address the spatial irregularities found in ecological phenomena, including the heterogeneous canopy sizes found in ecosystems and abstract ecological community sizes to which coarse satellite-based rasterized pixels are ill-equipped and single sensors applications lack versatility.

The spatial continuity or spatial explicitness of satellite inference offers an unprecedented readiness to conduct analyses of diversity patterns across a wide range of multiple scales. The multi-scalar analyses presented in this dissertation illustrate the gradual transition of what are traditionally considered separate drivers of alpha versus beta diversity while omitting the need for arbitrary decisions of a fixed optimal plot area. Subsequently, these findings question whether the traditional ecological focus of discrete ‘within’ versus ‘between’ community diversity (alpha vs beta) should be maintained or whether we need new more continuous concepts.

Further validation of plant diversity estimates from satellite remote sensing will remain necessary with the inclusion of large sample sizes, more ecosystem and vegetation types, a wider range of traits to ensure adequate functional differentiation and multi-temporal analyses. With growing adequate validation, ongoing advances in sensors, and methodological improvements, the large-scale repeated and spatially explicit monitoring of plant diversity patterns through remote sensing techniques is going to become an integral part of global biodiversity observatory systems and planetary models to quantify our impacts and monitor Earth’s ecological healthspan.

# Chapter 7.: Supplementary Materials

*Fig. S. 1. Field photography illustrative of different locations and land use types*

Forested land use (Oak forest: left, Mixed pine forest: right)

Shrubland (Mixed with Holm oak: left, Cistus spp. shrubs: right)

Chestnut Plantations (managed: left, abandoned: right)

## S. 2: Cross-validation of Plant Area Index

We cross-validated the Plant Area Index (PAI) measurements from hemispherical photography with above and below canopy measurements taken with Photosynthetically Active Radiation (PAR) sensor (Apogee MQ-301; handheld device), quantifying the relative quantity of incident solar radiation absorbed by vegetation. PAR measurements were taken above and below the canopy to calculate the canopy absorbed light. A strong correlation was been found between PAR measurements and the PAI derived hemispherical photography. PAR measurements, however, did show high susceptibility to cloud cover and changing weather conditions resulting in a number of outliers as also indicated by Garrigues et al. (2008).

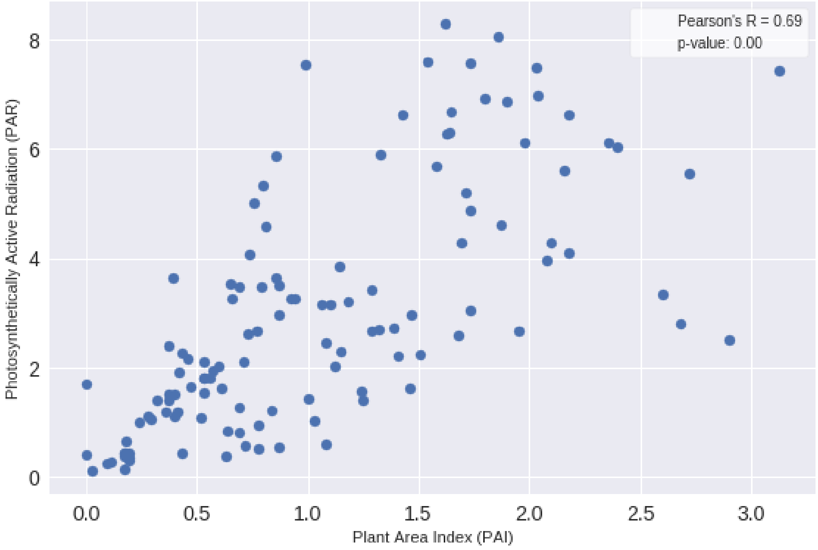


*Fig. S. 2a: Comparison of Plant Area Index (PAI) measurements derived from hemispherical photography against Photosynthetically Active Radiation (PAR) measurements.*

Further cross-validation was performed through comparison of PAI measurements against the fraction of vegetation/soil through spectral unmixing. Spectral unmixing was conducted using the HSDAR package in R (Lehnert et al., 2018). The principles behind the linear spectral unmixing approach are based on Sohn and McCoy (1997). Two endmember signals were considered in the unmixing exercise; the in-situ soil spectral reflectance, and the leaf spectral reflectance signals generated by running the PROSPECT RTM in forward mode based on in-situ measured field traits. To facilitate the former, we collected handheld hyperspectral reflectance data of representative soils in the study area using the RS-3500 spectroradiometer (350-2500 nm, 8 nm resolution) developed by Spectral Evolution.

The spectral unmixing analysis resulted in a fraction (%) of leaf vegetation signal, a fraction (%) of the soil spectral signal and an ‘error’ signal (%) that may indicate that endmember spectra do not fit well to the predefined endmember spectra. The fraction of vegetation was used to cross-validate the Plant Area Index measurements as an indicator of the vegetation density. As expected, high PAI strongly correlates with a high fraction of vegetation, inversely this results in a negative correlation with the fraction of soil in the spectral signal.

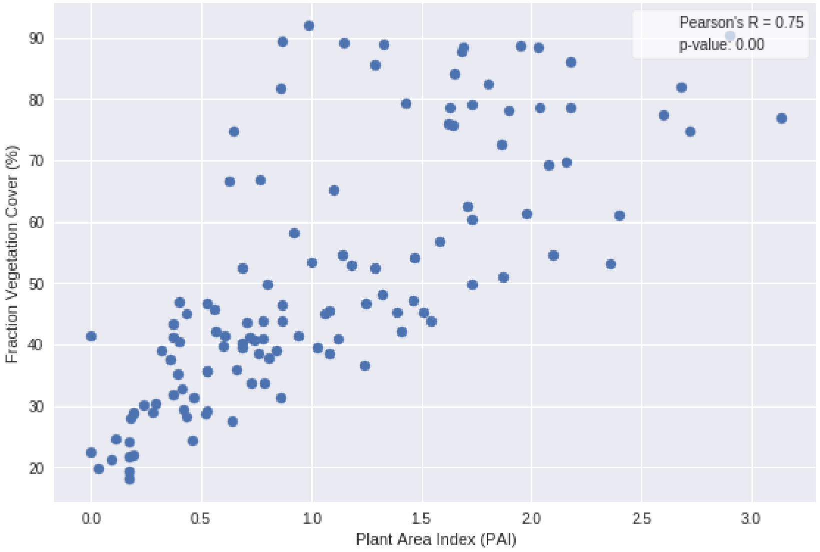


*Fig. S. 2b: Comparison of Plant Area Index (PAI) measurements derived from hemispherical photography against Fraction of Vegetation Cover (%) derived from spectral unmixing*

*Table S. 3: Spectral characteristics of the Sentinel-2 bands used*

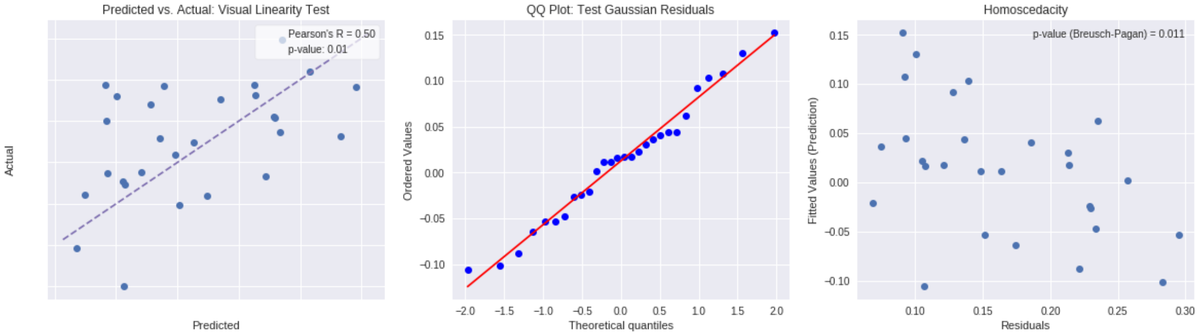
| Acronym | Central (nm) | Width (nm) | Spatial resolution (m) |
|---|---|---|---|
| B2 | 490 | 65 | 10 |
| B3 | 560 | 35 | 10 |
| B4 | 665 | 30 | 10 |
| B5 | 705 | 15 | 20 |
| B6 | 740 | 15 | 20 |
| B7 | 783 | 20 | 20 |
| B8a | 865 | 20 | 20 |
| B11 | 1610 | 90 | 20 |
| B12 | 2190 | 180 | 20 |

*Table S. 4: Overview of the configuration of input parameters using in PROSAIL-simulated spectral diversity which includes the two SAIL implementations; with fixed parameters and with variable (Genetic algorithm-optimized) parameter values.*

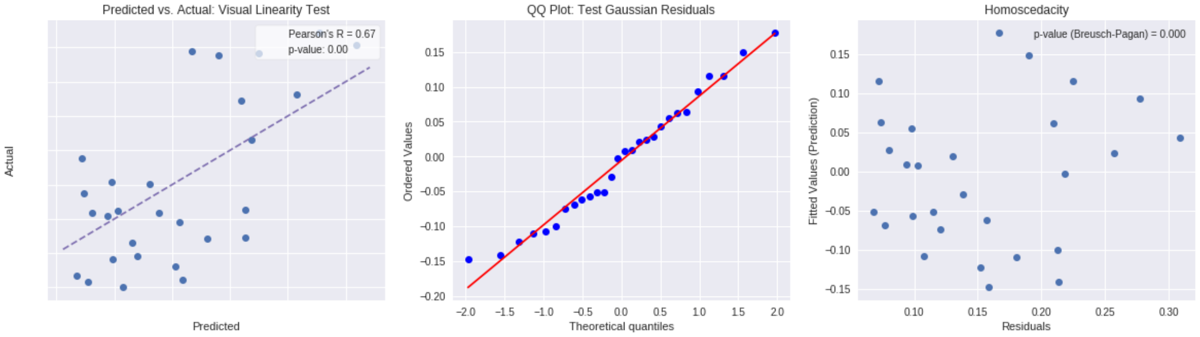
| Model | Parameter | Unit | Implementation: Fixed SAIL parameters | Implementation: Variable SAIL parameters |
|---|---|---|---|---|
| PROSPECT | Leaf structure | - | Fixed: 1.6 | Fixed: 1.6 |
|  | Chlorophyll a+b | ug/cm$^2$ | In-situ measurements | In-situ measurements |
|  | Carotenoids | ug/cm$^2$ | In-situ measurements | In-situ measurements |
|  | Equivalent water thickness | g/cm$^2$ | In-situ measurements | In-situ measurements |
|  | Dry matter content | g/cm$^2$ | In-situ measurements | In-situ measurements |
|  | Brown pigment | - | Fixed: 0.01 | Fixed: 0.01 |
| SAIL | Leaf area index | m2 / m2 | In-situ measurements: PAI-derived | In-situ measurements: PAI-derived |
|  | Average leaf angle | o | Fixed: Planophile | Search range: 20-85 |
|  | Hotspot | - | Fixed: 0.01 | Fixed: 0.01 |
|  | Dry/wet soil ratio | - | Fixed study area soil reflectance | Search range: 0-1 |
|  | Soil brightness | - | Fixed study area soil reflectance | Search range: 0-2 |
| Positional | Solar zenith | o | Sentinel-2 derived | Sentinel-2 derived |
|  | Observer zenith | o | Sentinel-2 derived | Sentinel-2 derived |
|  | Relative azimuth | o | Sentinel-2 derived | Sentinel-2 derived |

*Fig. S. 5: Review of assumptions for linear mixed-effect regression analyses: Linearity, Normality of residuals, Homoscedasticity*

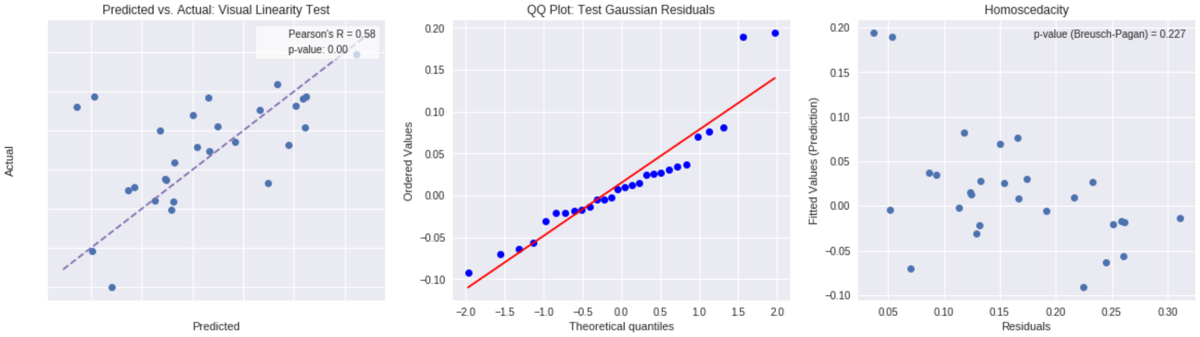
Trait Diversity - Convex Hull



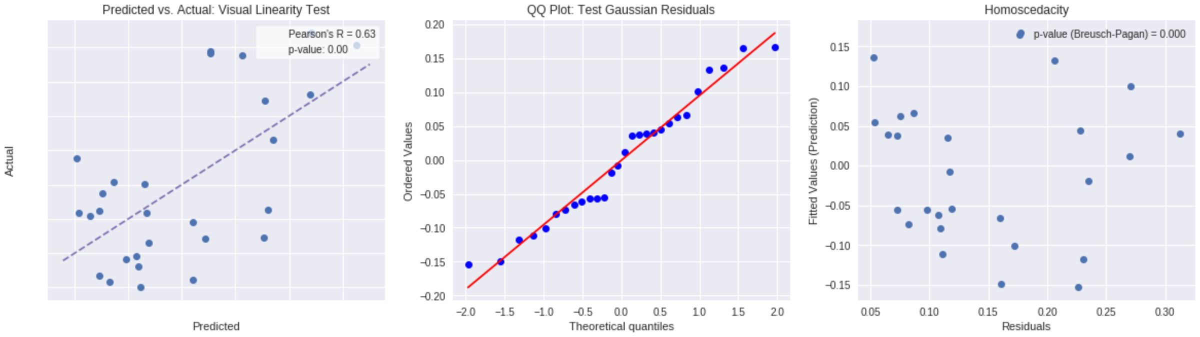
Trait Diversity - Rao's Q



Shannon's H - Convex Hull



Shannon's H - Rao's Q



## S. 6: Linear mixed-effect models; the role of plant diversity, vegetation cover, and landscape morphology in explaining Sentinel-2 spectral diversity observations

*Table S. 6a: Linear mixed-effect model summary and relative weights analysis with spectral diversity calculated based on the Convex Hull Volume (CHV) as the dependent variable and vegetation cover, landscape morphology, and CHV-based calculation of trait diversity as predictors, while location is set as the random effect. τ00 - random factor intercept variance (i.e. between-subject variance of the location), ICC – random factor intraclass correlation coefficient*

| | | **Spectral Diversity (CHV)** | | | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *β* | *p* | *VIF* | *Relative weights* |
| (Intercept) | 0.10 | 0.01 – 0.19 | **0.00** | **0.035** | - | - |
| Trait diversity (CHV) | 0.16 | -0.19 – 0.51 | 0.19 | 0.332 | 2.60 | 6.36 |
| Vegetation Cover | 0.95 | 0.19 – 1.72 | **0.59** | **0.019** | 1.29 | 84.46 |
| Landscape Morphology | 0.72 | -0.60 – 2.03 | 0.24 | 0.254 | 2.19 | 9.18 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.00 | | | | | |
| $\tau_{00\ \text{Location}}$ | 0.00 | | | | | |
| ICC | 0.00 | | | | | |
| $N_{\text{Location}}$ | 14 | | | | | |
| Observations | 28 | | | | | |
| $R^2_{\text{Marginal}}$ / $R^2_{\text{Conditional}}$ | 0.221 / 0.221 | | | | | |

*Table S. 6b: Linear mixed-effect model and relative weights analysis summary with spectral diversity calculated based on the Rao's quadratic entropy (Rao's Q) as the dependent variable and vegetation cover, landscape morphology, and Rao's Q-based trait diversity as predictors, while location is set as the random effect. τ00 - random factor intercept variance (i.e. between-subject variance of the location), ICC – random factor intraclass correlation coefficient*

| | **Spectral Diversity (Rao's Q)** | | | | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *β* | *p* | *VIF* | *Relative weights* |
| (Intercept) | -0.04 | -0.16 – 0.08 | 0.00 | 0.508 | - | - |
| Trait diversity (Rao's Q) | 0.25 | -0.12 – 0.62 | 0.24 | 0.161 | 1.71 | 5.83 |
| Vegetation Cover | 2.07 | 0.86 – 3.29 | **0.73** | **0.003** | 1.20 | 63.23 |
| Landscape Morphology | 2.90 | 0.72 – 5.08 | **0.56** | **0.014** | 1.52 | 30.93 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.01 | | | | | |
| $\tau_{00\ \text{Location}}$ | 0.00 | | | | | |
| ICC | 0.18 | | | | | |
| $N_{\text{Location}}$ | 14 | | | | | |
| Observations | 28 | | | | | |
| $R^2_{\text{Marginal}}$ / $R^2_{\text{Conditional}}$ | 0.400 / 0.507 | | | | | |

*Table S. 6c: Linear mixed-effect model summary and relative weights analysis with spectral diversity calculated based on the Convex Hull Volume (CHV) as the dependent variable and vegetation cover, landscape morphology, and Shannon's H taxonomic diversity as fixed effect predictors, while location is set as the random effect. τ00 - random factor intercept variance (i.e. between-subject variance of the location), ICC – random factor intraclass correlation coefficient*

| | | **Spectral Diversity (CHV)** | | | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *β* | *p* | *VIF* | *Relative weights* |
| (Intercept) | 0.10 | 0.04 – 0.16 | **0.00** | **0.003** | - | - |
| Shannon's H | 0.24 | 0.02 – 0.45 | **0.40** | **0.032** | 2.19 | 42.24 |
| Vegetation Cover | 0.86 | 0.20 – 1.52 | **0.53** | **0.015** | 1.28 | 52.98 |
| Landscape Morphology | 0.53 | -0.67 – 1.73 | 0.18 | 0.354 | 1.84 | 4.78 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.00 | | | | | |
| $\tau_{00\ \text{Location}}$ | 0.00 | | | | | |
| ICC | 0.00 | | | | | |
| $N_{\text{Location}}$ | 14 | | | | | |
| Observations | 28 | | | | | |
| $R^2_{\text{Marginal}}$ / $R^2_{\text{Conditional}}$ | 0.342 / 0.342 | | | | | |

*Table S. 6d: Linear mixed-effect model summary and relative weights analysis with spectral diversity calculated based on the Rao's quadratic entropy (Rao's Q) as the dependent variable and vegetation cover, landscape morphology, and Shannon's H taxonomic diversity as fixed effect predictors, while location is set as the random effect. τ00 - random factor intercept variance (i.e. between-subject variance of the location), ICC – random factor intraclass correlation coefficient*

| | **Spectral Diversity (Rao's Q)** | | | | | |
|---|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *CI* | *β* | *p* | *VIF* | *Relative weights* |
| (Intercept) | 0.01 | -0.11 – 0.13 | 0.00 | 0.916 | - | - |
| Shannon's H | 0.11 | -0.32 – 0.54 | 0.16 | 0.585 | 2.19 | 2.98 |
| Vegetation Cover | 1.81 | 0.48 – 3.13 | **0.63** | **0.012** | 1.28 | 66.53 |
| Landscape Morphology | 2.39 | -0.03 – 4.82 | 0.46 | 0.053 | 1.84 | 30.49 |
| **Random Effects** | | | | | | |
| $\sigma^2$ | 0.01 | | | | | |
| $\tau_{00\ \mathrm{Location}}$ | 0.00 | | | | | |
| ICC | 0.33 | | | | | |
| $N_{\mathrm{Location}}$ | 14 | | | | | |
| Observations | 28 | | | | | |
| $R^2_{\mathrm{Marginal}}$ / $R^2_{\mathrm{Conditional}}$ | 0.327 / 0.552 | | | | | |

## S. 7. Isolating biodiversity signals in spectral diversity

Spectral diversity approaches tend to circumvent the challenges and difficulties in isolating direct biodiversity signals, e.g. functional traits or species discrimination, in the spectral signal. This makes spectral diversity relatively straightforward to deploy. However, as shown here, the approach risks the spectral diversity signal to be dominated by other factors and, in the end, only poorly relate to in-situ plant diversity. Our ability to account for spectrally dominant confounding factors, such as vegetation cover, could improve the robustness and relationship of spectral diversity approaches to in-situ plant diversity across spatial, spectral, geographic, and temporal resolutions. We suggest three main techniques that can be integrated or complement spectral diversity indices to control for components of vegetation cover including the abundance of soil signals, variation in vegetation density, and canopy architecture (morphological traits) in multispectral satellite-based observations. These techniques include spectral unmixing techniques, radiative transfer model inversion, and data fusion (Musavi et al., 2015).

The separation of the soil signal from the effects of vegetation (morphology and biochemistry) can be done through spectral unmixing (Asner and Heidebrecht, 2002; Clasen et al., 2015). Gholizadeh et al. (2018) proposed a metric of spectral diversity that is soil abundance normalized and applicable to high-resolution observations to allow for the removal of ‘pure’ soil pixels. In coarser satellite observations, pixels are commonly mixed aggregates of both soil and vegetation spectra. In those cases, spectral unmixing and the normalization of the fraction of soil signal can help limit the confounding role of vegetation cover to some degree. Yet, representative and extensive spectral libraries are required to go beyond coarse soil/vegetation fractional patterns to assess the role of different growth forms and canopy architecture (Nidamanuri and Ramiya, 2013).

RTMs, specifically those intended for (heterogeneous) canopies, partition and parameterize the spectral reflectance of canopies into different layers and components of soil background and vegetation (Jacquemoud et al. 2009; Myneni et al. 1995). In figures 2-3, we applied *forward* radiative transfer modeling to simulate leaf and canopy spectra. The *inversion* of such models, on the other hand, enables the retrieval of plant traits from spectral information which are of specific interest for functional diversity assessments. This could allow to assess and adjust spectral diversity indices in consideration of soil signal abundance, and canopy architecture. Alternatively, it can facilitate a direct comparison of spectrally retrieved leaf trait values against in-situ leaf trait measurements (e.g. Ali et al., 2020a, 2020b; Brown et al., 2019; Rossi et al., 2020). In addition, recent advances have proposed the possibility of leaf-canopy models using the Directional Area Scattering Factor to specifically correct spectral data for canopy structural effects (Adams et al., 2018). Although still in their infancy, these models could facilitate targeted decoupling of spectra in canopy structure and biochemistry signals.

The inversion of canopy RTMs to estimate plant traits and biophysical parameters from spectra and radiometry is far from trivial (Musavi et al., 2015). It relies on a parameterization of the canopy structure characteristics (Table S. 4). The inversion is often ill-posed and prone to a range of equally possible solutions which challenges the correct simultaneous estimation of the parameters, especially in the case of multispectral information (Combal et al., 2003; Koetz et al., 2007). The forthcoming launch of hyperspectral satellite imagers (e.g. EnMAP, SBG, CHIME; Cavender-Bares, Gamon, and Townsend 2020) offers prospective on more detailed spectral information that might benefit inversion exercises.

Alternatively, empirical relationships between different spectra and plant traits can be established through the use of machine learning, Partial Least Squares Regression, and spectral vegetation indices (Durán et al., 2019; Ma et al., 2019; Schneider et al., 2017; Verrelst et al., 2019a, 2015). These methods, however, require large training datasets which hampers their scalability and vegetation indices have been found to be site- and time-specific with limited generality, and potentially relevant spectral information is disregarded (Ali et al., 2020a; Verrelst et al., 2015)

Ancillary data (e.g. on soil and vegetation) and data assimilation can help overcome the ill-posedness in solving RTM inversion by constraining canopy models with a priori information (Lahoz and Schneider, 2014; Lewis et al., 2012; Rivera et al., 2013). In our study, we relied on forward modelling by including in-situ measurements to generate simulated leaf and canopy spectra, but those will not be available for large-scale applications. The ingestion of LIDAR data is interesting to complement pixel-based optical reflectance for better characterization of the canopy structure including its morphological traits and vertical profile (Hakkenberg et al., 2018; Koetz et al., 2007). Such information can help further understand the role of vegetation cover as a confounding factor (Combal et al., 2003).

*Fig. S. 8. Field photography illustrative of different locations and land use types*

| **Forested locations** | **Shrubland locations** |
|---|---|
| Oak forest:<br> | Holm oak:<br> |
| Mixed forest:<br> | Mixed shrubland:<br> |
| Mixed pine forest:<br> | Cistus spp. Shrubs:<br> |

## S. 9: Cross-validation of Leaf Area Index (LAI) against Photosynthetically Active Radiation (PAR) measurements

We cross-validated the Leaf Area Index (LAI) measurements from hemispherical photography with above and below canopy measurements taken with Photosynthetically Active Radiation (PAR) sensor (Apogee MQ-301; handheld device), quantifying the relative quantity of incident solar radiation absorbed by vegetation. PAR measurements were taken above and below the canopy to calculate the canopy absorbed light. A strong correlation was been found between PAR measurements and the LAI-derived hemispherical photography. PAR measurements however did show high susceptibility to cloud cover and changing weather conditions resulting in a number of outliers as also indicated by Garrigues et al. (2008).

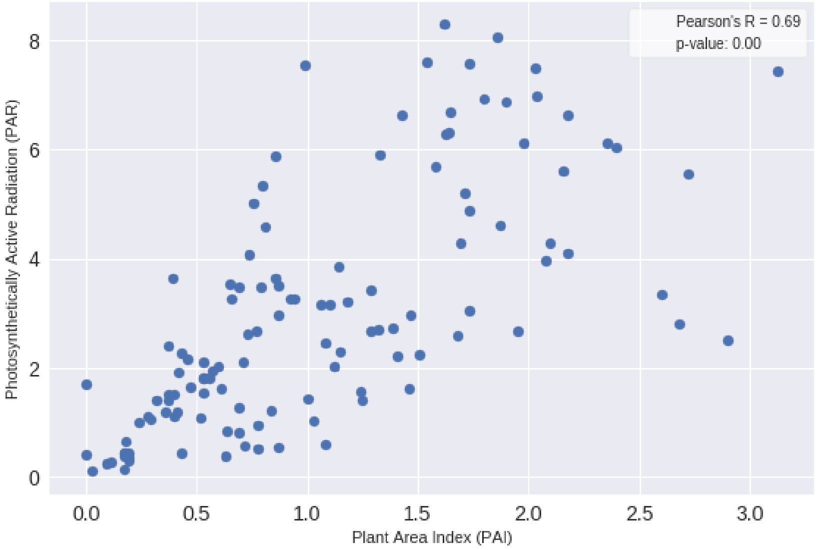


*Fig. S. 9: Comparison of LAI Area Index (LAI) measurements derived from hemispherical photography against Photosynthetically Active Radiation (PAR) measurements.*

## S. 10: Plot-wise linear correlation between satellite-based single trait estimates and in-situ field measurements

*Table S. 10: Overview of bivariate correlation (Pearson's r) and coefficient of determination (R2) between plot-wise satellite-based trait estimates and in-situ measured trait observations. Root Mean Square Error (RMSE) quantifies the deviations in estimated traits. Moran's I is indicative of the spatial association in the residuals of neighbouring points. Moran's I null-hypothesis assumes spatial independence.*

| Pixel-level trait estimates | | | | | |
|---|---|---|---|---|---|
| Algorithm | Trait | Pearson's R | $R^2$ | RMSE | Moran's I |
| SVR (Hybrid) | Leaf Area Index (m2/m2) | $0.76^{**}$ | 0.58 | 0.49 | $0.73^{**}$ |
| | Leaf Mass per Area (mg/$cm^2$) | $0.81^{**}$ | 0.66 | 6.36 | $0.69^{**}$ |
| | Leaf Chlorophyll (μg/$cm^2$) | $0.56^{**}$ | 0.31 | 7.07 | $0.63^{**}$ |
| ARTMO (LUT) | Leaf Area Index (m2/m2) | $0.79^{**}$ | 0.63 | 0.51 | $0.64^{**}$ |
| | Leaf Mass per Area (mg/$cm^2$) | $0.82^{**}$ | 0.68 | 31.06 | $0.69^{**}$ |
| | Leaf Chlorophyll (μg/$cm^2$) | $0.30^{**}$ | 0.09 | 12.03 | $0.68^{**}$ |
| SNAP | Leaf Area Index (m2/m2) | $0.74^{**}$ | 0.55 | 0.62 | $0.73^{**}$ |
| | Leaf Mass per Area (mg/$cm^2$) | $0.71^{**}$ | 0.51 | 5.94 | $0.69^{**}$ |
| | Leaf Chlorophyll (μg/$cm^2$) | $0.43^{**}$ | 0.19 | 13.79 | $0.69^{**}$ |
| **: Significant correlation (p <0.01) | | | | | |

## S. 11: Plot-wise regression between satellite-based single trait estimates and in-situ field measurements based on spatial error modelling

*Table S. 11. Overview of spatial error model regression between plot-wise satellite-based trait estimates and in-situ measured trait observations (Coefficient, St.Error and Nagelkerke's Pseudo-R2). Root Mean Square Error (RMSE) quantifies the deviations in estimated traits. Moran's I is indiciative of the spatial association of in the residuals neigboring points. Moran's I null-hypothesis assumes spatial independence.*

| **Pixel-level trait estimates** | | | | | |
|---|---|---|---|---|---|
| Algo-rithm | Trait | Spatial Error Model | | | Moran's I |
| | | Estimate | St.Error | Pseudo-R$^2$ | |
| SVR (Hybrid) | Leaf Area Index (m2/m2) | $0.30^{**}$ | 0.04 | 0.93 | $0.43^{ns}$ |
| | Leaf Mass per Area (mg/cm$^2$) | $0.33^{**}$ | 0.10 | 0.91 | $0.41^{ns}$ |
| | Leaf Chlorophyll (μg/cm$^2$) | $0.17^{**}$ | 0.06 | 0.76 | $0.43^{ns}$ |
| ARTMO (LUT) | Leaf Area Index (m2/m2) | $0.51^{**}$ | 0.07 | 0.86 | $0.43^{ns}$ |
| | Leaf Mass per Area (mg/cm$^2$) | $1.45^{**}$ | 0.28 | 0.89 | $0.42^{ns}$ |
| | Leaf Chlorophyll (μg/cm$^2$) | $0.15^{ns}$ | 0.14 | 0.35 | $0.41^{ns}$ |
| SNAP | Leaf Area Index (m2/m2) | $0.38^{**}$ | 0.05 | 0.93 | $0.43^{ns}$ |
| | Leaf Mass per Area (mg/cm$^2$) | $0.06^{**}$ | 0.04 | 0.81 | $0.37^{ns}$ |
| | Leaf Chlorophyll (μg/cm$^2$) | $0.08^{**}$ | 0.06 | 0.88 | $0.41^{ns}$ |

$^{**}$: Significant correlation ($p < 0.01$), $^{ns}$: Not significant ($p > 0.05$)

## S. 12: SNAP biophysical processor retrieval of single trait estimates compared against field measurements

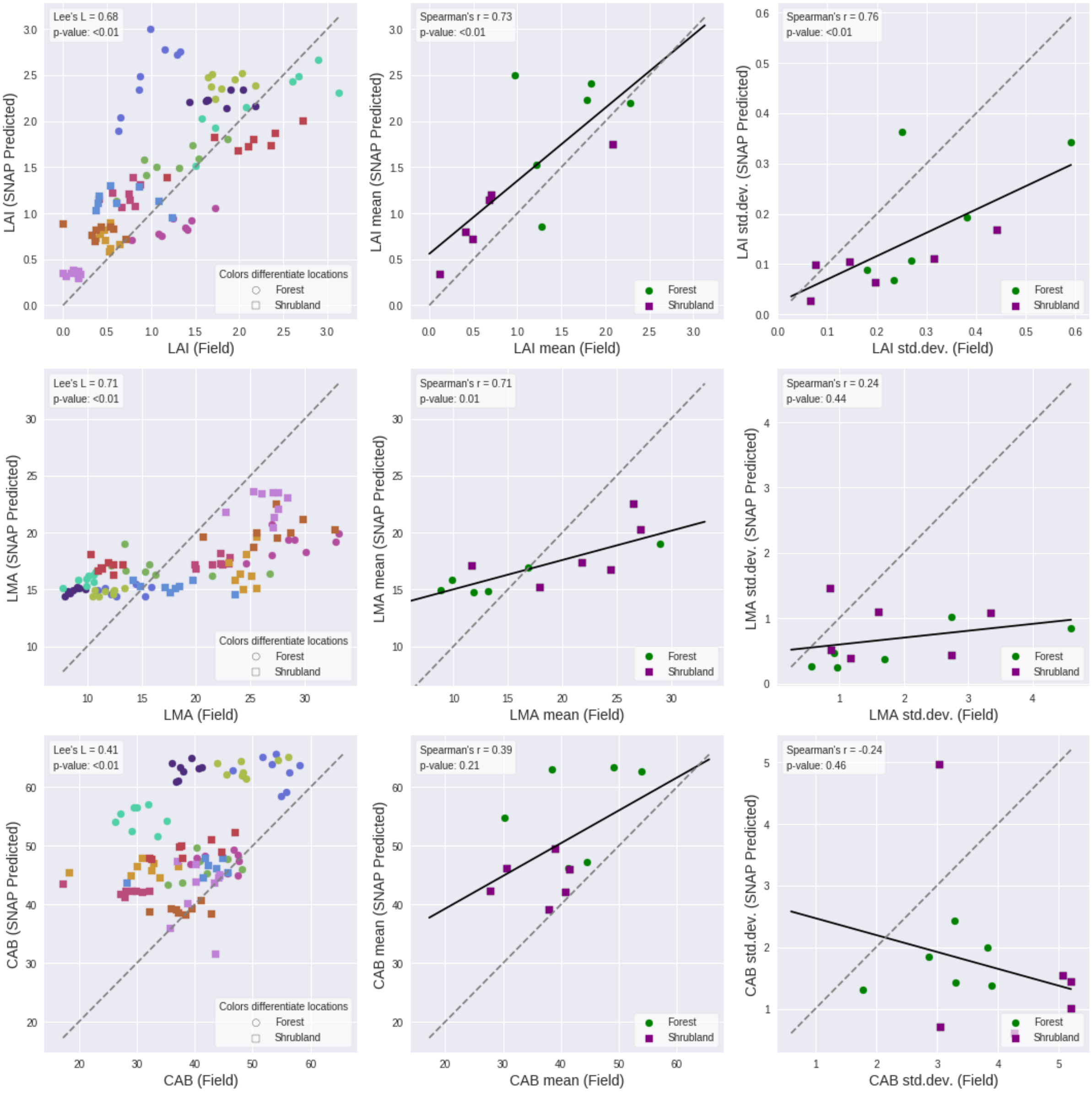


*Fig. S. 12: Comparison of Sentinel-2-based trait estimates (y-axis) retrieved using the SNAP biophysical processor against in-situ field measurements (x-axis). The left column shows pixel-level (in-situ: plot) comparisons of traits, where different colors indicate plots of respective locations. The middle column depicts trait means per location and the right column presents trait standard deviations per location. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the fitted linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

## S. 13: SNAP biophysical estimates of functional diversity compared against in-situ observations of functional diversity and taxonomic diversity

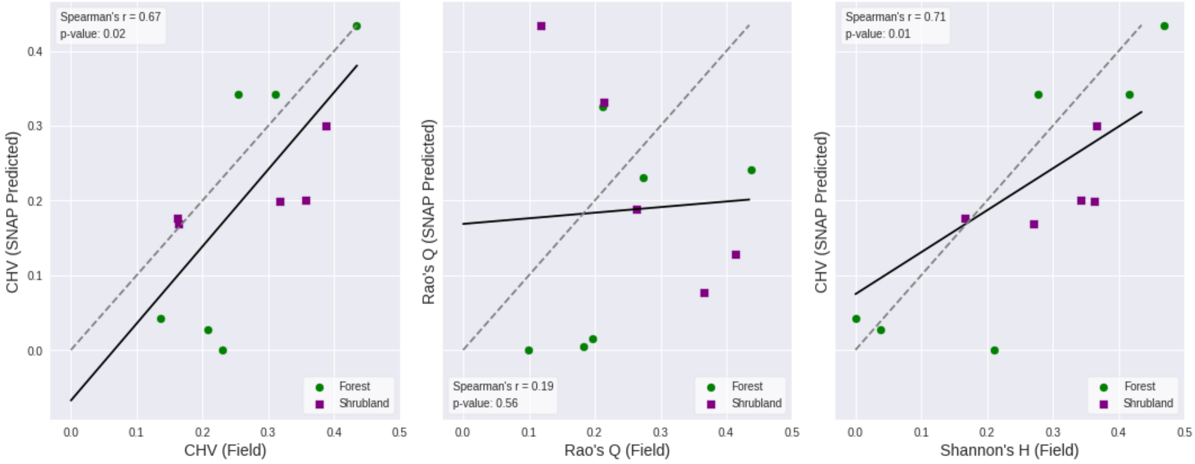


*Fig. S. 13: Left and center panels present remotely sensed functional diversity estimates (CHV and Rao's Q) calculated from Sentinel-2 derived traits (LAI, LMA, and CAB) by the SNAP biophysical processor compared against in-situ functional diversity measurements. The rightmost plot compares SNAP-derived remotely sensed functional diversity (CHV) against in-situ taxonomic diversity (Shannon's H). The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

## S. 14: In-situ correlations between functional diversity (CHV and Rao's Q) and community taxonomic diversity (Shannon' H)

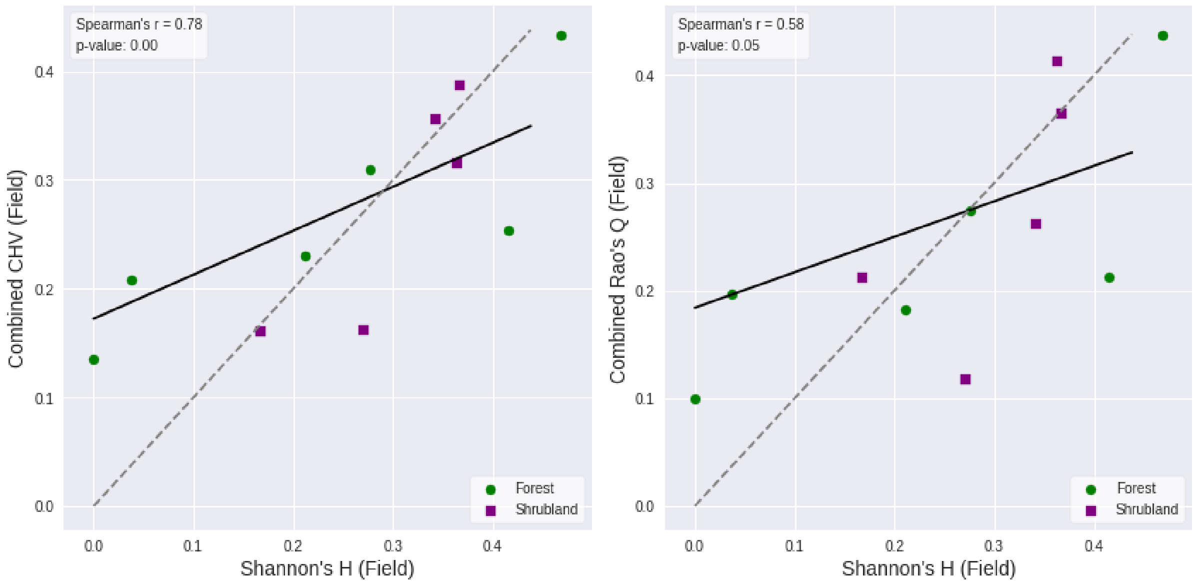


*Fig. S. 14: Correlations of in-situ observations of functional diversity, CVH (left column) and Rao's Q (right column), with taxonomic diversity Shannon's H) as observed on the ground. Purple and green markers represent shrubland and forested locations, respectively.*

## S. 15: Alternative scaling (leaf versus canopy) of traits for functional diversity estimates retrieved by SVR hybrid inversion.

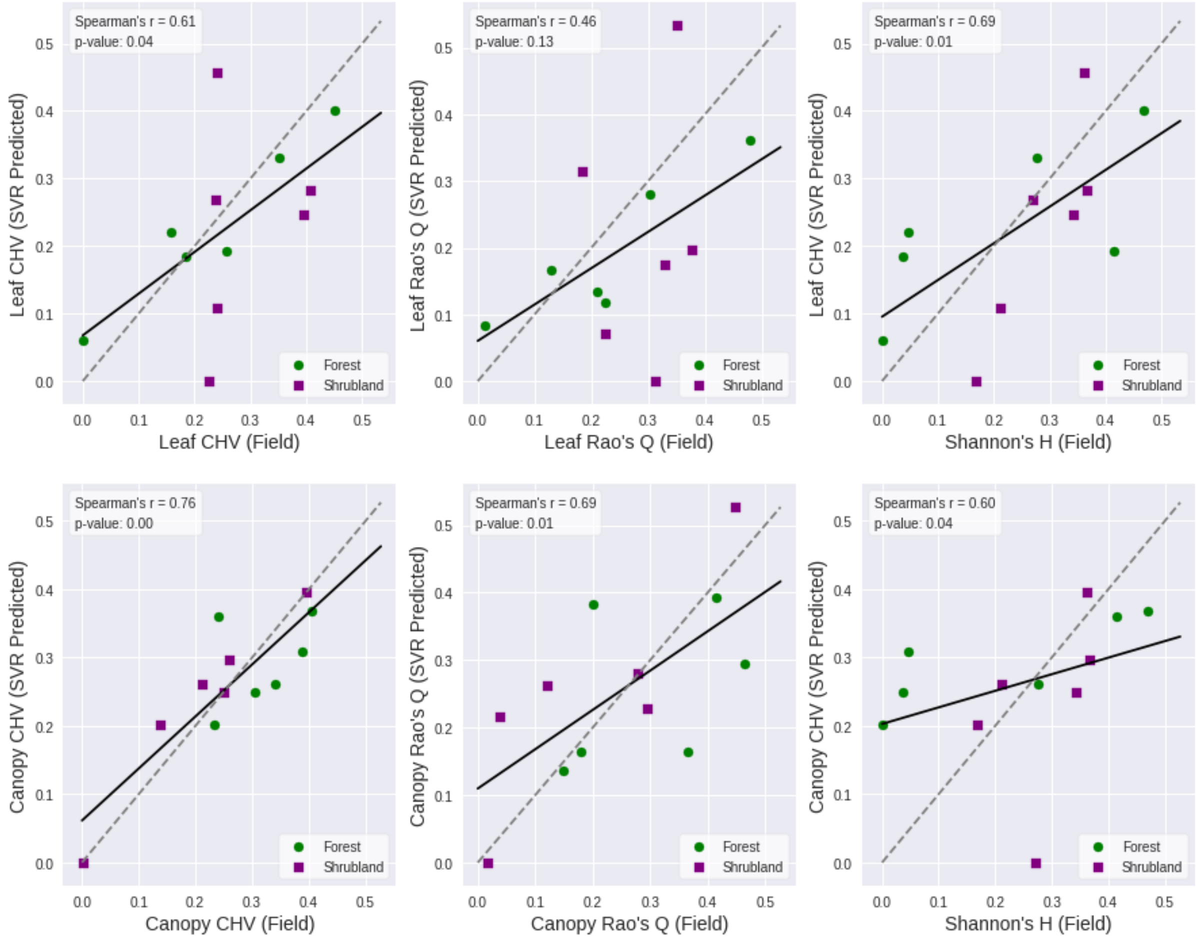


*Fig. S. 15: Remotely sensed functional diversity estimates (CHV and Rao's Q) calculated from Sentinel-2 derived leaf-level (top row) versus canopy-level (bottom row) scaling of traits through SVR hybrid inversion. The top row compares estimated functional diversity based on leaf-level traits (LMA and CAB) against in-situ observations of functional diversity and taxonomic diversity. The bottom row does the same comparing estimated functional diversity based on canopy-level traits (LMA*LAI and CAB*LAI) against in-situ observations. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

## S. 16: Alternative scaling (leaf versus canopy) of traits for functional diversity estimates retrieved by ARTMO LUT-based inversion.

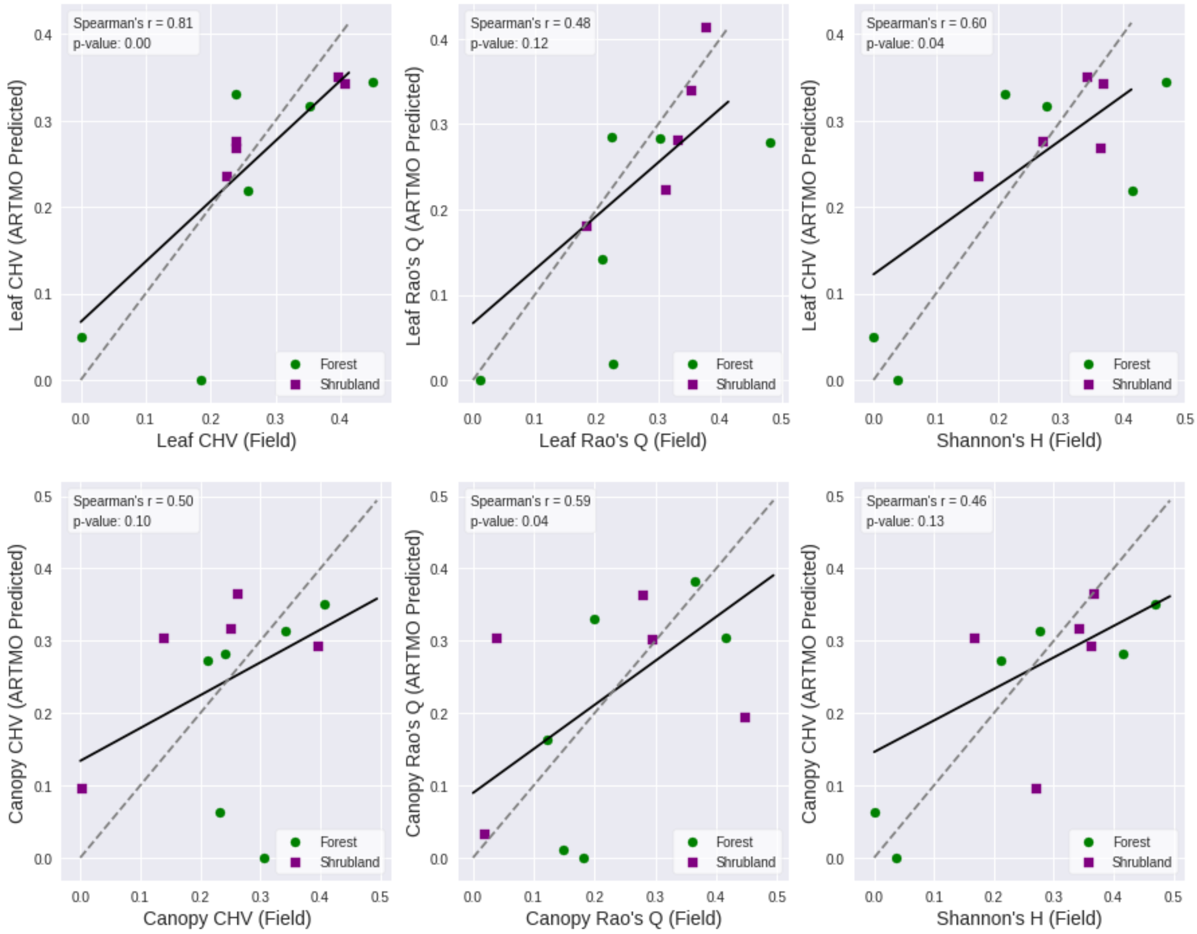


*Fig. S. 16: Remotely sensed functional diversity estimates (CHV and Rao's Q) calculated from Sentinel-2 derived leaf-level (top row) versus canopy-level (bottom row) scaling of traits through ARTMO LUT-based inversion. The top row compares estimated functional diversity based on leaf-level traits (LMA and CAB) against in-situ observations of functional diversity and taxonomic diversity. The bottom row does the same comparing estimated functional diversity based on canopy-level traits (LMA*LAI and CAB*LAI) against in-situ observations. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

## S. 17. Alternative scaling (leaf versus canopy) of traits for functional diversity estimates retrieved by the SNAP biophysical processor.

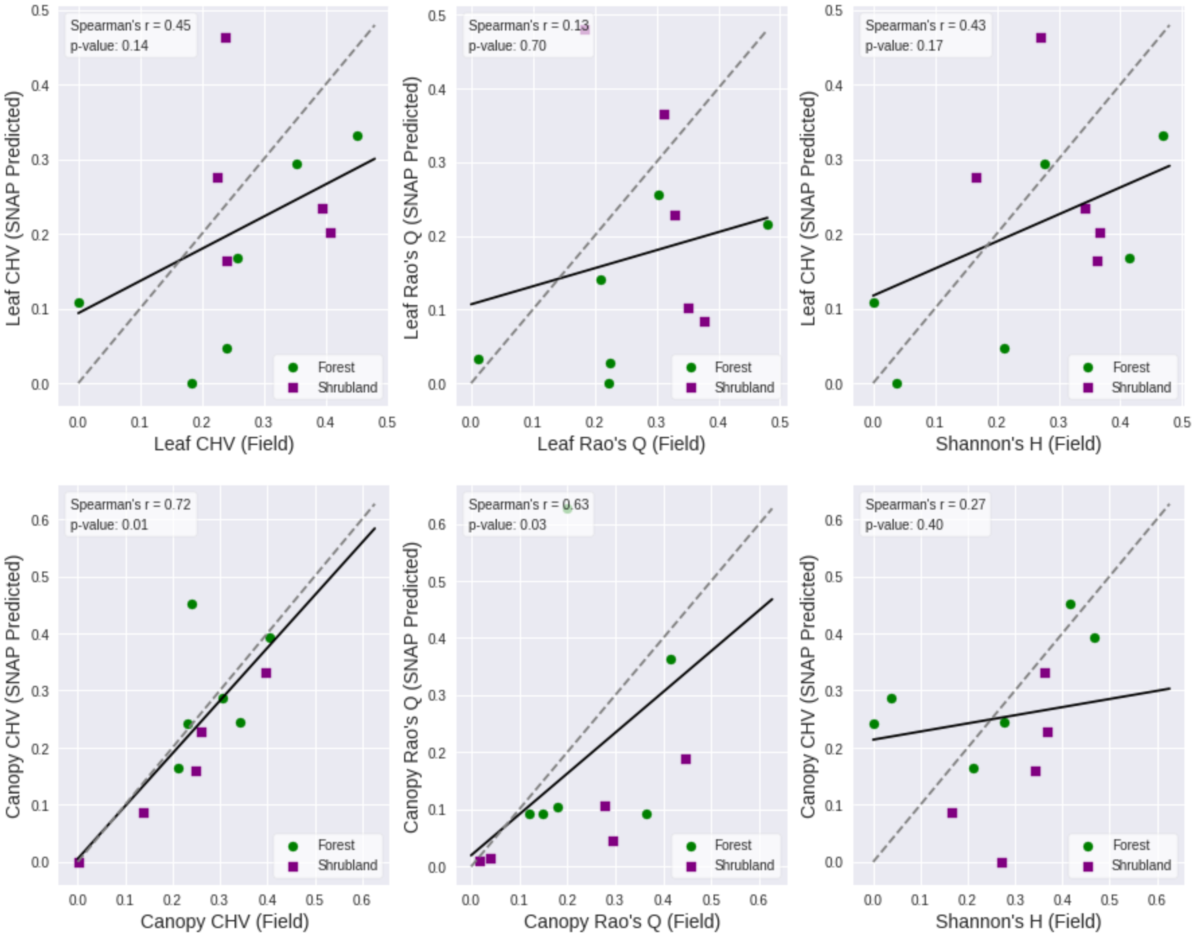


*Fig. S. 17: Remotely sensed functional diversity estimates (CHV and Rao's Q) calculated from Sentinel-2 derived leaf-level (top row) versus canopy-level (bottom row) scaling of traits through the SNAP biophysical processor. The top row compares estimated functional diversity based on leaf-level traits (LMA and CAB) against in-situ observations of functional diversity and taxonomic diversity. The bottom row does the same comparing estimated functional diversity based on canopy-level traits (LMA*LAI and CAB*LAI) against in-situ observations. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

### S. 18: Alternative scaling (leaf versus canopy) of traits for in-situ correlations between functional diversity (CHV and Rao’s Q) and community taxonomic diversity (Shannon’ H).

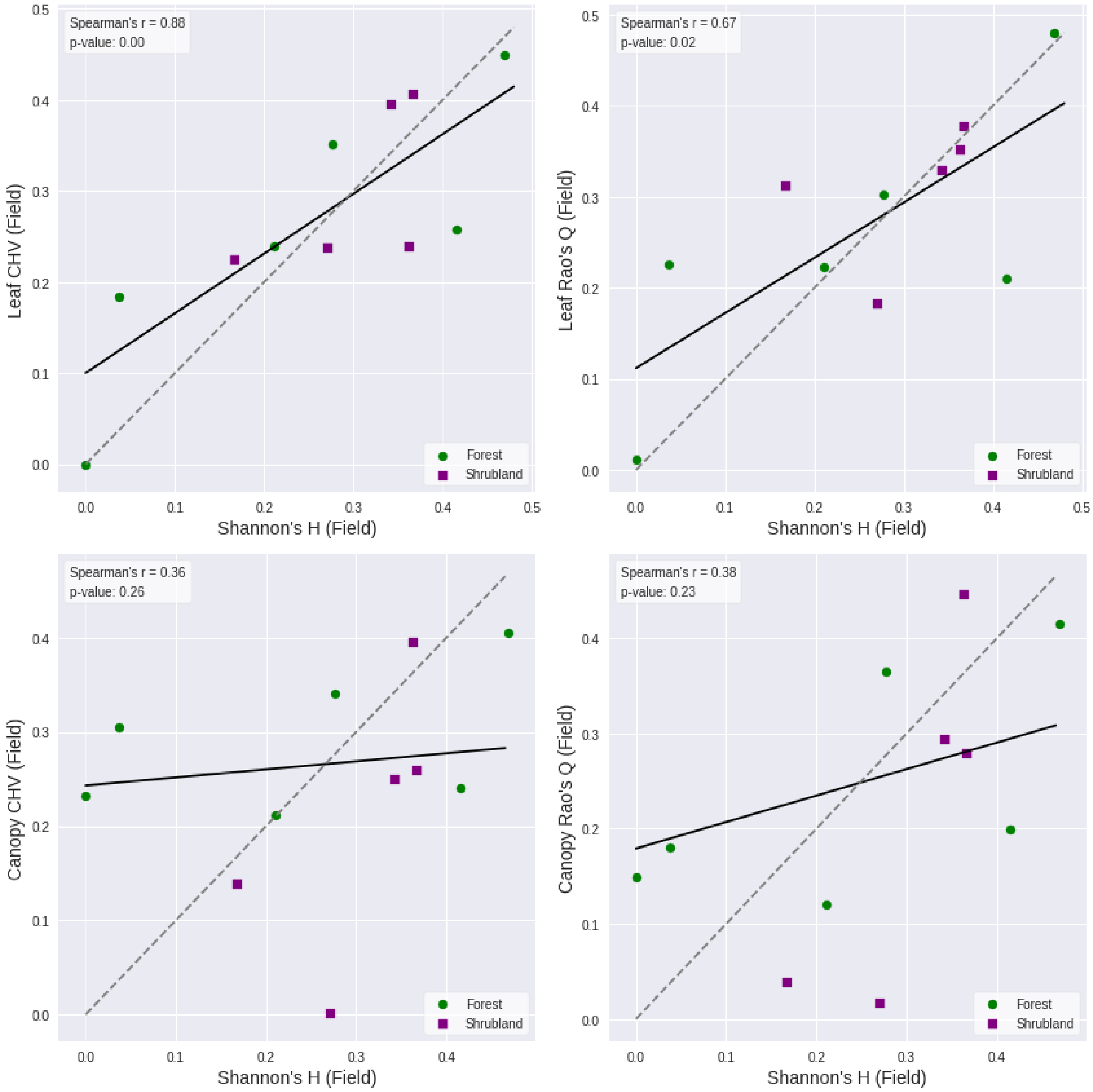


*Fig. S. 18: Correlations of CVH (left column) and Rao’s Q (right column) with taxonomic diversity Shannon’s H) as observed in-situ. The top row compares in-situ observations of functional diversity based on leaf-level traits (LMA and CAB) against in-situ observations of taxonomic diversity. The bottom row does the same comparing canopy-level traits (LMA*LAI and CAB*LAI) in-situ functional diversity against in-situ taxonomic diversity. The grey dotted line shows the 1:1 relationship, whereas the black line indicates the linear relationship between the remotely sensed estimates and field data. Purple and green markers represent shrubland and forested locations, respectively.*

*Fig. S. 19: a) Map of the Sentinel-2 observation, as seen through a true visible range composite image, over the study area in Sabah, Malaysia on the 9th of July 2017 after atmospheric corrections. b) Map of the three land use classes within the Sabah study area used for analysis.*

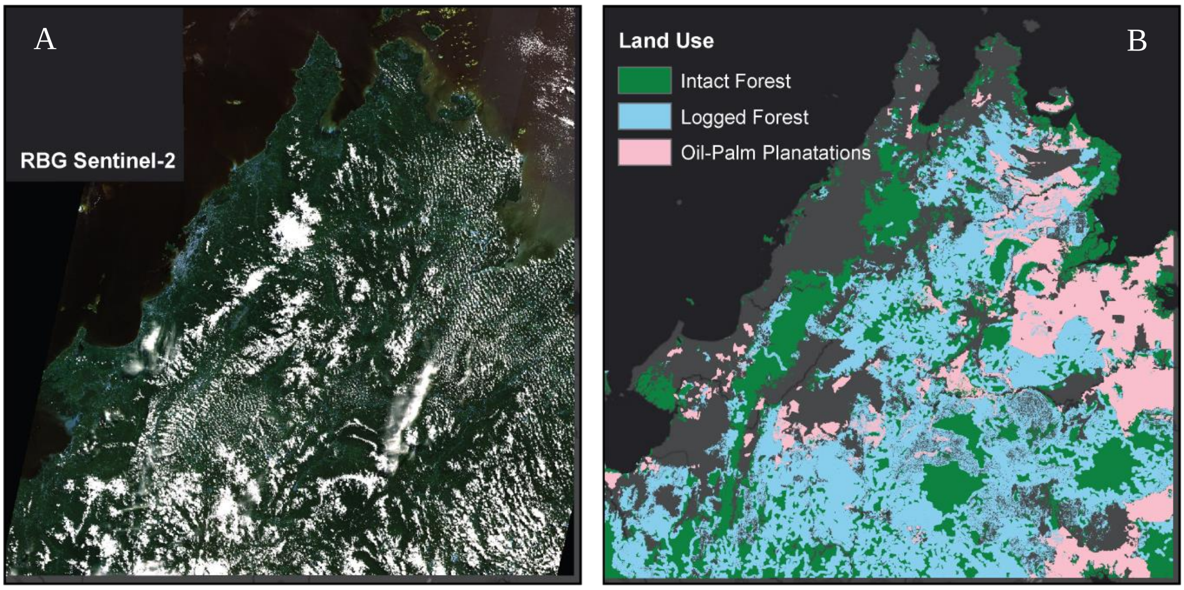


*Table S. 20: Descriptive statistics of elevation and slope observed between plots across land use types. Data is derived from digital elevation models observed by the 30m spatial resolution Shuttle Radar Topography Mission (SRTM).*

| | | N | Mean elevation (m) | Mean slope (% change) |
|---|---|---|---|---|
| 🟩 | Intact Forest | 1192 | 439.90 | 1.88 |
| 🟦 | Logged Forest | 3018 | 419.71 | 1.30 |
| 🟥 | Oil-Palm Plantations | 1416 | 63.84 | 0.74 |

## S. 21: Qualitative assessment of the validity of spectral trait indicators

To assess the plausibility of the derived spectral trait indicators on which we based functional diversity estimates, the performance of the inversion of SNAP's biophysical processor retrieval from spectra to traits was examined.

Firstly, we conducted a sensitivity analysis to assess the spectral layout of Sentinel-2 bands in terms of receptiveness to retrieve these traits (Fig. S. 21a). The analysis is based on repeated PROSAIL simulations with random variations of the trait values while mapping the spectral responses and the correlation between Sentinel-2's spectral bands and trait variation. The findings demonstrate significant spectral sensitivity to the studied traits (LAI, EWT/LWC, and CAB) (Fig. S. 21a). These findings match the sensitivity analyses of Sentinel-2 for retrieval of the traits under study (LAI, CAB and EWT/LWC) demonstrated in previous sensitivity analyses (de Sá et al., 2021; Gu et al., 2016; Rossi et al., 2020; Verrelst et al., 2019b).

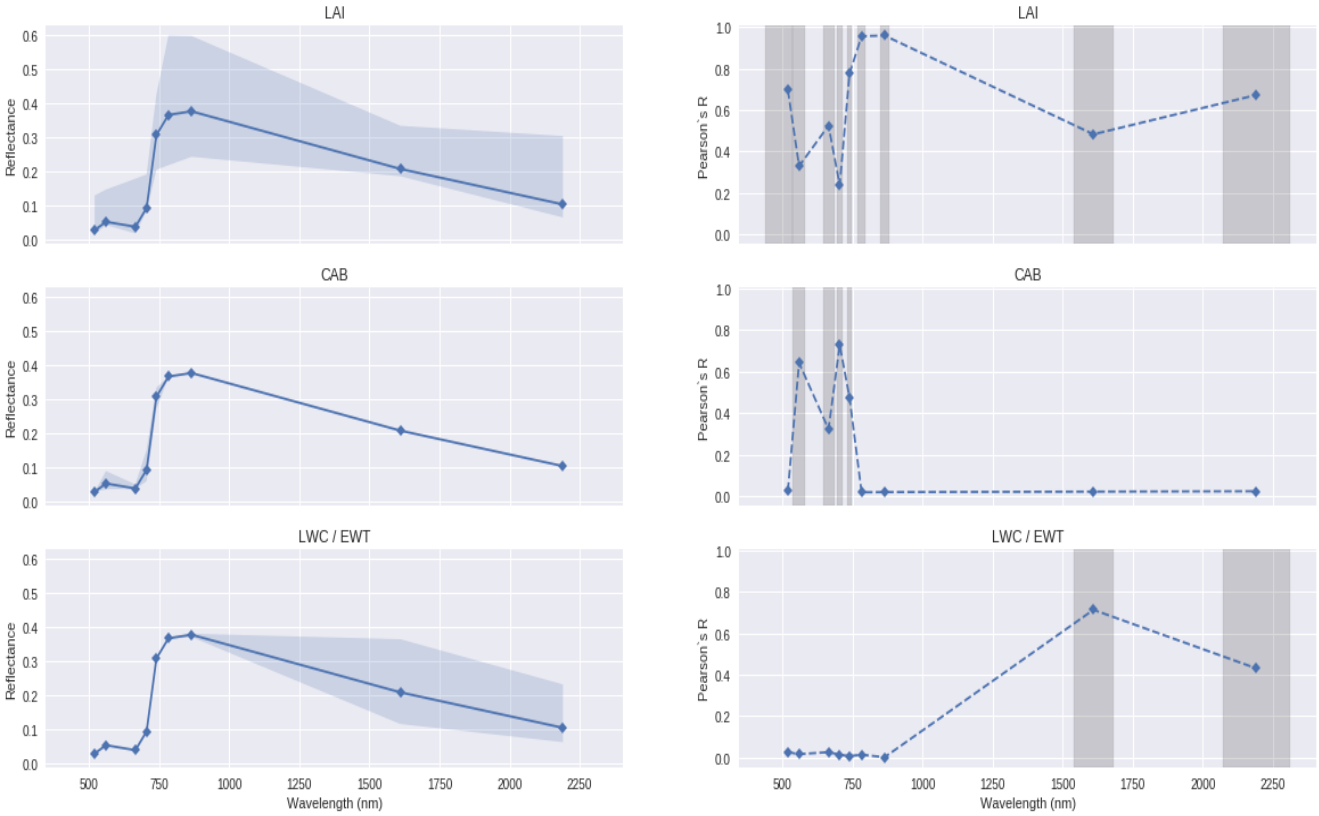


*Fig. S. 21a: Sensitivity analysis of PROSAIL's LAI, CAB and EWT/LWC parameters to the spectral lay-out of Sentinel-2 MSI bands used in this study. The left pane illustrates the range of variability in spectral response to changes in the parameters while all other parameters are kept constant at modes defined in Weiss & 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). Significant correlations are indicated by the grey highlighted bars.*

Secondly, the presence of biases in the derived spectral trait indicators across land use types was examined by reversing the inversion process. From the spectrally retrieved trait estimates obtained through inversion, we re-modeled spectra based on PROSAIL in forward-mode. The simulated spectra were compared against the actual observed Sentinel-2 spectra to assess the performance (size of the error) between different land use types/canopy types. This was done for 20,000 randomly drawn pixels over the study area. Search ranges for the remaining PROSAIL traits were constrained to the distribution of input variables described by Weiss & Baret (2016). We used Spectral Angle Mapper (SAM), Mean Absolute Error (MAE), and Root Mean Squared Error (RMSE) to assess the deviation between the simulated and actual spectra. We evaluated differences in the size of errors across land use types to examine whether such biases could have affected our results. On average, across the land use types, a RMSE of 0.012 is observed which is a 7.6 percent mean deviation from the actual observed spectra (See table S3.2). No profound differences in errors were observed between the individual land use types which suggest there is no structural bias in the inversion performance for approximation of the vegetation present in different land use.

*Table S. 21b: Comparison of errors between simulated spectra with retrieved trait estimates as input and actual Sentinel-2 reflectance spectra stratified across land use types.*

| | RMSE | | MAE | | %nRMSE | Sampled pixels (N) |
|---|---|---|---|---|---|---|
| Land Use | µ | σ | µ | σ | µ | |
| Intact Forest | 0.012 | 0.009 | 0.007 | 0.005 | 7.6 | 4774 |
| Logged Forest | 0.014 | 0.01 | 0.008 | 0.006 | 8.9 | 4274 |
| Oil-Palm Plantations | 0.012 | 0.01 | 0.007 | 0.006 | 7.2 | 3952 |

Thirdly, we compared the distributions of spectral trait indicators against in-situ measured traits of common species in the different studied land use types. Figure S3.3 indicates that the spectral trait indicators are to a large degree in line with the range of measurements from field studies.

The most notable deviance is an overestimation in oil-palm plantations of LAI compared to Hadi et al. (2017)'s effective LAI measurements. Hadi et al. (2017)'s measurements are conducted in relatively recently planted oil-palm plantations. Differences in LAI between young plantations versus older plantations might be responsible for this discrepancy. In our study, observed LAI values –were the highest in plantations rather than tropical evergreen broadleaf forests. This was also reported by Asner et al. (2003). Intensive management regimes -through planting schemes, fertilizer, and pest management- aim to maximize production in these plantations and both resonate with relatively high chlorophyll and LAI ranges. Furthermore, early studies by Hardon et al. (1969) have demonstrated a positive correlation between the leaf area and the yield of different palms. Industrial oil-palm plantations are often located on more favorable lands for high productivity in terms of elevation and slope.

In terms of LWC/EWT and CAB, we find much larger variation in the species measurement conducted in the field. Notably, these measurements consist of a variety of individual species whereas our observations are based on pixel-based aggregation of multiple species possibly levelling out some of the variation. In consideration of this convergence, the range of spectral trait indicators is reasonable with the exception of an overestimation of LWC/EWT compared to Martin et al. (2018)'s in-situ measurements.

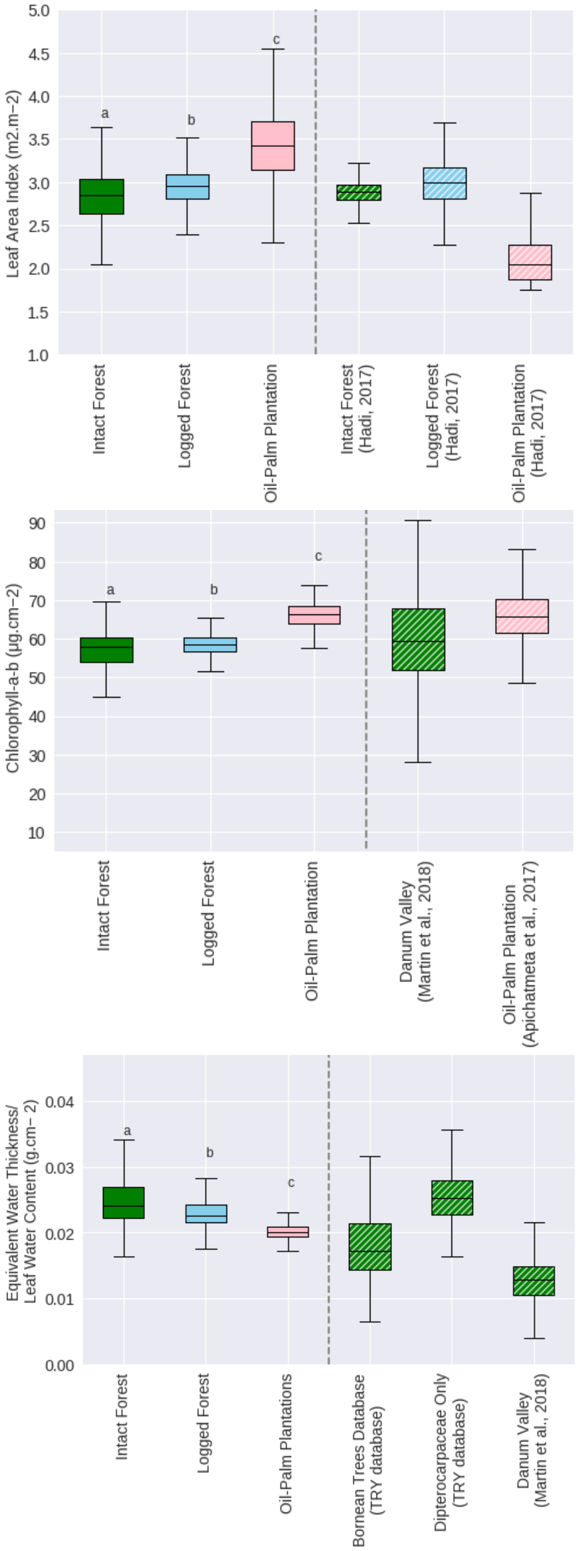


*Fig. S. 21c: Comparison of retrieval of spectral trait indicators from SNAP's biophysical processor derived from Sentinel-2 reflectance spectra to relevant in-situ trait ranges in the TRY plant trait database (Kattge et al., 2011; Kurokawa and Nakashizuka, 2008) and other regionally relevant field campaigns (Apichatmeta et al., 2017; Azzeme et al., 2016; Hadi et al., 2017; Martin et al., 2018). Differences in retrieved trait estimates between land use types according to a post-hoc Tukey's HSD test are indicated with different letters.*

## S. 22: Functional diversity across elevation

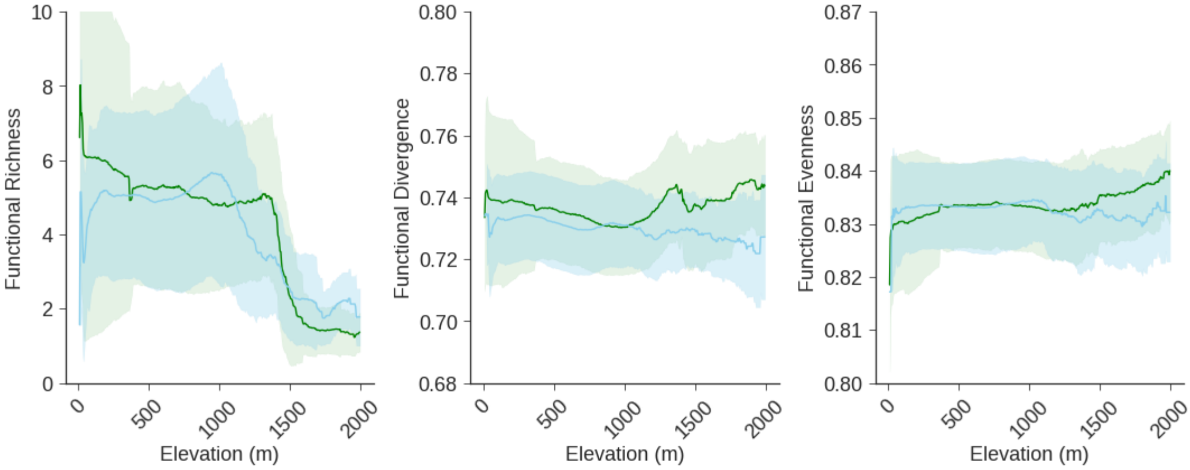


*Fig. S. 22: Variation of functional diversity metrics along average elevation of plot. Green represents intact forests; blue indicates logged forests. Oil-palm plantations were only found below 500m ASL.*

Functional richness decreases along the elevational gradient. In line with ecological theory, this indicates a stronger functional convergence with elevation linked to a stronger environmental filtering of fitness in higher altitudes (Durán et al., 2019). A steep drop in functional richness is particularly observable above 1400m ASL. These findings correspond with earlier studies on elevational patterns of tree species richness on Mount Kinabalu, Borneo (Aiba and Kitayama 2010; Grytnes and Beaman 2006; Kitayama 1992). Similar to functional richness in our study, tree species were found to decrease rapidly with elevation above 1500m (Grytnes and Beaman, 2006). Moreover, using airborne remote sensing, studies have shown a lower functional richness at higher elevation suggesting a smaller range of resource availability at higher altitudes, whereas, again, functional divergence remained relatively unaffected by elevation (Durán et al., 2019).

Generally, we observe a negative correlation of functional richness and elevation of Pearson's R = -0.18 for both land use types and of Pearson's R = -0.31 for Intact Forests specifically. For Logged Forests, we observe an initial increase in functional richness before following a similar decrease as seen in intact forests. Functional divergence and functional evenness, on the other hand, indicate little variation with elevation. Oil-palm plantations were not found to be grown at elevations above 500m above sea level (Table S. 20). This therefore did not allow for studying elevational effects in oil-palm plantations.

## S. 23: Non-log-transformed functional-area relationships

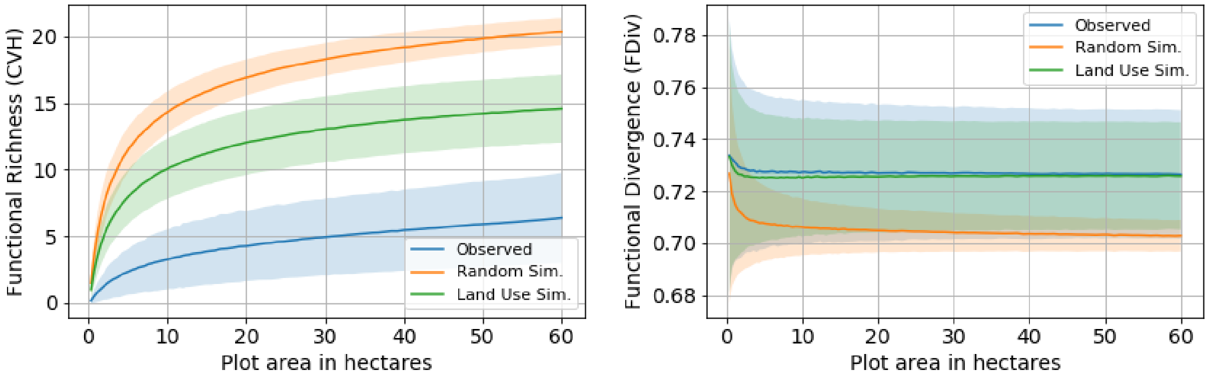


*Fig. S. 23a: Non-log-transformed scale dependency of the two studied functional diversity metrics. Comparisons are made between observed remotely sensed diversity in Sabah, Borneo, versus null-models based on randomly drawn trait combinations from observed trait values. The 'Random Sim.' model (orange) draws random trait combinations irrespective of land use type, whereas the 'Land Use Sim.' model draws random trait combination in consideration of land use. Dark lines represent the mean and standard deviations are represented by the respective shaded areas.*

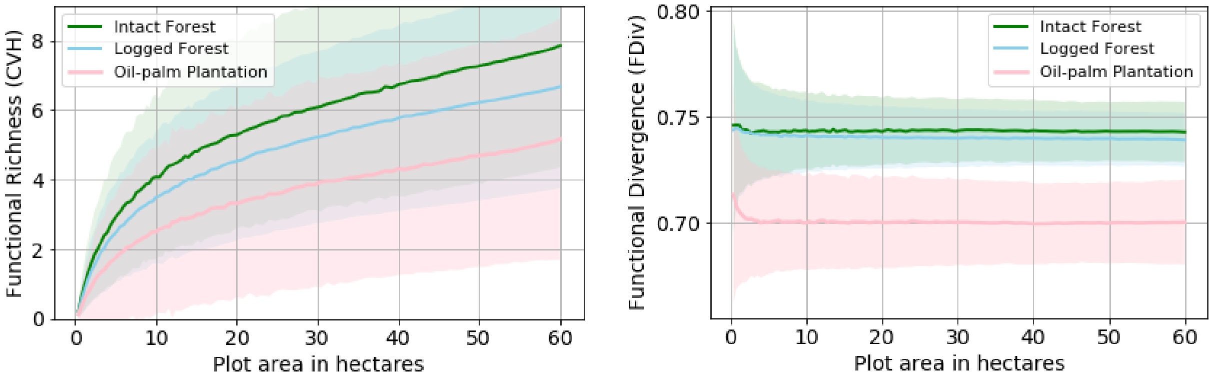
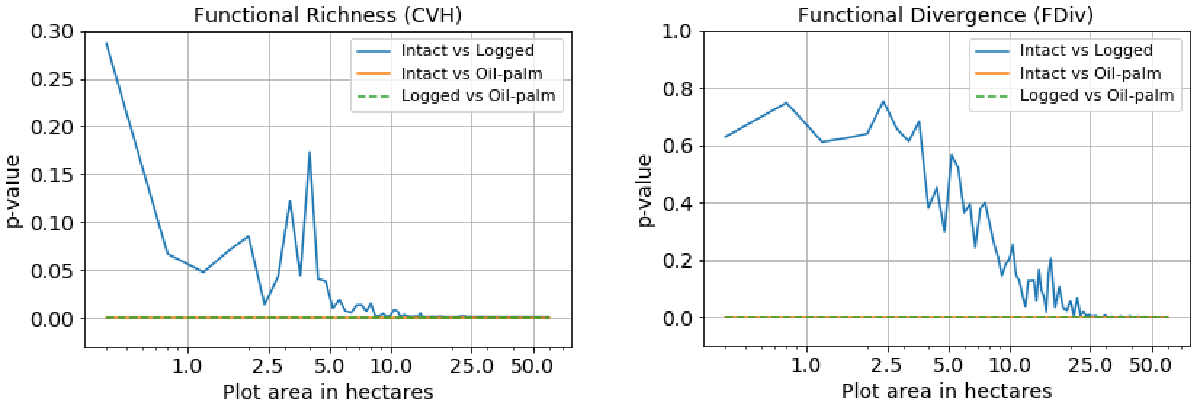


*Fig. S. 23b: Non-log-transformed scale dependency of the two studied functional diversity metrics stratified across land use types. Functional diversity calculations were done over continuous plots of one land use type over a range from 0.4 to 60 ha sized plots. Dark lines represent the mean and standard deviations are represented by the respective shaded areas.*

## S. 24: Posthoc analysis of functional diversity differences between land use types

*S. 24: Posthoc analysis of ANOVA to assess the significant differences between land use pairings. P-values below 0.05 are considered to signal significant differences between individual land use types.*



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# I. Summary

Biodiversity enables ecosystems to thrive through the synergy of functional differences among organisms. Human well-being is strongly dependent on biodiversity and related ecosystem services. At the same time, human activities over the past centuries have resulted in the current unprecedented biodiversity declines. To understand the interaction between anthropological pressures and biodiversity, new comprehensive and scalable methods are of urgent importance. Sole reliance on traditional field sampling methods to meet this challenge is widely considered to be unfeasible given the spatial and temporal scales involved. This has inspired a growing body of research on the application of remote sensing for large-scale monitoring of plant biodiversity, thus far mostly with an emphasis on airborne remote sensing and anticipated future hyperspectral satellite missions. This thesis studied the overlooked capabilities of currently operational satellite observations to conduct large-scale monitoring of plant diversity, with a focus on the European Space Agency's flagship Sentinel-2 satellite.

Remote sensing of plant diversity patterns largely hinges on the notion that plant spectral profiles are integral representations of plant phenotypes and the underlying functional variation. Indeed, this thesis showed that the diversity in spectral signals, as observed from satellite measurements, relates to in-situ taxonomic plant diversity patterns at a landscape scale in forests and shrublands. However, the findings also illustrated the need for a cautious application and refinement of the presumed relationship between spectral diversity and plant diversity patterns. Heterogeneous vegetation cover (including canopy architecture, density, and background) dominated the spectral diversity signals observed with Sentinel-2 and overpowered actual plant functional diversity signals. Therefore, methods that isolate such confounding factors from the actual functional and taxonomic diversity patterns in the spectral signal are advantageous despite generally requiring a more complex data processing chain.

This thesis examined the use of physics-based radiative transfer models (RTMs) that simulate the propagation of light within canopies and leaves. The implementation of RTMs allowed us to isolate canopy plant traits from other signals to estimate plant diversity patterns. The quantitative comparisons revealed a strong correlative relationship to the in-situ plant functional richness patterns, yet still with an average 20-21% deviation from field measurements. Qualitatively, the spatial patterns of plant functional diversity revealed significant differences along a land use gradient based on different degrees of human disturbance which followed ecological expectations. In addition, the application of RTMs helped to overcome the dependence on scarce in-situ trait data for training and calibration. Further validation of RTM-based approaches across vegetation types and ecosystems will still be needed to assess its actual scalability across regions.

Spatial ecological processes are known to depend on the scale and means of observation. The 20m spatial resolution of Sentinel-2 is relatively coarse in comparison to the detail found in vegetation heterogeneity. As such, this spatial scale challenged the interpretation and validation of the satellite-derived plant diversity estimates. The 20m spatial resolution was ill-equipped to delineate individual canopies and instead presented pixel-based aggregations of multiple canopy crowns. These aggregations sit in between and mix the traditional ecological units of observation based on individual organisms and the communities thereof. Hence, this

complicated the interpretation following traditional ecological diversity concepts. The multi-scale analyses presented in this dissertation illustrated the scale dependency and gradual transition of what are traditionally considered separate drivers of ‘*within’* versus ‘*between’* plant community diversity. The multi-scale approach allowed us to bypass the need for arbitrary decisions of a fixed optimal plot area to calculate diversity metrics. Subsequently, the findings question whether the traditional ecological focus of discrete ‘*within’* versus ‘*between’* community diversity should be maintained in remote sensing applications or whether we need new more continuous concepts.

Moreover, the adequately scaled ground validation of the studies presented here required a dedicated field study campaign to match composite plots georeferenced to the pixel raster of Sentinel-2 observations. Given the laboriousness of this campaign, the feasibility and repeatability of such efforts will be limited. Future studies that seek to overcome challenges in the validation and interpretation of satellite remote sensing observations of plant diversity may benefit from relying on multi-sensors integration. For instance, two-tier validation using drones can aid field validation campaigns with spatial scales that are more feasible to match on the ground. Additionally, multi-sensor approaches can offer help addressing the spatial irregularities found in ecological phenomena, e.g.: heterogeneously shaped canopies and communities, to which coarse satellite-based rasterized pixels are ill-equipped and single sensors applications lack versatility.

While this thesis makes important steps in the development of concepts and techniques to address biodiversity patterns via remote sensing, further extensive validation of plant diversity estimates from satellite remote sensing remains necessary with the inclusion of larger sample sizes, more ecosystem and vegetation types, and a wider range of traits to ensure adequate functional differentiation. Further consideration of the role of different spatial and spectral resolutions will be necessary as well as the inclusion of multi-temporal dynamics. The maturation and acceptance of satellite-derived plant diversity estimates will evolve with growing adequate validation, advances in sensors, and further methodological improvements. With these ongoing developments, the large-scale and frequent monitoring of plant diversity patterns through remote sensing can become an integral part of global biodiversity observatory systems to quantify our biodiversity footprints and our impact on the ecosystem systems that support our wellbeing.

# II. Samenvatting

Menselijk welzijn is sterk afhankelijk van biodiversiteit en de ecosysteemdiensten gefaciliteerd door biodiversiteit. Echter, menselijk handelen heeft tegelijkertijd geleid tot de huidige zorgwekkende biodiversiteitsverliezen. Beknopte en schaalbare methodes om de staat van biodiversiteit (van lokaal tot globaal) te inventariseren zijn in toenemende mate van urgent belang. De volledige afhankelijkheid van traditionele veldstudies hierin zal ontoereikend zijn gezien de ruimtelijke en temporele schaal van deze opgave. Onderzoek naar het gebruik van remote sensing (d.w.z. aardobservatie door middel van sensoren) voor grootschalige biodiversiteitsinventarisatie is daarom van belang. Dusver heeft de focus echter vooral gelegen op hyperspectrale metingen vanuit vliegtuigen of drones en discussies omtrent toekomstige satellietmissies. In aanvulling daarop bestudeert deze thesis juist de mogelijkheden van de huidige multispectrale satellieten (d.w.z. satellieten waarbij informatie van verschillende golflengten wordt gebruikt) met de focus op de Sentinel-2 constellatie.

Remote sensing van ruimtelijke plantbiodiversiteitspatronen is gebaseerd op het idee dat spectrale metingen van vegetatie vertegenwoordigingen zijn van hoe planten eruitzien en de onderliggende variatie in functionele plantkarakteristieken. In overeenkomst met dit idee laten de studies in deze thesis zien dat de diversiteit in dergelijke spectrale signalen inderdaad gekoppeld kan worden aan ruimtelijke landschapspatronen van plantensoortenrijkdom in bossen en struikgewassen. Echter, de bevindingen laten ook zien dat spectrale signalen geobserveerd door Sentinel-2 gedomineerd worden door met name de variatie in vegetatiedichtheid. De koppeling van spectrale diversiteit aan plantbiodiversiteit werkt dus alleen in overeenstemming met de variatie in vegetatiedichtheid. Een behoedzame toepassing en karakterisering van de relatie tussen spectrale diversiteit en plantbiodiversiteit is daarom vereist. Methodes die elementen van plantbiodiversiteit in spectra isoleren van verstorende signalen zoals vegetatiedichtheid kunnen daarbij helpen, maar vereisen complexere dataverwerking en extra handelingen.

Deze thesis past de inversie van vegetatie stralingsmodellen (radiative transfer models, RTMs) toe op het schatten van plantbiodiversiteit. Deze modellen simuleren op basis van universele natuurkundige principes de interactie tussen zonlicht en vegetatie. Door het gebruik van deze modellen is een schaalbare methode ontwikkeld om ecologisch relevante planteigenschappen te karakteriseren, te isoleren en interfererende factoren te scheiden ten behoeve van het schatten van landschapspatronen van plantbiodiversiteit. De resultaten laten zien dat de inschattingen kwantitatief sterk relateren met functionele plantbiodiversiteit gemeten in veldstudies, maar wel gemiddeld 20-21% afwijken van veldmetingen. Kwalitatief volgen de inschattingen vanuit satelliet-observatie de ecologische verwachtingen volgens ruimtelijke landgebruik gradiënten. Een belangrijk bijkomend voordeel van het gebruik van modellen voor simulatie is de verminderde afhankelijkheid van schaarse velddata voor het trainen en kalibreren van methodes voor het schatten van plantbiodiversiteit. De daadwerkelijke schaalbaarheid van de gepresenteerde methodes vereist verdere toetsing in verschillende vegetatietypen en ecosystemen.

De 20m ruimtelijke resolutie van Sentinel-2 is relatief grof gezien de fijnmazige heterogeniteit van vegetatie. Daarom blijft de interpretatie van dergelijke observaties op dit schaalniveau voor

het schatten van plantbiodiversiteit een uitdaging. De resolutie is ontoereikend voor het identificeren van individuele plantentoppen. In plaats daarvan ‘’zien’’ we op deze resolutie het signaal van meerdere plantentoppen tezamen. Enerzijds bemoeilijkt dit de validatie en training van plantbiodiversiteitsmodellen. Anderzijds mixt deze aggregatie de diversiteit van planten met plantengemeenschappen tot een moeilijk te interpreteren geheel. Dit maakt geobserveerde ruimtelijke patronen van biodiversiteit moeilijk te koppelen aan de traditionele focus van ecologische concepten op de biodiversiteit *binnen* (alpha) en *tussen* (beta) plantengemeenschappen.

Het ruimtelijk expliciete en grootschalige bereik van satelliet-observaties biedt mogelijkheden om diversiteit te inventariseren over plots van verschillende grootte. De analyses op verschillende schaalniveaus gepresenteerd in deze thesis illustreren hoe landschapspatronen van plant functionele biodiversiteit zich verhouden tot schaal. Hierbij laten de studies zien dat beta-diversiteit in toenemende mate kan worden geobserveerd bij grotere schalen in de mix van traditionele alpha- en beta- plantbiodiversiteit. De multi-schaal analyses illustreren ook dat de discrete concepten uit ecologie worden uitgedaagd door de ruimtelijk expliciete observaties van remote sensing. Dit daagt de traditionele focus op arbitraire plantgemeenschappen als de noemer van biodiversiteit uit en roept op tot de ontwikkeling van nieuwe en meer continue en graduele schaalconcepten. Om deze schaaluitdagingen verder te begrijpen kunnen toekomstige studies meerdere sensoren integreren. Met name de fusie van hoge resolutie spectrale metingen vanuit vliegtuigen of drones met satelliet-data biedt potentiële oplossingen om de ruimtelijke onregelmatigheden en fijnmazigheid van vegetatie in kaart te brengen en om het valideren en kalibreren van plantbiodiversiteitsschattingen beter te kunnen faciliteren. De rol van ruimtelijke schaal op hoe wij biodiversiteit waarnemen kan daarbij verder en in meer detail worden onderzocht.

Voorlopig zal verdere veldvalidatie van belang blijven om enerzijds het vertrouwen in satelliet-gebaseerde schatters van plantbiodiversiteit te versterken en anderzijds om methodes verder te verfijnen. Dit zal gedaan moeten worden door studies op te zetten met grotere steekproefsomvangen, met een wijder bereik van verschillende vegetatietypes en ecosystemen, verschillende sensors, een multi-temporele aanpak, en in een achtneming van een grotere verscheidenheid aan functionele rollen in plantbiodiversiteit. Met toenemende adequate validatie, de ontwikkeling van sensortechnologie, en methodologische voortgang, zal de rol van grootschalige en ruimtelijke expliciete inventarisatie van landschapspatronen van plantbiodiversiteit vanuit satelliet remote sensing steeds meer erkenning kunnen gaan genieten. Uiteindelijk kan satelliet aardobservatie daarmee een integrale rol gaan spelen in een globaal en gestandaardiseerd raamwerk om onze biodiversiteitsafdruk en onze impact op de ecosystemen te kwantificeren.

# III. Acknowledgements

In a week from writing this, I am running the Vietnam Mountain Marathon in Mộc Châu. PhD pursuits have often been compared to resembling a trail marathon: it’s a long journey on lonely winding uphill roads. I will soon find out to what extent this metaphor is accurate. While every PhD project is different, my journey has largely felt like a lonesome and daunting struggle. Nevertheless, looking back at the entire journey I realize there were many people along the way to hand me the much-needed metaphorical water and motivation to keep pushing. I want to start by thanking Peter and Nadia for allowing me to embark on this PhD journey. I think now it is safe to admit that I arrived at the starting line pretty much untrained for this distance. I had little to no experience in the fields of biology, conservation, remote sensing, or any coding knowledge. You trusted me to quickly acquire those skills. Joris provided major guidance and help in developing these skills for which I am very thankful.

So many people have played a crucial role in helping me stay positive and luminous, no matter how dim the progress. First off, I want to thank my friends, family, brothers, and sisters, that have made me feel at home in Leiden; Sandesh, Jessie, Aydin, and everybody from LUSV who embraced me like a family in Leiden, Guangchao and crew as a true inspiration for living a balanced life, Riccardo, Marco, Luca, Francesco (pampering me with Italian cuisine and fratellanza), Daniel and Bea. I am very grateful to my brother Mucahid as a friend and brave guide in this academic landscape. I want to thank my friends in Vietnam that provided many of my most cherished memories, gave me a place to escape, and uplifted my spirit on every visit. I want to especially thank my brother Phát and his family, and my comrade Khôi. Special acknowledgments to chị Hòa, Bình, Trang, for all your inspiration and support, as well as the larger group of STI and HCMIRG. I want to thank my extended family, my grandparents, Anne, Andre for their inspiration and support. Special thanks to Christian (and Andrea) for being a great friend and a very valuable academic sparring partner. I have learned so much from you and always felt inspired through our conversations on Skype or in the mountains of Zernez. The world needs to get ready for all our future collaborations!

I want to thank the many people within CML that supported me on a daily basis with tea breaks, healthy office vibes, and the preparations leading up to the defense. Special thanks to Sammy and Suzanna, Kevin, the RS group, Nuno, Maarten, Glenn, Emily, and all my dear office mates over the years: Anne, Bertram, Georgios, Bill, Yingji, Laura, and Sam. You have been wonderful to me. I want to thank my co-authors of the manuscripts and publications. I want to give a special thank you to Niels, you saved me literally when got injured in the forest of the Montesinho national park doing fieldwork sampling, but also figurately, by saving my PhD by helping me build a very impressive field data validation dataset. Thank you Myrthe, it felt like a true victory to play my first competitive basketball again after 2,5 years of rehab post-injury. I want to thank KNAW for financial support for the Montesinho field campaign. I want to thank Amie and Famoussa among others for a wonderful time in Ghana and of course my brother Nathan in Accra for always supporting me. I want to thank the reviewers for rejecting multiple versions of my papers initially and firing up my motivation. I would like to acknowledge the synergy of events that helped align a path for me to accomplish the PhD journey with many lessons that truly shaped me into who I am today as a more resilient and balanced person.

I left my final and most important thank you to my family (Wil, Otto, and Elke) because these words involve the deepest and whole of my heart. I am so thankful for you and how you have supported me in every possible way and surrounded me with unconditional love. Perseverance, being resilient, and having the curiosity to learn more and adapt, all started with you. Netherlands, Australia, or Austria, inside or outside academia, I believe I would have been able to make it anywhere with the mindset and support that you have given me. My love and gratitude are infinite. The doctor’s title will be in front of my name, but honestly, you deserve it just as much so considered it a shared title! Special thanks to Elke and Ross for the beautiful dissertation cover.

Lastly, a little warning to those who want to pursue a PhD; do not seek academic titles, money, and possession for the sake of it as those will never satisfy. What I value in hindsight is the strength and resilience I have shown and developed through the many adversities I faced over these years. Hustle-and-grind culture might be toxic, and I paid its price, so be aware. Yet, in the end, it still was the perseverance and hard work that led me to obtain my PhD title.

I am thankful for everyone that stuck with me when the soil remained bare no matter how many seeds I planted and the water I gave. First seedlings have sprouted and an even bigger harvest is coming soon, let’s celebrate together and keep empowering each other to grow. I am forever grateful, also to the many people I failed to mention here. Thank you all from the bottom of my heart.

# IV. Curriculum Vitae

Leon T. Hauser was born in Subiaco, Perth, Western Australia and moved to the Netherlands with his younger sister and parents timely before enjoying his formal education. After completing his Latin school at Gymnasium Camphusianum in Gorinchem, he enrolled in a bachelor's studies in ‘Human Geography’ at Utrecht University. After graduation and a brief return to Australia, Leon proceeded with a joint research master's programme in ‘Sustainable Development’ shared between Basel University and Utrecht University matching his interest in sustainable societal transition. Leon wrote his master thesis at the Alterra Green World Research Centre in Wageningen on how farm management shapes the Dutch rural landscape through the presence of semi-natural landscape elements and biotopes combining insights from aerial photography and farmer interviews.

Following M.Sc. graduation with cum laude distinction in 2013, Leon engaged in consultancy projects related to urban agriculture and invasive water species infestations. In late 2014, Leon took up a role as an ‘Environmental Research Officer’ at the Space Technology Institute based in Hanoi, Vietnam, funded by the Australian Department of Foreign Affairs and Trade. The projects within Leon’s portfolio focused on the monitoring of coastal land use changes in relation to market and policy decisions. The assignment resulted in numerous collaborations with ministries and national research institutes, publications in SCOPUS-listed journals and presentations at international conferences and the OECD headquarters.

Halfway into 2016, Leon returned to the Netherlands in pursuit of a PhD at the Institute of Environmental Sciences, Leiden University. He researched and developed physics-based scalable methods for Sentinel-2 to map plant biodiversity patterns over large geographic extents. During his doctoral candidacy, Leon was involved in instructing computer lab courses in GIS and Environmental Biology. His PhD project has resulted in four manuscripts of which two were published in ‘Remote Sensing of the Environment’ (IF: 10.2) and oral presentations at the EGU in Vienna (2019) and the World Biodiversity Forum in Davos (2020). Before finishing his PhD, Leon commenced a postdoctoral research position within the Institute of Environmental Sciences of Leiden University funded and supported by the Centre for Sustainability and ACCEZ (Accelerating the Circular Economy in Zuid-Holland) with a focus on quantitative ecosystem services modelling for agricultural land-use scenarios.

Coming September, Leon will start a postdoctoral position at the Remote Sensing Laboratories of the University of Zurich (Switzerland) linking satellite-based ratings of company footprints in biodiversity and water to support sustainable finance. At the same time, Leon has received a European Space Agency (ESA) grant for Initial Support for Innovation (EISI*)* to further develop satellite-based biodiversity metrics into applicable data products in supply chain management and life-cycle assessment *(*www.biodiv-watch.space).

# V. Publications

## Peer-reviewed journals:

**Hauser, L. T.**, Timmermans, J., Soudzilovskaia, N. A., & P. M. van Bodegom (2022). *Linking Land Use and Plant Functional Diversity Patterns in Sabah, Borneo, through Large-Scale Spatially Continuous Sentinel-2 Inference.* Land, 11(4), 572. https://doi.org/10.3390/land11040572

Nguyen An Binh, **Hauser, L.T.**, Pham Viet Hoa, Giang Thi Phuong Thao, Nguyen Ngoc An, Huynh Song Nhut, Tran Anh Phuong & J. Verrelst (2022). *Quantifying mangrove leaf area index from Sentinel-2 imagery using hybrid models and active learning.* International Journal of Remote Sensing, pp. 1-22. https://doi.org/10.1080/01431161.2021.2024912

Bayrak, M.M., Marks, D., **Hauser, L.T.**, & D. Marks (2022). *Disentangling the concepts of global climate change, adaptation, and human mobility: a political-ecological exploration in Vietnam's Mekong Delta*. Clim. Dev. 0, 1–10. https://doi.org/10.1080/17565529.2022.2028596

**Hauser, L.T.**, Timmermans, J., van der Windt, N., Sil, Â.F., César de Sá, N., Soudzilovskaia, N.A., & P.M. van Bodegom (2021). *Explaining discrepancies between spectral and in-situ plant diversity in multispectral satellite earth observation*. Remote Sens. Environ. 265, 112684. https://doi.org/10.1016/j.rse.2021.112684

**Hauser, L.T.**, Féret J.B., Nguyen An Binh, Van der Windt, N., Timmermans J., Sil A., Soudzilovskaia N.A., & P.M. van Bodegom (2021). *Towards scalable estimation of plant functional diversity from Sentinel-2 imagery: In-situ validation in a heterogeneous (semi-) natural landscape*. Remote Sensing of Environment, Volume 262, 1 September 2021, 112505. https://doi.org/10.1016/j.rse.2021.112505

De Sá, N.C., Baratchi, M., **Hauser, L.T.**, & P.M. van Bodegom (2021). *Exploring the Impact of Noise on Hybrid Inversion of PROSAIL RTM on Sentinel-2 Data*. Remote Sens. 13(4), 1–20. https://doi.org/10.3390/rs13040648

**Hauser, L.T.**, Nguyen An Binh, Pham Viet Hoa, Nguyen Hong Quan & J. Timmermans, (2020). *Gap-free annual monitoring of mangrove forest dynamics in Ca Mau province, Vietnamese Mekong delta using the LandSat-7-8 Archives and post-classification temporal optimization*. Remote Sens. 2020, 12(22), 3729. https://doi.org/10.3390/rs12223729

Pham Viet Hoa. Nguyen Vu Giang, Nguyen An Binh, Nguyen Minh Hieu, Nguyen Trang Thi Quynh & **L.T. Hauser**, (2017). *Mangrove Species Discrimination in Southern Vietnam Based on in-situ Measured Hyperspectral Reflectance*. International Journal of Geoinformatics, 13(3).

**Hauser, L.T**, Nguyen Vu Giang, Nguyen An Binh, Dade, E., Nguyen Minh Hieu, Nguyen Thi Quynh Trang, Vu Huu Long, Tong Thi Huyen Ai, & Pham Viet Hoa (2017). *Uncovering the spatio-temporal dynamics of land cover change and fragmentation of mangroves in the Ca*

*Mau peninsula, Vietnam using multi-temporal SPOT satellite imagery (2004-2013).* Applied Geography, 86, pp. 197–207. http://doi.org/10.1016/j.apgeog.2017.06.019

**Hauser, L.T.**, Van Der Sluis, T. & Giezen, M., (2016). *The Role of Farm Management Characteristics in Understanding the Spatial Distribution of Landscape Elements: A Case Study in the Netherlands*. Rural Landscapes: Society, Environment, History. 3(1), pp.7. http://doi.org/10.16993/rl.14

## Conferences:

Invited speaker at World Biodiversity Forum, 23-28 February, 2020. Davos, Switzerland. Session: 'Remote Sensing for Biodiversity Monitoring'.

Invited speaker at SENSE Symposium, 11 October 2019, University of Twente. Session: 'Innovative research techniques in Environmental Sciences'.

Invited speaker at 11th International Convention of Asia Scholars. 16-19 July 2019, Leiden University, Leiden, The Netherlands. Session: 'Engaging with Vietnam'.

**Hauser, L.T**. (2019), *Vietnam's Voyage into Space; Motives and Pathways Towards building a New Satellite Technology Powerhouse.* 11th International Convention of Asia Scholars. Leiden University, Leiden, The Netherlands

Invited speaker at European Geosciences Union General Assembly, 7–12 April 2019, Vienna, Austria. Session: 'Remote sensing of interactions between vegetation and hydrology'.

**Hauser, L.T**., Timmermans, J., Soudzilovskaia, N.A. & P.M. van Bodegom (2019). *Mapping plant functional diversity across land use types and along elevation through satellite remote sensing*. 21st EGU General Assembly, EGU2019, Proceedings from the conference held 7-12 April, 2019 in Vienna, Austria.

Invited speaker at Data to Decisions: Valuing the Societal Benefit of Geo-Spatial Information: A workshop organized by the GEOValue community in collaboration with OECD, NASA, and USGS. March 10-11, 2016, OECD, Paris, France.

Invited speaker at 6th DAAD and VNU international conference for 'Remote Sensing and GIS Application and Integration', 6-9 Oct. 2015, Hanoi

**Hauser L.T.** et al. (2015), *Spectral Discrimination of Common Mangrove Species in the Ca Mau Peninsula, Vietnam; Using a large sample-set of hyperspectral in-situ canopy data*. Proceedings of the 6th DAAD and VNU international conference for 'Remote Sensing and GIS Application and Integration', 6-9 Oct. 2015, Hanoi; Vietnamese National University, pp. 649-656. DOI: 10.13140/RG.2.1.4535.3683

Invited speaker at International Conference on "Conservation, Sustainable Community Livelihood and Climate Change Mitigation". December 2013, Chinese University of Hong Kong, Hong Kong.

Biodiversity enables ecosystems to thrive through the synergy of functional differences among organisms. While human well-being strongly depends on biodiversity-driven ecosystem services, human actions are also at the root of current unprecedented biodiversity declines. Comprehensive methods to assess the dynamics and state of biodiversity are therefore increasingly urgent. This thesis studies the overlooked capabilities of current satellite observations to conduct large-scale monitoring of plant functional diversity, with a focus on the European Space Agency's flagship Sentinel-2 satellite. Specifically, it addresses the use of spectral diversity metrics, radiative transfer model inversion, the need for adequate in-situ validation, and the role of spatial scale in our perception and estimation of satellite-derived plant functional diversity patterns.