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Satellite remote sensing of plant functional diversity

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

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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 km²) 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 phylogenetic <https://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 ($\mu\text{g}/\text{cm}^2$) 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 Eta² values which is a measure of effect size for use in ANOVA, analogous to R² 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).

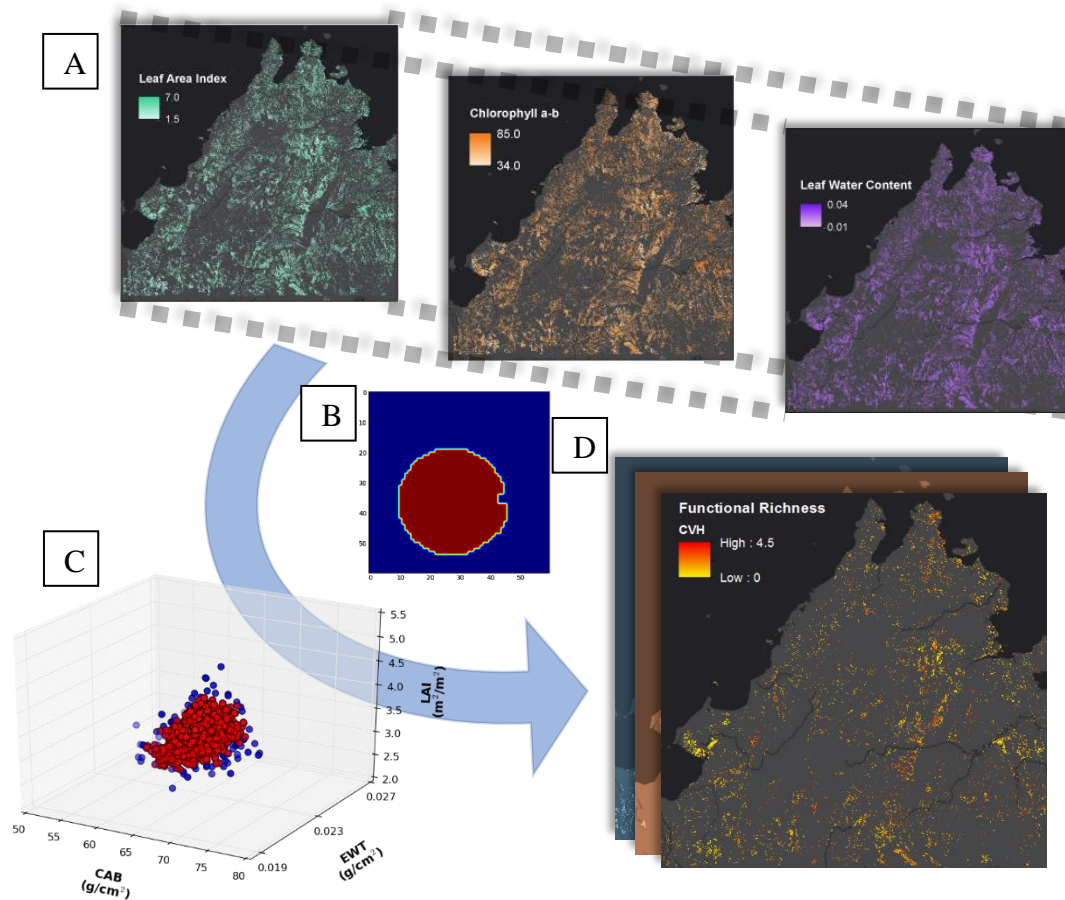


Fig. 4.1: The data pipeline from satellite remotely sensed traits to functional diversity metrics maps; (A) maps of Leaf Area Index (m^2/m^2) (LAI), leaf Chlorophyll-a-b Content ($\mu g/cm^2$) (CAB), and leaf Equivalent Water Thickness (g/cm^2) (EWT). Masks are portrayed in dark grey. (B) Zoom-in on 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).

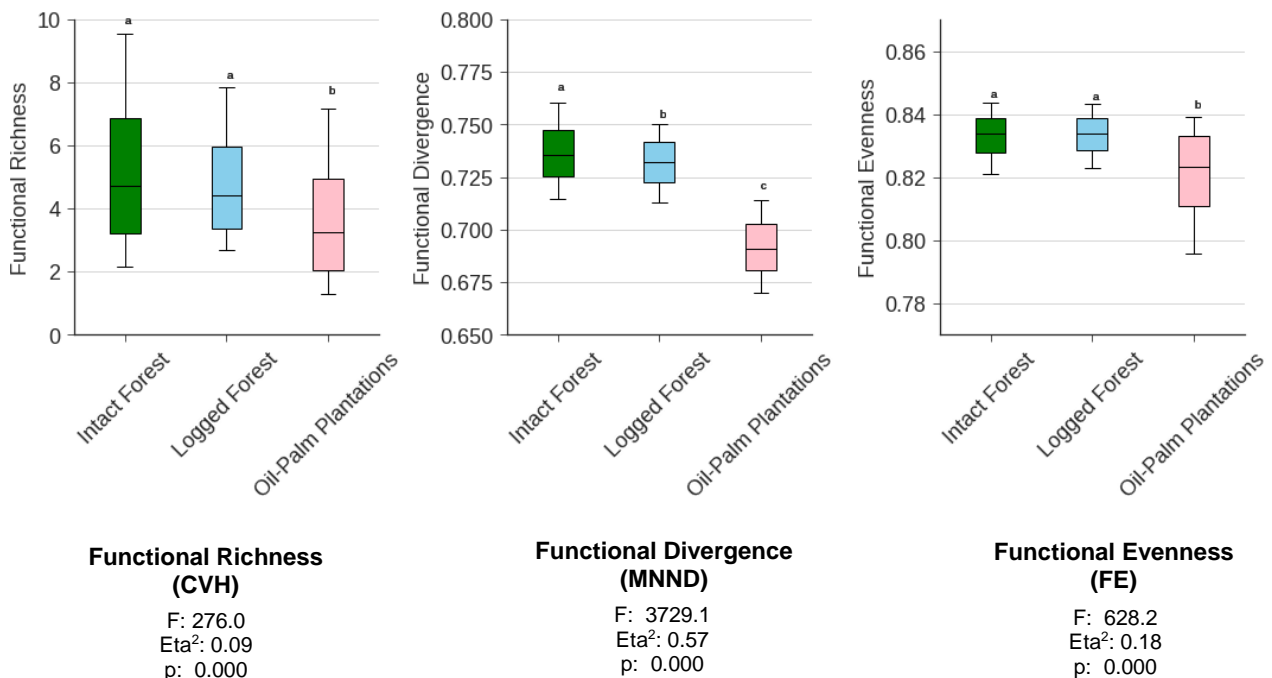


Fig. 4.2: Differences in functional diversity metrics across land use types (below 500m ASL) in boxplots and ANOVA results. Boxplots' box represents 25, 50 and 75 percentiles and the whiskers depict the 10, 90 percentiles. Differences in retrieved trait estimates between land use types according to a 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.

	N	Functional Richness		Functional Divergence		Functional Evenness	
		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.