# Satellite remote sensing of plant functional diversity

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# 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

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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).

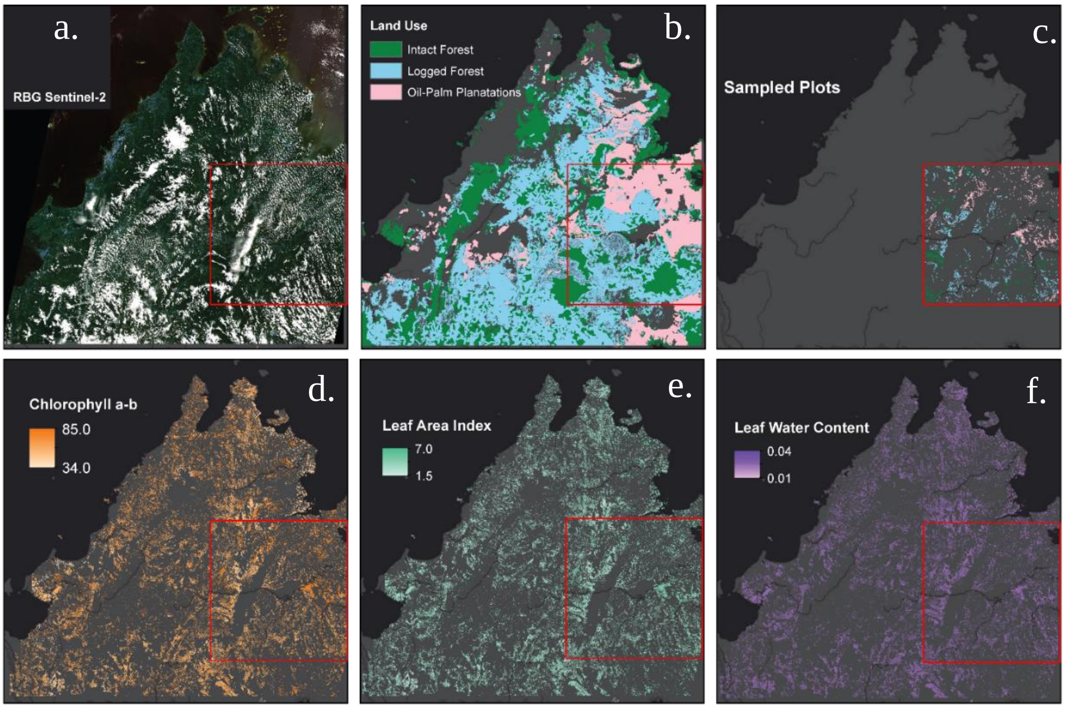

*Fig. 5.1: a) Map of the Sentinel-2 observation, as seen through a true visible range composite image, over the study area in Sabah, Malaysia on the 9th of July 2017 after atmospheric corrections. b) Map of the three land use classes within the Sabah study area used for analysis. c) Map of study area 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):

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

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

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 $\bar{dG}$ 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).

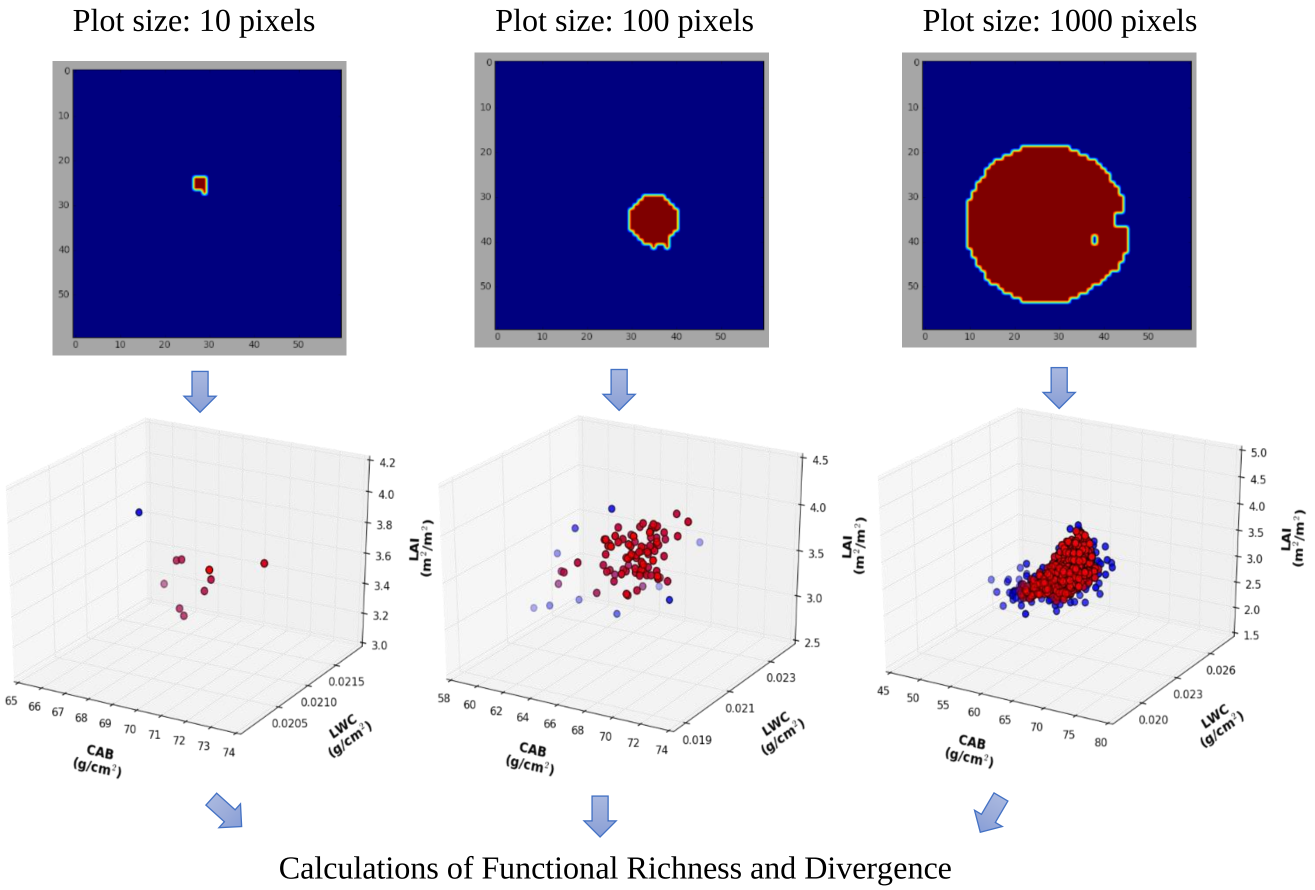

*Fig. 5.2: Three different plot sizes are exemplified for functional diversity calculations. All plots (N = 1713) are grown based on a nest radial nearest neighbour search and plot locations are chosen in which plot sizes van be varied from 0.4ha to 60ha continuously without masks transecting the plots.*

### 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.

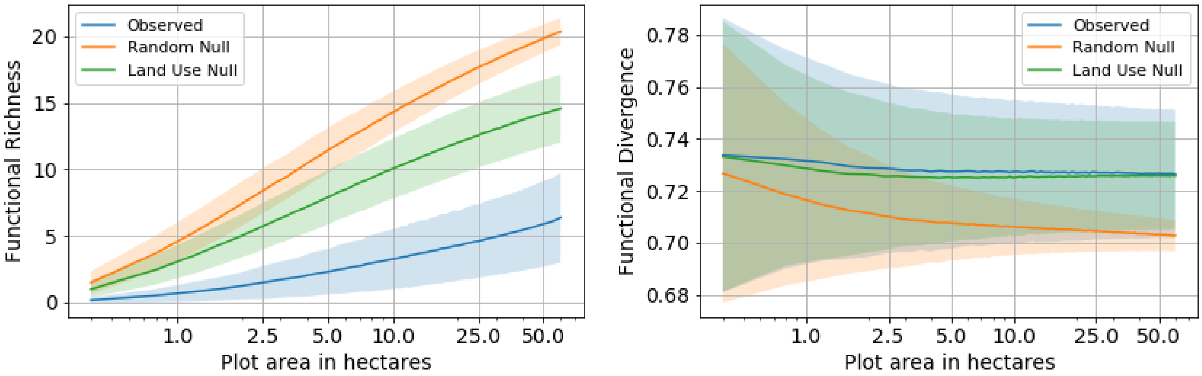

*Fig. 5.3: Scale dependency of the functional richness (left) and divergence (right) metrics comparing observed remotely sensed diversity in Sabah, Borneo, versus null-models based on randomly drawn trait combinations from observed trait values. The 'Random Null' model (orange) draws random trait combinations 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

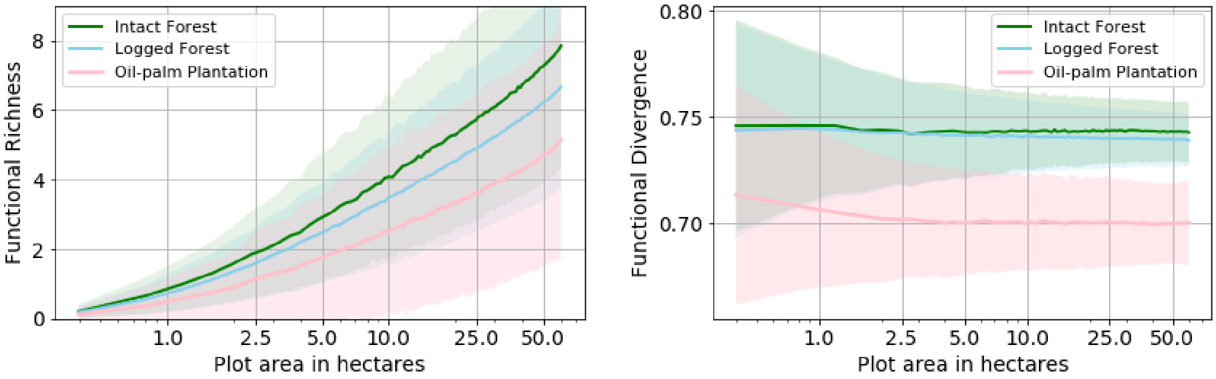

*Fig. 5.4: Scale dependency of the functional richness (left) and divergence (right) metrics stratified across land use types. Functional diversity calculations were done over continuous plots of one land use type over a range from 0.4 to 60 ha. Dark lines represent the mean and standard deviations are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

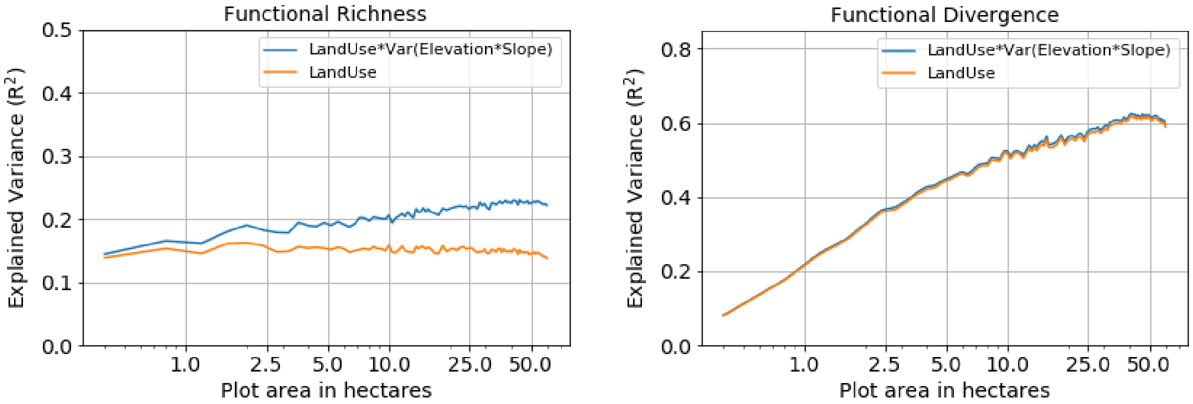

*Fig. 5.5: Explained variance of two sets of linear regression models as predictors of spatial functional richness (left) and divergence (right) patterns across plot area size. The first set of models (orange) includes land use as a predictor of functional diversity. The second set of models (blue) expands 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.