




RESEARCH ARTICLE

Spectral characterization of plant diversity in a biodiversity-enriched oil palm plantation

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Keywords

canopy diversity, imaging spectroscopy, remote sensing, spectral diversity, understory vegetation

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Editor: Prof. Mat Disney

Associate Editor: Dr. Javier Lopatin

Received: 23 December 2024; Revised: 29 July 2025; Accepted: 12 September 2025

doi: 10.1002/rse2.70034

Abstract

Assessing plant diversity using remote sensing, including airborne imaging spectroscopy, shows promise for large-scale biodiversity monitoring in landscape restoration and conservation. Enriching plantations with native trees is a key restoration strategy to enhance biodiversity and ecosystem functions in agricultural lands. In this study, we tested how well imaging spectroscopy characterizes plant diversity in 37 experimental plots of varying sizes and planted diversity levels in a biodiversity-enriched oil palm plantation in Sumatra, Indonesia. Six years after establishing the plots, we acquired airborne imaging spectroscopy data comprising 160 spectral bands (400–1000 nm, at ~3.7 nm bandwidth) at 0.3 m spatial resolution. We calculated spectral diversity as the variance among image pixels and partitioned spectral diversity into alpha and beta diversity components. After controlling for differences in sampling area through rarefaction, we found no significant relationship between spectral and plant alpha diversity. Further, the relationships between the local contribution of spectral beta diversity and plant beta diversity revealed no significant trends. Spectral variability within plots was substantially higher than among plots (spectral alpha diversity ~82%–87%, spectral beta diversity ~11%–18%). These discrepancies are likely due to the structural dominance of oil palm crowns, which absorbed most of the light, while most of the plant diversity occurring below the oil palm canopy was not detectable by airborne spectroscopy. Our study highlights that remote sensing of plant diversity in ecosystems with strong vertical stratification and high understory diversity, such as agroforests, would benefit from combining data from passive with data from active sensors, such as LiDAR, to capture structural diversity.

Introduction

Quantifying plant diversity using remote sensing has become a high priority for landscape management and conservation research, particularly in the context of biodiversity loss and the need for scalable monitoring tools

(Asner, 2013; Draper et al., 2020; Roberts et al., 2022). Imaging spectroscopy, also known as hyperspectral remote sensing, measures the interaction between light and matter, including plants, across hundreds of contiguous spectral bands, typically ranging between 400 and 2400 nm, allowing for a detailed analysis of how light

interacts with various materials (Zahra et al., 2024). Spectral reflectance of plants depends on leaf chemistry, anatomy and morphology (Billings & Morris, 1951; Curran, 1989; Shull, 1929), and when measured from a distance, also on plant architecture (Ollinger, 2011). Detailed spectral data allow the identification of subtle differences in plant traits that are not detectable with other remote sensing methods (Asner & Martin, 2009; Serbin et al., 2015; Singh et al., 2015; Z. Wang et al., 2020). Imaging spectroscopy has emerged as a powerful tool for assessing biodiversity, addressing the challenges of comprehensive measurement and monitoring of different landscapes for large-scale studies (Massey et al., 2023; Skidmore et al., 2021; Turner, 2014).

The use of remote sensing to quantify plant spectral diversity is based on the spectral variation hypothesis (SVH) (Palmer et al., 2002). This hypothesis states that areas with high spectral variation exhibit high environmental variation and thus can harbour more species than areas with less spectral variation. Recent advances in imaging spectroscopy, which view plant spectra as integrated measures of their form and function (Kothari & Schweiger, 2022; Ustin & Gamon, 2010), have facilitated the derivation of spectral diversity metrics (Draper et al., 2020; Féret & Asner, 2014; Laliberté et al., 2020; Rocchini et al., 2021; Wang & Gamon, 2019). Although specifics vary, all of these metrics capture the variation of plant spectra within an ecosystem, serving as proxies for biodiversity (Féret & Asner, 2014; Laliberté et al., 2020; Wang & Gamon, 2019). However, the spectral diversity–biodiversity relationship can be complicated by mismatches between plant and pixel size (Schweiger & Laliberté, 2022; Wang et al., 2018) and complex canopy layering (Conti et al., 2021; Coverdale & Davies, 2023). In addition, factors such as changes in illumination, atmospheric conditions and instrument characteristics can influence the relationship between spectral and plant diversity (Camacho et al., 2019; Fassnacht et al., 2022).

The SVH has been tested using data from different platforms, including spaceborne (e.g. MODIS (Schmidtlein & Fassnacht, 2017)), airborne (e.g. HyMap; Crofts et al., 2024) and UAV-based systems (Xu et al., 2022). Each platform offers distinct advantages and trade-offs in terms of spatial, spectral and temporal resolution (Rossi & Gholizadeh, 2023; Schneider et al., 2017). Spaceborne sensors allow for broad-scale, frequent monitoring, but at coarse spatial resolution (Liu et al., 2024). UAV-based sensors can capture ultra-fine spatial detail at flexible time intervals but are limited in coverage (Torresani et al., 2024). Airborne platforms offer a balance between resolution and coverage, making them particularly relevant for landscape-scale biodiversity monitoring (Schneider et al., 2017). However, quantifying plant diversity

using spectral diversity from airborne platforms can be challenging in ecosystems with multiple vertical vegetation strata, as in forests, where only a subset of trees may reach the top canopy (e.g. due to different growth rates or specific species traits), limiting the ability of airborne surveys to capture the full spectrum of biodiversity below the canopy (Torresani et al., 2024).

Despite the demonstrated potential of imaging spectroscopy for assessing plant diversity in forest ecosystems (e.g. Asner & Martin, 2009; Féret & Asner, 2014; Hill et al., 2019; Torresani et al., 2024), its application in the agroforestry and restoration context remains a developing field (e.g. Adão et al., 2017; Piironen et al., 2017; Torresani et al., 2024). The imperative to quantify and understand plant diversity within these restoration efforts has intensified, driven by the need for effective landscape management and ecosystem restoration (UN, 2021). Agroforestry systems integrate diverse trees and woody vegetation into cultivated crops (FAO, 2019), for example through woodland islets (i.e. tree islands), which are introduced as small patches of native trees within conventionally managed agricultural matrices (Benayas et al., 2008). These systems have been shown to promote the recovery of biodiversity and ecosystem functions while maximizing ecosystem services (Holl et al., 2020; Moreno et al., 2018; Torralba et al., 2016; Zemp et al., 2023), and are therefore recognized as an efficient strategy for restoring degraded landscapes (Dagar et al., 2020; Pashkevich et al., 2022). However, the complexity of agroforestry systems, characterized by multiple vegetation layers, presents challenges for remote sensing techniques that primarily capture information from the top of the canopy (Schweiger & Laliberté, 2022).

Here, we test the degree to which airborne imaging spectroscopy can predict plant diversity in biodiversity-enriched oil palm plantations at alpha- and beta diversity scales. For this, we used airborne imagery obtained from an oil palm plantation, enriched with 52 plots varying in size (from 25 to 1600 m²) and planted with tree diversity levels ranging from zero to six species, 6 years before image acquisition (Teuscher et al., 2016). These plots represent a type of agroforestry in the form of tree islands that combine oil palms (*Elaeis guineensis*, *Jacq.*), planted native trees, and naturally regenerated plants. We tested the hypothesis that spectral diversity (as defined by Laliberté et al., 2020) correlates with plant diversity, as found in other forest ecosystems (Draper et al., 2020; Frye et al., 2021; Schweiger & Laliberté, 2022). Further, we hypothesized that larger tree islands would exhibit higher spectral alpha diversity and support greater taxonomic diversity, due to greater environmental heterogeneity (Paterno et al., 2023; Zemp et al., 2023), even after controlling for sampling effort. Finally, we

hypothesized that the dissimilarity in species composition among tree islands is linked to their spectral dissimilarity, that is spectral beta diversity (He et al., 2009).

Materials and Methods

Study site

The study site is located in the state of Humusindo Makmur Sejati near the Bungku village in Jambi province, Sumatra, Indonesia (1.95° S, 103.25° E; 47 ± 11 m a.s.l.). The area is characterized by a humid tropical climate with a mean annual temperature of 26.7 ± 1.0°C and a mean annual precipitation of 2235 ± 385 mm (1991–2011) (Teuscher et al., 2016). The study site is part of EFForTS-BEE (Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems, <https://www.uni-goettingen.de/efforts>, part of the global network of tree diversity experiments TreeDivNet, <https://treedivnet.ugent.be>), a large-scale, long-term biodiversity enrichment experiment in oil palm plantations. It consists of 52 plots in the form of tree islands (Benayas et al., 2008) randomly distributed within a 140-ha African oil palm monoculture (*Elaeis guineensis*, Jacq.), six to 12 years of age at the establishment of the experiment in December 2013. The quadratic plots are located at least 84 m apart (Fig. 1). They vary in size from 25, 100, 400, and 1600 m², and in the number of tree species planted at the onset of the experiment (i.e. the diversity level), ranging from no tree planted (i.e. the treatment consisted of palm tree removal to make space for natural regeneration) to one, two, three, and six native tree species planted. Before establishing the plots, 40% of palms were removed in all but the 25 m² plots (Teuscher et al., 2016). The experiment follows a random partition design (Bell et al., 2009), where four plots were assigned to diversity level 0, 24 were planted with one, 12 with two, eight with three, and four with six tree species per plot. After establishment, fertilization, herbicide and pesticide application stopped, resulting in plants establishing spontaneously from natural regeneration. Manual weeding around the planted trees stopped about 2 years after tree planting to increase the chance of survival of the planted trees (Teuscher et al., 2016; Zemp et al., 2023).

Ground-based plant inventory

In January and February 2020, we recorded species identity, stem diameter and tree height for all woody plant individuals, that is all trees, shrubs and lianas, planted or naturally regenerated, including all oil palms inside the tree islands (Table S1). Stem diameter was measured at 5 cm above the ground for seedlings <1.3 m and at

1.3 m (diameter at breast height, DBH) for taller individuals. Tree height was measured from the base of the trunk to the top of the crown, and for oil palms, it was measured from the base of the trunk to the base of the youngest leaf.

Imaging spectroscopy data processing

We acquired airborne imaging spectroscopy data with a Neo HySpex VNIR-1600 sensor (HySpex, Oslo, Norway) installed on a BN2T research aircraft flying at around 1780 m a.s.l. The airborne campaign was carried out by Dimap HK Pty Limited (Kowloon, Hong Kong) on January 27, 2020. The spectral imagery covered the 400–1000 nm wavelength region (visible to near-infrared, VNIR) in 160 bands with a spectral sampling interval of 2.5 nm and a spatial resolution of 0.3 m (for technical specifications, see Table S2).

Imaging spectroscopy data were radiometrically, geometrically and atmospherically corrected (Table S2). First, the raw data were calibrated to radiance. The data were further ortho-rectified and georeferenced with ground control points, a digital surface model retrieved from the airborne laser scanning data (acquired in the same campaign) and a boresight correction. Finally, the geocoded images were atmospherically corrected using the ATCOR-4 algorithm with the scan angle and an assumed water vapour column of 2 g/cm². The aerosol type used in the algorithm was rural areas.

Visual inspection revealed significant cloud effects and blurring, so we decided to work with four flight lines covering 37 of the 52 plots. We excluded noisy spectral bands at the beginning and the end of the spectrum (wavelengths <450 and >930 nm), keeping 132 bands for the subsequent analysis. Data were visually checked with *spectrolab* (Meireles et al., 2023) in R (R Core Team, 2024). Since our study plots were scattered across the oil palm plantation (Fig. 1B), we constructed an artificial landscape by assembling the spectral images of our 37 plots next to each other for the calculation of spectral diversity indices (Fig. S1; Text S1). We applied vector normalization to all images to correct illumination differences between flight lines, as implemented in *spectrolab* (Meireles et al., 2023).

Calculating spectral and plant diversity

First, we used principal component analysis (PCA) with type-I scaling to check spectral variation among all pixels from the images. PCA in spectral analysis helps to minimize noise, reduce artefacts due to illumination, and highlight meaningful spectral variation (Laliberté et al., 2020; Ustin & Gamon, 2010). We retained 24 principal components (PCs) that together explained more

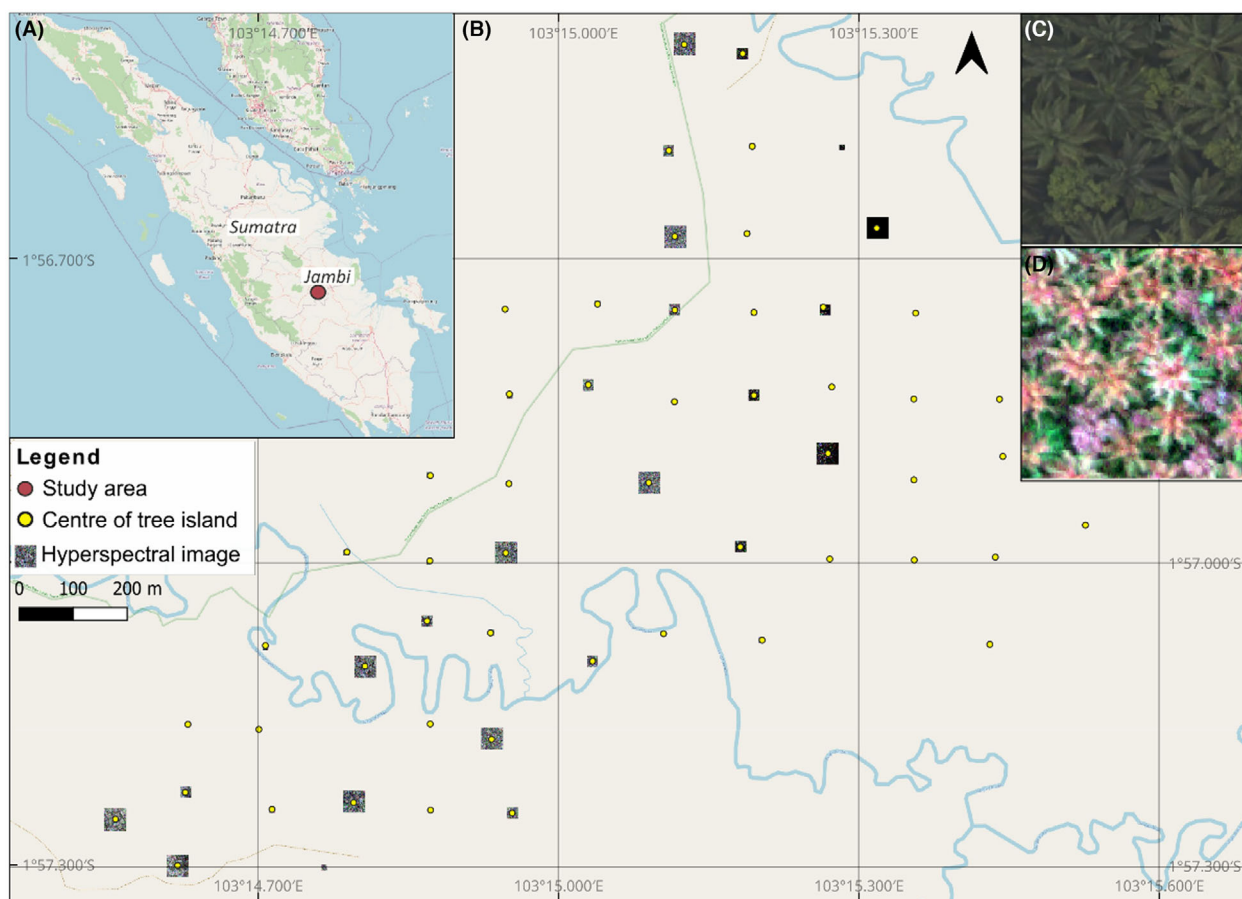


Figure 1. Map of the study area and spatial distribution of tree islands (experimental plots) in the biodiversity-enriched oil palm plantation. (A) Location of the study area (red point) within Sumatra, Indonesia. (B) Distribution of the tree islands across the plantation, with yellow points indicating the centre of each tree island and squares showing the hyperspectral images. (C) One example of a tree island shown using a true-colour orthophoto captured in 2020 at a resolution of 5 cm. (D) Colour-infrared (CIR) image created from imaging spectroscopy data using near-infrared (NIR) 752.5 nm, red 654.5 nm, and green 557.1 nm bands, with a pixel size of 30 cm. The true-colour orthophoto is included only for illustrative purposes and was not used in the analysis. For CIR images of all 37 studied plots (see Fig. S1).

than 95% of the total spectral variation. This threshold ensured that most of the relevant spectral information was preserved while excluding lower-variance components likely dominated by noise or atmospheric interference (Laliberté et al., 2020). We then calculated spectral diversity as the variance among all image pixels within the study region, capturing the spread of spectral signatures among pixels, following the concept and R functions outlined in Laliberté et al. (2020) and available online (<https://github.com/elaliberte/specdiv>).

Next, we partitioned the total spectral variation, that is spectral gamma diversity, into spectral alpha (within-plot spectral variation) and beta (among-plot spectral variation) components. Spectral alpha diversity is a measure standardized to the number of pixels per plot, allowing for comparison among plots of different sizes and numbers of pixels. We grouped plots by size and calculated

the plot-wise local contribution to spectral beta diversity (LC beta diversity), which represents how much each plot contributes to the overall beta diversity (Legendre & De Cáceres, 2013). Finally, we calculated the contribution of spectral alpha and beta diversity to spectral gamma diversity for all plots grouped by plot size.

We calculated plant taxonomic diversity at the plot level using tree inventory data, including the planted trees, regenerated trees and oil palms, for the same 37 plots available for spectral diversity calculations (Table S1) using the *vegan* package (Oksanen et al., 2022) in R (R Core Team, 2024). Species richness was calculated as the total number of different species present in each plot. To account for differences in sampling area, we used individual-based rarefaction (Gotelli & Colwell, 2001). We calculated rarefied species richness per plot using the *vegan::rarefy()* function (Oksanen et al., 2022), based on

the minimum number of individuals found in any plot. This approach allowed for unbiased comparisons of species richness across plots of varying sizes.

Shannon diversity was calculated based on differences in species abundance, and Simpson diversity was calculated as the probability that two individuals randomly selected from a plot belong to different species (Chao et al., 2006; Oksanen et al., 2022). We calculated beta diversity using the Jaccard dissimilarity index, which quantifies the uniqueness of species composition between the different plots (Chao et al., 2006). Then, we calculated the local contribution to beta diversity (LC beta diversity).

We used linear regression models to test how well spectral diversity indices predicted plant alpha diversity (i.e. rarefied species richness, Shannon and Simpson diversity) and the local contribution to plant beta diversity using all 37 plots combined and separated by plot sizes. To test for any significant differences among results grouped by plot size, we performed post hoc analyses using Tukey's honest significant difference (HSD) test. Additionally, to test whether the relationship between spectral diversity and plant diversity was stronger for canopy-emergent individuals, we repeated the analysis using a subset of the inventory filtered to include only trees taller than 5 m to represent canopy-layer vegetation (Reiner et al., 2023; Vehmas et al., 2011). All analyses were performed in R version 4.3.2 (R Core Team, 2024). For graphics, we used the package *ggplot2* (Wickham et al., 2021).

Results

Across the 37 plots, we recorded 4274 trees from 55 species (Table S1), of which 266 were oil palms, 2088 planted trees, and 1920 regenerated trees. On average, plots of 5 × 5 m had 3.7 ± 1.6 plant species, plots of 10 × 10 m had 5.4 ± 1.8 species, plots of 20 × 20 m had 8.8 ± 2.7 species, and plots of 40 × 40 m had 16.1 ± 4.3 species. Around 64% of all individual trees and 91% of all species were found in the height class 0–5 m, 26% of all individual trees and 51% of all species were found between 5 and 10 m, 9% of all individual trees and 15% of all species were found between 10 and 15 m, 1% of all individual trees and only 4 species were found between 15 and 20 m, and less than 1% of all individual trees, which were either oil palms or *Hibiscus macrophyllus*, *Parkia speciosa*, and *Peronema canescens*, reached heights greater than 20 m (Fig. 2). Mean tree height was 4.7 ± 3.4 m, planted trees measured on average 6 ± 4 m, naturally regenerated trees 3 ± 1.7 m, and oil palms 6.3 ± 0.9 m (Fig. S2, Text S2). While species richness increased with plot size (Fig. S3), rarefied species richness did not. Similarly, neither Shannon nor Simpson

diversity, nor spectral alpha diversity showed significant differences depending on plot size (Fig. 3B–D).

Further, we found no significant relationships between spectral alpha diversity and plant diversity (rarefied species richness, Shannon or Simpson diversity) for all 37 plots combined or for different plot sizes analysed separately (Fig. 4A–C, Table S3). However, when repeating our analyses including only trees taller than 5 m, we found consistent positive trends between spectral alpha diversity and plant diversity, which were stronger for Simpson and Shannon diversity compared to species richness (Fig. 4D–F and Table S4). These trends also remained statistically non-significant. Here, we used observed species richness (Fig. 4D) rather than rarefied diversity metrics due to the small number of individuals in some plots.

We found that the total spectral diversity within the experiment (gamma diversity) was mainly driven by differences in pixels within plots (i.e. spectral alpha diversity) rather than spectral differences among plots (i.e. spectral beta diversity). Spectral alpha diversity accounted for 87%, 89%, 88% and 82% of the total spectral variance for plots measuring 25, 100, 400 and 1600 m², respectively, while spectral beta diversity accounted for only 11%–18%. Additionally, all correlations between the local contributions to spectral (LCSD beta) and taxonomic beta diversity (LC beta diversity) were non-significant across plot size class independently from including all trees (Fig. S4) and only trees >5 m (Fig. S5).

Discussion

We used spectral diversity calculated as the variance among pixels derived from imaging spectroscopy to test how far we could capture plant diversity in an oil palm plantation enriched with tree islands of varying sizes and diversity levels. We found no significant relationships between spectral diversity and plant diversity (measured as rarefied species richness, Shannon, and Simpson diversity). This is likely because the reflectance signal captured by imaging spectroscopy depends primarily on the chemistry and structure at the uppermost canopy levels, while most species richness in the tree diversity experiment was concentrated in the understory <5 m (Fig. 2).

According to the spectral variation hypothesis (SVH), greater variability in remotely sensed spectral reflectance can serve as a proxy for environmental heterogeneity and plant diversity (Palmer et al., 2002; Rocchini et al., 2010). However, this relationship is context-dependent and influenced by factors, including vegetation structure and composition, as well as the distribution of species diversity across different canopy layers and canopy gaps (Fasnacht et al., 2022; Perrone et al., 2023; Rocchini

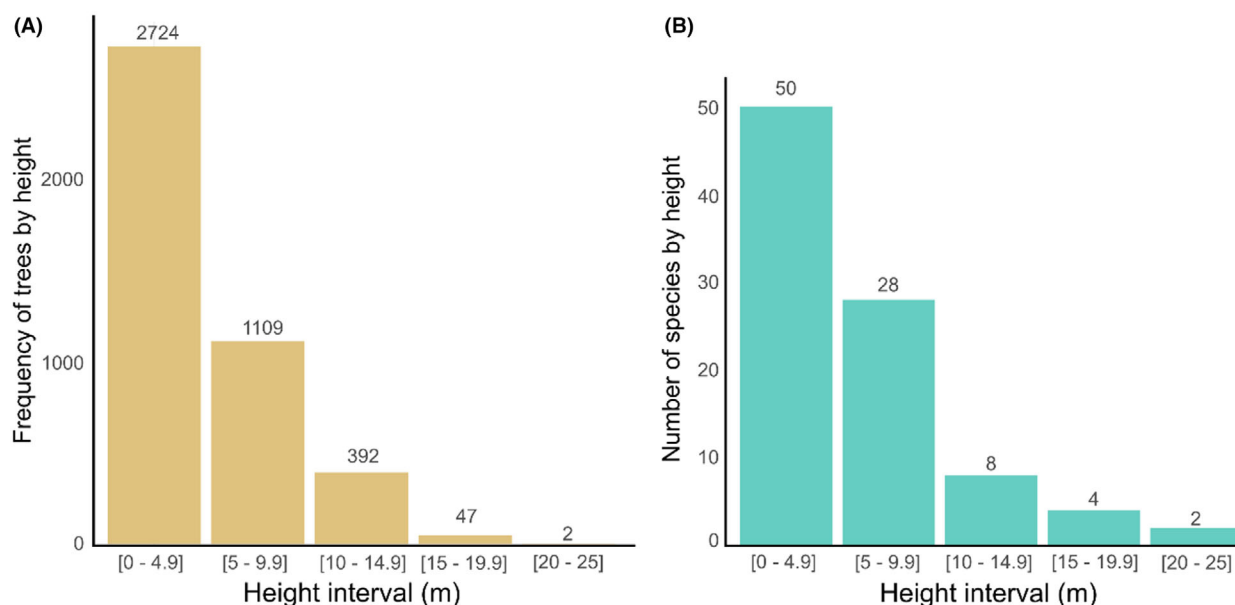


Figure 2. Distribution of the number of trees and species across height classes. (A) Frequency distribution of all individual trees (including planted, naturally regenerated and oil palms) recorded across the 37 study plots. (B) Number of unique plant species found per height class.

et al., 2010; Schmidlein & Fassnacht, 2017). In our study, tree islands exhibited enhanced structural complexity due to the initial thinning of the tall oil palms and subsequent planting and natural establishment of native trees. Six years after planting, the experimental trees had reached mid-canopy level, while naturally regenerating vegetation led to a dense and heterogeneous understory, overtopped by the remaining tall oil palms (Kikuchi et al., 2024; Zemp et al., 2019). This multi-layered complexity, while beneficial for ecosystem restoration, presents challenges for optical remote sensing methods as only small fractions of light can reach the diverse lower canopy layers (Hernandez-Santin et al., 2019; Yang et al., 2023). Most of the reflected radiation captured by the sensor comes from the dominant upper canopy, with complex scattering limiting the detectability of vegetation below.

While we attempted to isolate the canopy vegetation by filtering for individuals taller than 5 m, this only removed understory diversity from our calculations. Although the strength of the relationships between spectral diversity and plant diversity increased and showed consistent trends, they remained statistically non-significant (Fig. 4D–F). This is likely due to the structural dominance of oil palm crowns (Hernandez-Santin et al., 2019), which likely occluded most emergent trees from the sensor's view and cast shadows on the remaining trees in the canopy gaps. Moreover, in our ground-based inventory, palm height measurement was recorded only up to the base of the youngest leaf, likely underestimating the actual crown

height. We observed that oil palms, having more voluminous crowns than the other trees, dominated the canopy cover (Fig. 1C,D), as confirmed by a drone-based assessment 3 years post-enrichment, where 56% of the canopy was dominated by oil palms compared to only 15% by other trees (Khokthong et al., 2019). Additionally, our inventory revealed that 64% of all individuals and 50 of 55 species were found in the 0–5 m height layer, further highlighting the vertical complexity and concentration of tree diversity in the lower layers of the canopy. Moreover, while raw species richness increased with plot size, this pattern was not mirrored in Shannon or Simpson diversity, nor in rarefied species richness. This suggests that observed differences in richness across plot sizes were primarily driven by sampling effort rather than underlying ecological variation, which is supported by us not finding any significant differences in tree diversity across plot sizes after accounting for sampling effort (Fig. 3).

The overall limited variation in tree diversity across the experiment further complicates estimating diversity from afar. We found that spectral diversity within islands exceeded spectral diversity between islands, suggesting a relatively homogeneous spectral landscape across the study area. The absence of significant correlations between the local contribution of each community to spectral and plant beta diversity further corroborates that the structural dominance of oil palm crowns limited the ability of imaging spectroscopy to capture most of the understory vegetation, where most of the diversity resides

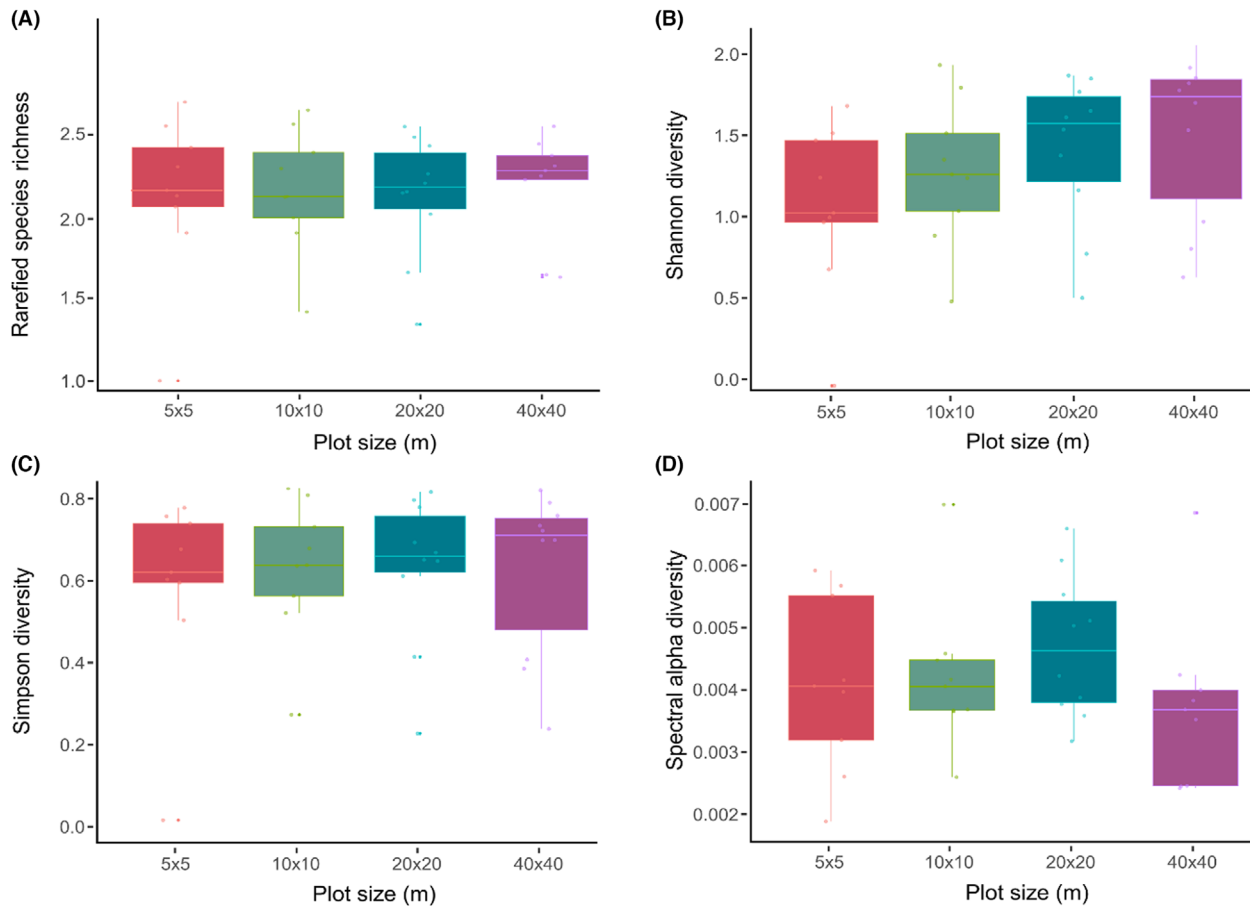


Figure 3. Diversity patterns in the enriched oil palm plantation in relation to plot size. (A) Rarefied plant species richness; (B) Shannon diversity; (C) Simpson diversity; and (D) spectral alpha diversity. Values are shown by plot size categories (5' × 5' m, 10' × 10' m, 20' × 20' m, and 40' × 40' m). Statistically significant differences among plot sizes were tested using Tukey's HSD test. We found no significant differences at $p < 0.05$.

in this agroforestry system. In addition to canopy occlusion of lower layers, image blurring, fog and shadows could have led to the mixing of spectral signals and reduced distinctiveness of spectral signatures across the landscape (Li et al., 2022). This homogenization of spectral signals poses challenges specifically in the tropical ecosystems.

Our results underscore the limitations of imaging spectroscopy in capturing plant diversity in multi-layered and structurally complex (agro-)forests. While imaging spectroscopy offers valuable insights into top-of-the-canopy diversity, which can be useful for understanding habitat structure and the maintenance of ecosystem functionality and stability (Fornoff et al., 2021), it falls short in detecting diversity within lower vegetation strata. In our study, most plant diversity resided below the oil palm canopy, and this vertical stratification limited the ability of airborne optical sensors to detect understory species. Until

relationships between top-of-the-canopy tree diversity and the diversity of lower canopy layers are better understood, it is unlikely that canopy reflectance alone can capture plant diversity in complex, multi-layered ecosystems.

Future plant diversity monitoring efforts should consider leveraging multi-sensor strategies combining airborne or satellite imaging spectroscopy with complementary technologies like light detection and ranging (LiDAR), which provide vertical structural information (Ming et al., 2024; Montoya-Sánchez et al., 2024). These approaches could offer a more comprehensive view of biodiversity across forest strata when integrated with ground-based inventories (Crespo-Peremarch et al., 2018; Yang et al., 2023). This is particularly important in the context of ecosystem restoration, where increasing structural complexity at lower canopy layers is an ecological goal but a methodological obstacle for passive remote sensing.

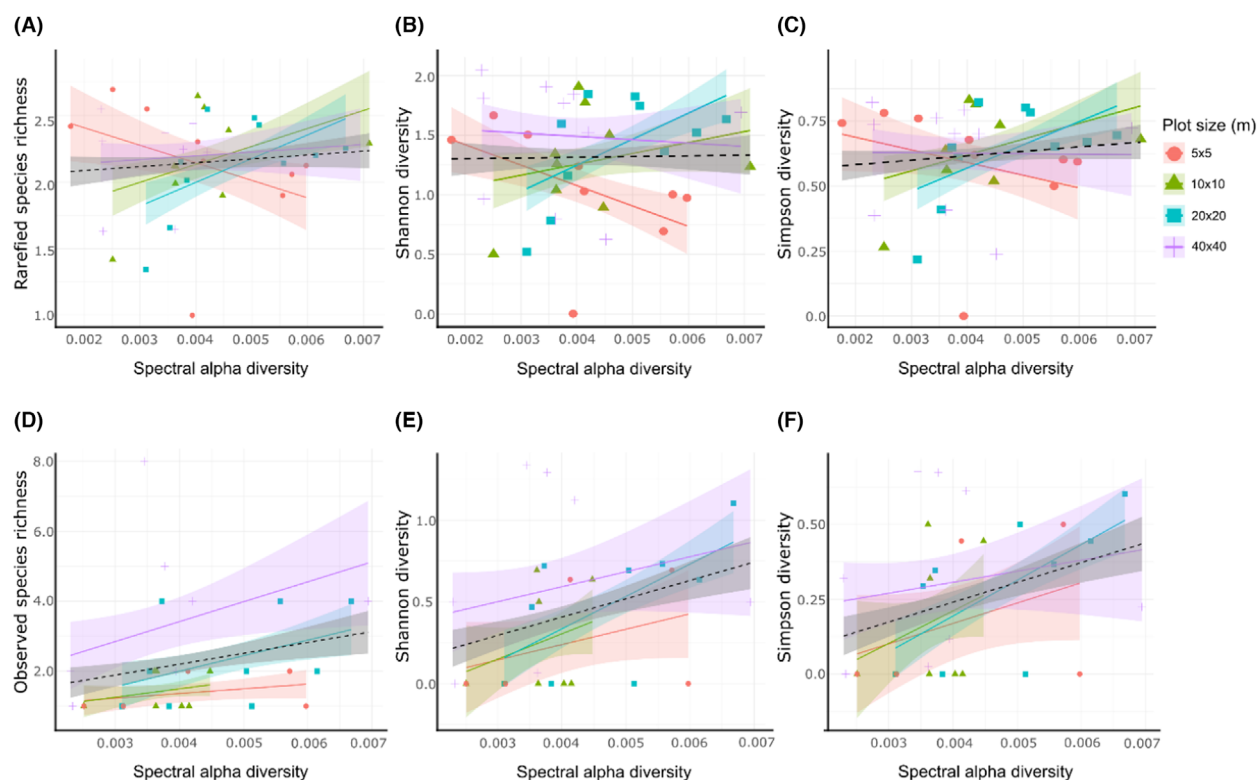


Figure 4. Relationships between spectral alpha diversity and plant alpha diversity, for trees of all height classes, showing (A) rarefied species richness (all plots: $r^2 = 0.02$, p -value = 0.39, $n = 37$); (B) Shannon diversity (all plots: $r^2 = 0.0007$, p -value = 0.87, $n = 37$); and (C) Simpson diversity (all plots: $r^2 = 0.019$, p -value = 0.41, $n = 37$), and for trees >5 m, showing (D) observed species richness (all plots: $r^2 = 0.061$, p -value = 0.187, $n = 30$); (E) Shannon diversity (all plots: $r^2 = 0.111$, p -value = 0.07, $n = 30$); and (F) Simpson diversity (all plots: $r^2 = 0.118$, p -value = 0.062, $n = 30$). The black dotted line indicates the overall relationship across all plots; the coloured lines indicate the relationships per specific plot sizes (see Table S3). The level of confidence interval used was 0.6; R -squared = r^2 ; sample size = n .

Conclusion

In this study, we attempted to quantify plant spectral diversity using airborne imaging spectroscopy in an oil palm plantation enriched with tree islands of varying sizes and diversity levels. We explored the relationship between remotely sensed spectral diversity and ground-based plant diversity but found no significant correlations, although positive trends became more apparent when removing understory vegetation from our analysis. This is likely due to the structural dominance of oil palm crowns, which predominantly contributed to the spectral signatures captured by airborne imaging spectroscopy. However, in our enriched oil palm plantation, much of the plant diversity was concentrated below the oil palm canopy, remaining less detectable. Our findings underscore the limitations of optical remote sensing in characterizing plant diversity in vertically structured ecosystems such as agroforests. Given the challenges posed by vertical canopy stratification, future research could focus on integrating complementary remote sensing approaches, such as LiDAR, to improve

plant diversity assessments. Our findings contribute to ongoing efforts to refine remote sensing approaches for ecological monitoring and sustainable landscape management in agroforestry systems.

Acknowledgements

We thank PT Humusindo Makmur Sejati and Pak Hasbi and his family for granting us access to and use of their properties. We thank the many field assistants for their support in the field. We are grateful for the logistical support by the EForTS staff and coordination. This study was financed by the Deutsche Forschungsgemeinschaft (DFG) German Research Foundation—project number 192626868—SFB 990 in the framework of the collaborative German–Indonesian research project CRC990 EForTS (<http://www.unigoettingen.de/crc990>). Research permit by the Indonesia Ministry of Research and Technology (337/SIP/FRP/E5/Dit.KI/IX/2016). EForTS-BEE is a member of the global network of tree diversity experiments TreeDivNet (<http://www.treedivnet.ugent.be>). Open

access publishing facilitated by Universite de Neuchatel, as part of the Wiley - Universite de Neuchatel agreement via the Consortium Of Swiss Academic Libraries.

Author Contributions

Vannesa Montoya-Sánchez: Conceptualization; methodology; formal analysis; visualization; writing – original draft; writing – review and editing. **Anna K. Schweiger:** Conceptualization; methodology; formal analysis; supervision; writing – review and editing; data curation. **Michael Schlund:** Formal analysis; methodology; writing – review and editing; data curation. **Gustavo Brant Paterno:** Writing – review and editing. **Stefan Erasmí:** Writing – review and editing. **Holger Kreft:** Writing – review and editing. **Dirk Hölscher:** Writing – review and editing. **Fabian Brambach:** Writing – review and editing. **Bambang Irawan:** Writing – review and editing. **Leti Sundawati:** Writing – review and editing. **Delphine Clara Zemp:** Conceptualization; supervision; writing – review and editing.

Conflict of Interest

The authors declare no financial or personal competing interests.

Data Availability Statement

The data and code to reproduce this work are publicly available via <https://doi.org/10.6084/m9.figshare.30135514.v1>.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1.