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Consequences of land use changes on ecological plant traits and strategies in Sumatra Indonesia

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Abstract

The deforestation and altering land use in Sumatra, Indonesia, have resulted in significant ecological shifts, especially in tropical rainforest ecosystems that play a crucial role in global biodiversity and carbon cycling. Based on species distribution and their ecological traits, plants' trait proportion, functional composition, and functional diversity across four land-use systems were calculated. The effects of land-use changes on each trait in species and individual plant levels, their variability, and functional diversity were observed using statistical tools such as Pearson's chi-squared test, ANOVA, Kruskal-Wallis rank sum test, Tukey's HSD and post-hoc multiple comparisons to detect the effects and relationships. The similarities and dissimilarities of traits were observed using NMDS ordination-based dissimilarity of traits. By examining 1382 plant species and 156,005 individuals in forest, jungle rubber, rubber plantations, and oil palm plantations, we found variations in the number of species, individual counts, and the mix of functional traits. The findings indicated that forests and jungle rubber had more incredible species richness and trait diversity than monocultures, particularly in pollination and seed dispersal syndromes. A significant association was discovered between functional and taxonomic diversity at the species level, exhibiting declining benefits at the individual level. The study emphasizes the need for sustainable land-use strategies to mitigate biodiversity loss and maintain ecosystem services.

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Introduction

Tropical rainforests, the most abundant and diverse terrestrial vegetation on Earth, are vital in preserving global biodiversity, regulating the carbon cycle, and supporting communities that rely on trees. Although tropical forests occupy a mere 6% of the Earth's land surface, these forests support around 80% of the documented worldwide species. Nevertheless, the rapid advancement of agriculture, changes in land use, and human practices such as logging and mining have resulted in substantial deforestation and degradation of forests, posing risks to biodiversity and the functioning of ecosystems (Gibbs *et al.*, 2010).

Southeast Asia, which covers 35% of the world's land area, is home to diverse species. It must confront substantial obstacles arising from logging activities and deforestation for agricultural reasons (Wilcove *et al.*, 2013). Indonesia is a significant part of the Indo-Malayan rainforest and is the third-largest country with a substantial amount of tropical rainforests. From 1990 to 2015, forest area has substantially decreased, resulting in a loss of around 27.5 million hectares (Mader, 2020). Indonesia experiences the highest rate of deforestation globally due to widespread land conversion for agricultural purposes, such as palm oil and rubber plantations (Hansen *et al.*, 2013).

The West Papua and Sumatra lowland rainforests in Indonesia pose unique challenges. These regions, characterized by a wide variety of plant and animal species, play a vital role in the conservation of biodiversity (Claudino-Sales 2019; Murdjoko *et al.*, 2021). However, these organisms face substantial hazards due to deforestation and degradation, leading to the loss of their native habitats and a decline in species diversity (Indrajaya *et al.*, 2022). The importance of conservation and restoration efforts cannot be overstated, particularly in involving local people to ensure the sustainability of these programs in the long run.

The deforestation of tropical rainforests has further ramifications. The issue not only reduces biodiversity by up to 42% in the impacted areas (Sodhi *et al.*, 2004) but also adversely affects ecological functions, economic prosperity, and the livelihoods of rural communities. The ban on rainforest conversion affects individuals who possess small parcels of land and those who hold customary land rights, forcing them to seek alternate livelihoods or relocate (Obidzinski *et al.*, 2012).

Land-use change in Sumatra, Indonesia

The transition from forest and agroforestry systems to monoculture plantations of rubber and oil palm in Sumatra, Indonesia, has led to significant environmental changes and a precarious equilibrium between biodiversity conservation and economic prosperity (Clough *et al.*, 2016; Grass *et al.*, 2020). The significant proliferation of oil palm plantations, particularly in South Sumatra, has been highlighted as a shift in agricultural dominance from traditional crops like rice to oil palm (Ngadi and Nagata, 2022). Expanding agricultural land, particularly in North Sumatra, has led to a rise in carbon dioxide emissions. The primary cause of this is predominantly attributed to land-use alterations and the transformation of wooded regions into agricultural terrain (Basyuni *et al.*, 2018).

Furthermore, converting forests into oil palm and rubber plantations in Sumatra has led to a significant decrease in biodiversity, particularly impacting the abundance of vascular epiphytes (Böhnert *et al.*, 2016). The creation of monoculture plantations dedicated to palm oil and rubber cultivation has caused the displacement of invaluable tropical rainforests, leading to substantial reductions in species diversity, population density, and plant biomass (Drescher *et al.*, 2016a; Foster *et al.*, 2011).

The agricultural landscape of Sumatra has seen a significant transformation due to the implementation of monoculture systems, such as rubber plantations and jungle rubber agroforestry systems. The rapid proliferation of monoculture rubber plantations, fueled by the global market demand, has replaced the more ecologically diversified jungle rubber systems (Feintrenie and Levang, 2009; Pye-Smith 2011).

Similarly, there has been a significant expansion in the extent of oil palm plantations, and the participation of small-scale oil palm farmers has been crucial in establishing Indonesia as a notable palm oil producer and exporter (Jelsma *et al.*, 2017). The changes in land use and agricultural practices in Sumatra substantially impact the ecosystem and animals. The studies emphasize the urgent requirement to immediately implement sustainable land-use policies to mitigate the negative environmental consequences arising from these changes (Basyuni *et al.*, 2018; Ngadi and Nagata, 2022). The collective repercussions of these activities impact the local ecosystems and possess worldwide significance due to their cumulative impact on biodiversity, climate, and the sustainability of natural resources.

Plant functional traits

Plants have a crucial role in the functioning of ecosystems, supporting ecological processes, structures, diversity, and stability (Masarovičová *et al.*, 2015). The functional approach to plant ecology combines physiological, population, and community ecology with environmental factors (Violle *et al.*, 2007). Plant functional features, encompassing morphological, physiological, and phenological characteristics, play a crucial role in comprehending plant behavior and classifying them into functional categories. The characteristics mentioned impact the functioning of individual plants, their interactions with the environment, and the overall activities of the ecosystem (Masarovičová *et al.*, 2015). Plant characteristics that relate to ecological interactions between plants and animals are influenced by biotic interactions and environmental conditions within plant communities (Webb *et al.*, 2002).

In their study, (Hodgson *et al.*, 1999) initially classified functional features into two categories: hard traits, such as photosynthesis and growth rates, and soft traits, such as woodiness and life cycle. This study specifically examines the correlation between measurable soft characteristics and ecological roles. These characteristics impact the interactions between plants and animals, affecting species' coexistence and the formation of community structure, composition, and ecosystem stability (Brooker *et al.*, 2008; Maestre *et al.*, 2005). It is crucial to understand how functional traits react to environmental conditions, as they indicate how plants adapt to these conditions and impact the functional makeup of plant communities. This connection between individual population dynamics and overall ecosystem functioning is essential for understanding the subject (Soliveres *et al.*, 2014).

Functional diversity and plant traits

Functional diversity, a vital component of biodiversity, incorporates the presence of different species and their competitive capacities within ecosystems, which in turn affect the functioning of the ecosystem and the distribution of traits across ecological groups (Goswami *et al.*, 2017; Song *et al.*, 2014). Understanding ecosystem dynamics, nutrient cycles, and stability significantly depends on this idea. Ecosystems are susceptible to even little changes in living and non-living variables. Functional plant features, such as pollination and seed dispersal, are crucial in ecological functioning. Disruptions to these traits can have negative impacts on ecosystem dynamics and the ability of plants to regenerate, which is a fundamental part of environmental conservation (Neuschulz *et al.*, 2016; Wang and Smith, 2002). The characteristics and their seasonal fluctuations substantially impact the germination of plants, their survival rates, the vegetation structure, and their dynamics (Cain *et al.*, 2000; Egerer *et al.*, 2018).

Ecological plant features, such as life cycle, growth shape, and pollination, are closely linked to ecological activities or services, enabling mutually beneficial interactions that are important for conservation (Egerer *et al.*, 2018). The features and roles mentioned are essential for preserving ecosystems' multifunctionality, shaping vegetation structure, and determining the evolutionary variety of plant communities (Midgley, 2012; Soliveres *et al.*, 2014).

This study is a part of the Collaborative Research Center 990 (CRC 990) called "Ecological and Socioeconomic Functions of Tropical Lowland Rainforest Transformation Systems" (EFForTS), which is funded by the Deutsche Forschungsgemeinschaft (DFG). The study investigates the ecological and socioeconomic consequences of converting rainforests into agricultural systems in Sumatra, Indonesia (Drescher *et al.*, 2016a). The research, carried out in Jambi Province, investigates the impact of this conversion on biodiversity, ecosystem functioning, and people's well-being. It comprises two lowland rainforest locations. The EFForTS project integrates environmental processes, biota, ecosystem services, and human factors into a comprehensive study method. Thirty-two core plots were surveyed across four land-use systems, each precisely measured and subdivided to enable thorough study. This worldwide project is a cooperative undertaking that involves institutions from Germany and Indonesia, including the University of Göttingen, the University of Jambi, Bogor Agricultural University, and Tadulako University. The DFG supports the initiative financially.

The rainforests in the Jambi province have had the fastest deforestation rate worldwide, primarily due to population growth, increased logging, and the expansion of agriculture (Drescher *et al.*, 2016a). In 2013, a substantial amount of the rainforest underwent reduction or conversion into agricultural land, highlighting the extent of land-use changes in the area.

An extensive vegetation survey was conducted across various land use systems, including forests, jungle rubber, rubber, and oil palm plantations. The survey provided information about the age of the plantations and emphasized the importance of smallholder management (Drescher *et al.*, 2016b; Kotowska *et al.*, 2016a; Rembold *et al.*, 2017). This study builds on a previous vegetation survey analyzing data on 1382 plant species across four land-use systems regarding species richness, composition, abundance, and physical traits (Rembold *et al.*, 2017). It involved an extensive review of ecological traits, using resources like Flora Malesiana and the TRY database, focusing on characteristics such as woodiness, life form, and pollination. The collected trait data, species abundance, and land-use information formed the basis for the final analysis. This study highlights the complex connection between land use, functional diversity, and ecosystem stability in the Jambi province.

Materials and methods

This research relied completely on a vegetation survey during which a total of 1382 species were documented. Among these, 312 species were not yet identified at the species level. This study focused on ecological plant characteristics, an extensive survey of the literature was conducted, encompassing a total of 992 species, 808 genera, and 91 families. This review sourced ecological plant traits from the published editions of Flora Malesiana, Tree Flora of Sabah and Sarawak, and Tree Flora of Java. Having an understanding of the distribution of each species across the four distinct land-use systems, we investigated the consequences of land-use changes on ecological plant traits and therefore functional diversity.

Study area

The study area was located in the EFForTS (Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems) project region in Jambi Province, which used to be one of the largest regions of tropical lowland rainforest in Southeast Asia, (Drescher *et al.* 2016)). Jambi, one of the 34 provinces of Indonesia, is situated on the eastern coast of central Sumatra. It covers 50160 km2 expanding from the southern Malacca Strait in the east to the Barisan Mountain range in the west (Fig. 1).

Eight plots were established in each of the four land use systems in 2012, resulting in a total of 32 study plots. Each core plot measures 50 × 50 m and contains five 5 × 5 m subplots at fixed positions (Drescher *et al.*, 2016a; Kotowska *et al.*, 2016b).

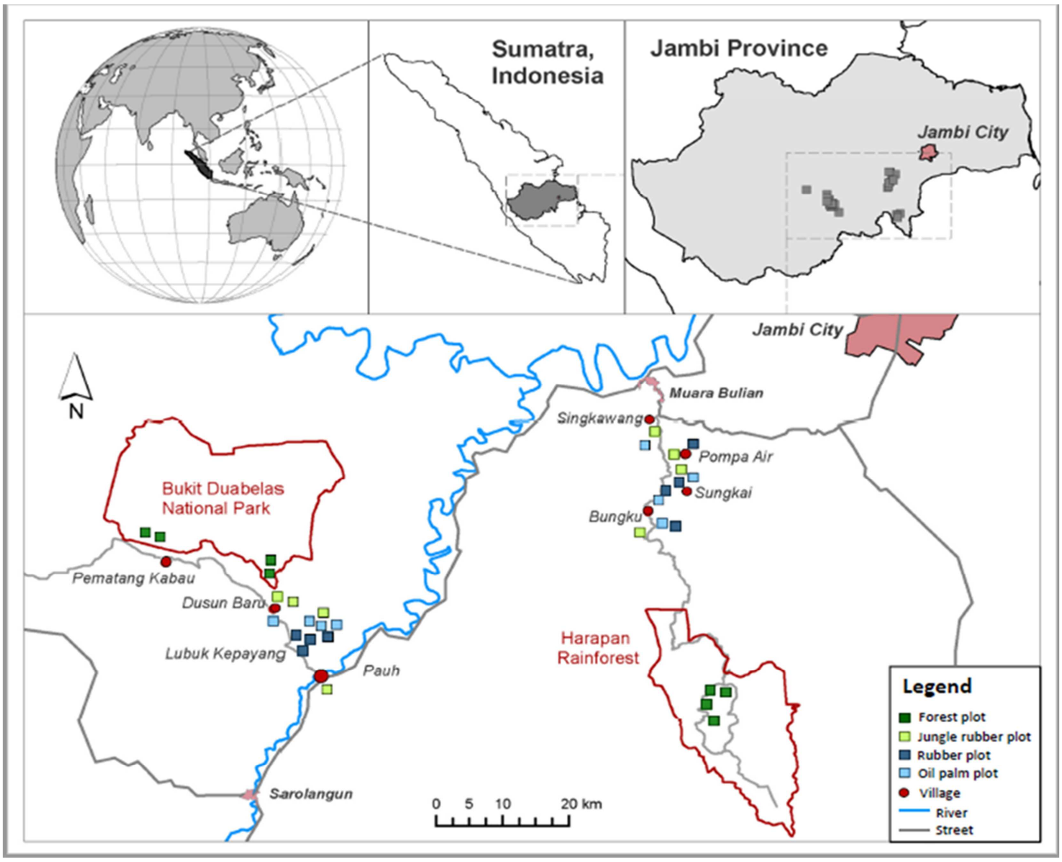

Fig. 1. Location of core plots near Bukit Duebelas National Park and Harapan Rainforest in the EFForTS study area in Jambi Province of Sumatra, Indonesia (Rembold *et al.*, 2017)

It was assured that the soil and climatic conditions were comparable and were representative of both study regions at 40-100 m a.s.l. The trees measured during the inventory of the respective plots were >10 cm Diameter at Breast Height (DBH) and plants with DBH <10 cm were measured in five subplots per plot (160 subplots in total).

Data collection

Vegetation survey

Data was collected on 1382 plant species in four distinct land-use systems: forest, jungle rubber, rubber plantations, and oil palm plantations. The survey recorded the number of different species present in each plot, along with their composition, abundance, as well as the height, growth type, diameter at breast height, and location of each tree.

Literature survey

This includes a comprehensive investigation to understand the ecological characteristics of species identified in the vegetation survey, specifically emphasizing aspects such as woody nature, life form, plant height, pollination syndrome, fruit type, dispersal syndrome, and reproduction. Information regarding these characteristics was gathered from published sources such as Flora Malesiana, Tree Flora of Sabah and Sarawak, and Tree Flora of Java.

The information was added using data from the plant trait database, which includes 992 recognized species. This database covers a wide range of features, including both categorical and numerical characteristics such as plant height, fruit and seed diameters, and chromosome counts. Additional information was obtained from online databases such as Naturalis, The International Plant Names Index (IPNI), and The Plant List. Data was gathered at the species, genus, and family levels, employing a hierarchical method to prioritize characteristic information. Species-level data inaccessible was replaced with information at the genus or family level. The gathered characteristic data was ultimately integrated with the species abundance and land use system databases, including information on species abundance and land use systems for analysis.

The analysis uses a classification system for functional plant features that encompasses Pollination Syndrome, encompassing categories for insect pollination (by bees, beetles, flies, and moths) and other pollination agents (bats, birds, and wind). Dispersal Syndrome is categorized into different types, including anemochory, autochory, hydrochory, and zoochory. This framework incorporates the previous approaches (Kattge *et al.*, 2020; Pérez-Harguindeguy *et al.*, 2016; Taudiere and Violle, 2016) and corresponds with the descriptions provided by (Pérez-Harguindeguy *et al.*, 2013).

Statistical analysis

The study evaluated the composition of ecological plant traits across four different land-use systems, utilizing Pearson's Chi-squared test using R software (Taudiere and Violle, 2016) to analyze count data for each trait. Analysis of Variance (ANOVA) and Kruskal-Wallis rank sum tests (Kraft and Ackerly 2010) assessed the significance of differences in trait percentages across land-use systems. Functional diversity was explored using species abundance and trait matrices through the 'functcomp' function from the FD package in R (Violle *et al.*, 2007), which returned numerical trait values for each system. The Shapiro-Wilk test examined the distribution of these values (Rabinowitz, 1975). and subsequent analyses, including ANOVA, Kruskal-Wallis Rank Sum Test, Tukey's Honest Significance Difference (HSD), and post-hoc tests Field (Kembel and Jr, 2011), elucidated differences in trait composition. The results were presented as box plots, indicating mean values and variability.

Further, non-metric multidimensional scaling (NMDS) via the 'metaMDS' function from R's 'vegan' package quantified trait dissimilarity, reflecting functional trait proximity and distribution patterns within the plots. The stress values associated with NMDS ordination gauged the non-metric fit quality of the trait data. Distance-based functional diversity indices, such as functional richness, evenness, dispersion, and Rao's quadratic entropy, were computed using the 'dbFD' function of the FD package, leveraging species-by-trait data. Correlations between functional diversity indices and species richness were visualized through a matrix and scatter plots, with significance testing conducted in Microsoft Excel, providing insights into the impact of land-use change on both functional and taxonomic diversity.

Results

We gathered and analyzed ecological plant traits data from a comprehensive dataset comprising 156,005 individuals and traits of 992 species, 808 genera, and 91 families. This dataset encompassed 999 trees, 362 shrubs, and 258 herbs across various species. Furthermore, the different land-use systems exhibited varying numbers of individuals per system. Among these, the most diverse in terms of species was the forest system (966 species), followed by jungle rubber (653 species), rubber (233 species), and oil palm (247 species). However, when considering the total number of individuals, the forest had the highest species diversity but the lowest individual count (17,043). In contrast, jungle rubber (18028) accounted for approximately half of the individuals found in rubber plantations (38,948) and less than a quarter of those in oil palm (81,986). Overall, forest and jungle rubber exhibited greater species richness with a more diverse trait composition and fewer individuals, whereas monoculture plantations (rubber and oil palm) showed lower species richness with a less diverse traits composition but a higher individual count.

The forest system exhibits the most incredible species diversity, with 963 species. Most of these species are woody plants, including trees and shrubs, contributing to 85% of the total species count. The jungle rubber system comprises 652 species, with woody plants being the most common, accounting for

83% of the total (Fig. 2a). The monoculture plantations of rubber and oil palm had a significantly lower species richness, with 230 and 219 species, respectively. Additionally, these plantations show a more even distribution of trees, shrubs, and herbs.

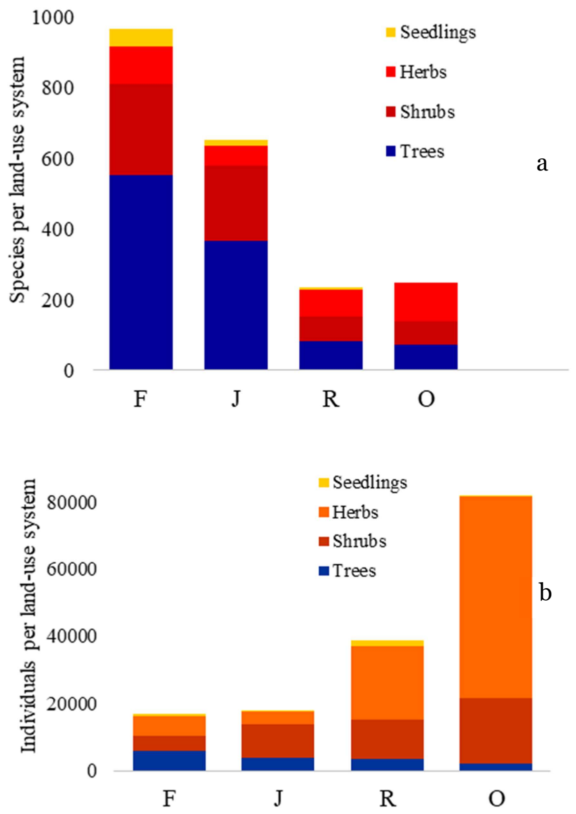

Fig. 2. Total species (a) and individual (b) numbers land-use system including trees (DBH ≥10 cm) and understorey vegetation. The group 'seedlings' combines several currently unidentified non-herbaceous seedlings that might either become a tree or a shrub. A total of 1382 plant species and 156,005 individuals across a land-use gradient measured as the proportion of each species in each of the four land-use systems: F – forest, J – jungle rubber, R – rubber plantation, O – oil palm plantation

The overall count of individual plants exhibits a contrasting trend. Forests and jungle rubber systems have around 50% fewer individual plants compared to rubber plantations, which have a count of 38,948 individuals. They also have less than 25% of the individual plants found in oil palm plantations, with the highest number at 81,986 individuals (Fig. 2b). This disparity indicates a greater concentration of herbaceous plants in plantation systems.

Although tree monocultures are prevalent in rubber and oil palm plantations, we unexpectedly discovered native tree seedlings in the lower vegetation layer. In oil palm plantations, we identified 63 different species, while in rubber plantations, we found 77 species. This discovery suggests a consistent if reduced, diversity of plant and animal species in these agricultural systems at the lower levels of vegetation.

The majority of the native tree seedlings found in the plantations are from genera characteristic of pioneer or secondary forest species, including Macaranga, Ficus, Artocarpus, and Alstonia. While most of these genera are often found in jungle rubber, a significant number of species more commonly found in forests were also discovered in the understories of the plantations. This indicates the ability of certain forest species to adapt and survive in different environments.

Among the 1382 plant species examined, 587 are found only in forests, accounting for a significant percentage (42%) of the total species and 61% of those in forests. This underscores the crucial importance of forests as a storehouse of biodiversity. Two hundred thirty-nine species are found only in forest and jungle rubber systems and are not present in plantation systems. The presence of several species in this shared pool highlights the significance of jungle rubber as a protective mechanism that supports the variety of forest-related organisms.

The analysis revealed that 230 species were recognized as indicators from the land-use systems examined. Among these, the forest system stood out with the most species, totaling 160. This finding further emphasizes the significance of the forest's exceptional biodiversity. In contrast, rubber and oil palm plantations exhibited the lowest indicator species, with only 6 and 33 species, respectively.

The results indicate a noticeable variation in the variety of plants, ranging from natural forests to managed agroforestry systems and monoculture plantations. As land use becomes more intensive, biodiversity decreases substantially, and the types of species present change.

Pollination syndrome

Species-level insect pollination and other pollination

Fig. 3 illustrates the differences in species-level pollination by insects and other agents in four unique land-use systems: Forests (F), Jungle Rubber (J), Rubber Plantations (R), and Oil Palm Plantations (O). Bees are the dominant insect pollinators throughout all land-use regimes (Fig. 3a), with the most incredible abundance in forested areas. Beetles rank second in frequency as pollinators, and they are particularly abundant in forested regions. Flies and moths also participate in pollination; however, their populations are significantly smaller than those of bees and beetles.

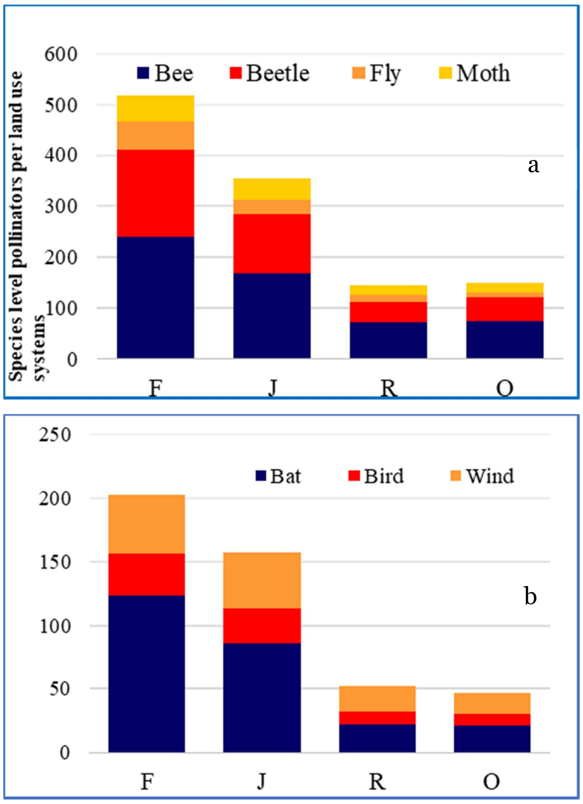

Fig. 2. Major species level pollinators involved in the pollination per land-use systems: F-Forests, J- Jungle Rubber, R- Rubber Plantation, and O- Oil Palm Plantation. a) shows the total numbers of insect pollinators: Bee, Beetle, Fly, and Moth, and b) other pollinators i.e. Bat, Bird, and Wind involved across four different land-use systems.

Bats play a significant role in forest ecosystems when considering non-insect pollinators. However, their presence in agricultural systems could be much higher. Bird pollination is present in all land use types, but it is not dominant in any system. Wind pollination is the least common in all systems, indicating that biotic pollination is more widespread than abiotic pollination in these conditions (Fig. 3b).

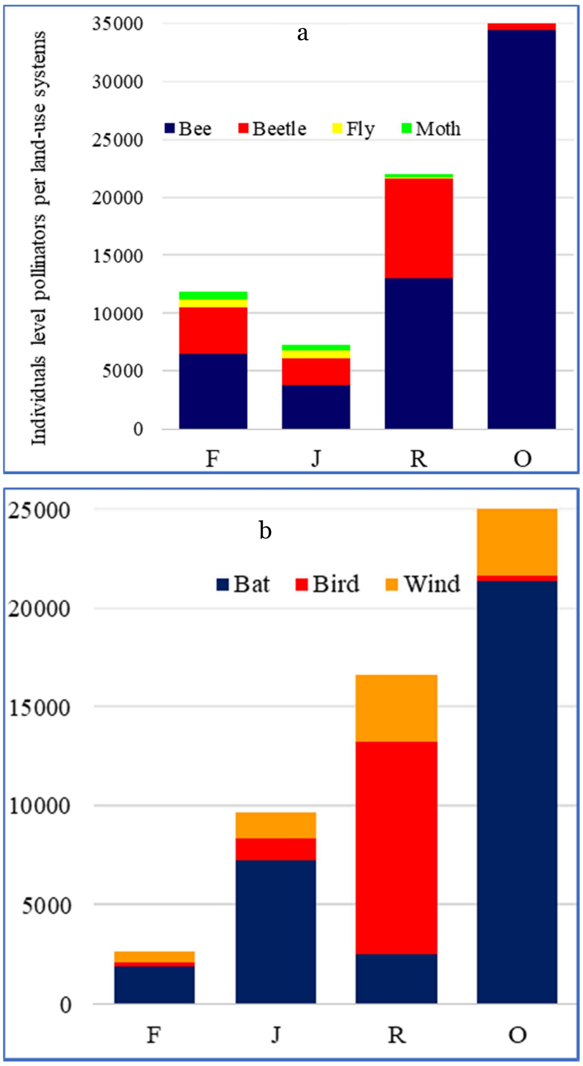

Fig. 4. Major Individual-level pollination per land-use systems: F-Forests, J- Jungle Rubber, R- Rubber Plantation, and O- Oil Palm Plantation. a) shows the total Individuals of insect pollinators: Bee, Beetle, Fly, and Moth, and in b) other pollinators: Bat, Bird, and Wind.

The pollination patterns observed suggest that there is a greater variety and number of pollinators in land-use systems that are less disturbed, such as forests. However, there is a decreasing tendency in the diversity and abundance of pollinators in monoculture plantations. This highlights the possible effects of altering land use on the communities of pollinators and the services they offer to the ecosystem.

Bees are the predominant insect pollinators in rubber and oil palm plantations, surpassing their population in forests and jungle rubber by a significant margin (Fig. 4a). Beetles, flies, and moths also participate in pollination, although their contribution is rather minor, primarily observed in the woodland ecosystem. Bats play a crucial role as pollinators in the forest ecosystem, whereas bird pollination is more prevalent in the oil palm plantations. Wind pollination is observed in many types of land-use systems, but it is especially common in oil palm plantations (Fig. 4b).

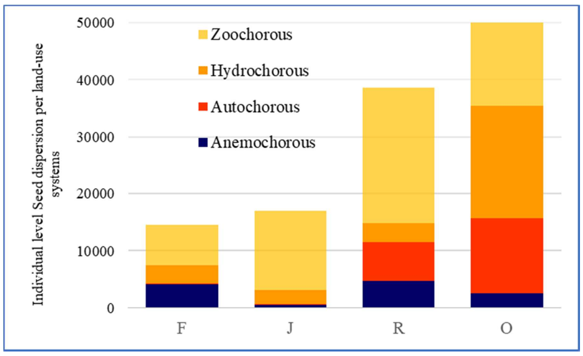

Fig. 3. Individual level seed dispersion per land-use systems. F-Forests, J- Jungle rubber, R-Rubber plantation and O-Oil Palm plantation

Seed dispersion syndrome

Fig. 5 illustrates the processes by which seeds disperse at the individual level in four distinct land-use systems: Forests (F), Jungle Rubber (J), Rubber Plantation (R), and Oil Palm Plantation (O). The data demonstrates that zoocorous (animal-assisted) seed dispersal is the most common mechanism across all forms of land use, with the greatest numbers observed in oil palm plantations. Following this, anemochorous seed dispersal, which is facilitated by wind, occurs. This process is particularly prominent in rubber and oil palm plantations, suggesting a dependence on wind for spreading seeds in these more exposed habitats.

Hydrochorous seed dispersal, which involves the assistance of water, is consistently less common in all ecosystems, with the lowest frequency observed in jungle rubber and rubber plantations. Autochorous, or self-dispersion, is a dispersal mechanism that is present but represents the smallest fraction among all dispersal methods. This shows transition from seed dispersal by living organisms to dissemination by non-living factors when we transition from natural ecosystems to those modified by human activities. In particular, oil palm plantations mainly depend on wind and animal dispersal methods. Functional composition of plant traits at species level across land-use systems.

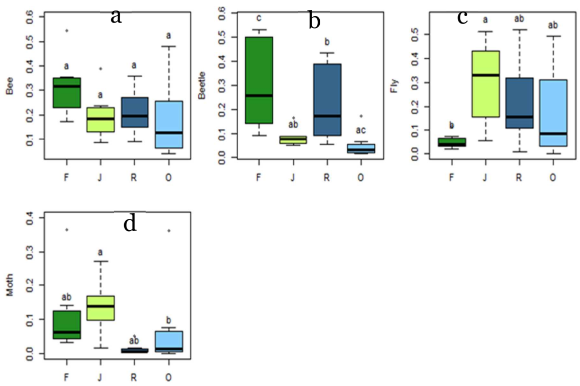

Fig. 6. Ecological plant traits insect pollination (a), bee (b), beetle (c), fly and (d), moth in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed significance level of differences; (a), p=0.002 (b), p=0.0011 (c), p=0.1129 and d), p=0.023

Pollination syndrome

Insect pollination

The figure illustrates that bee functional composition varies significantly across different land-use systems, with forests showing the highest median value. Beetles are most abundant in jungle rubber, significantly more so than in other systems, especially compared to the lowest median found in oil palm plantations. Flies have their highest presence in jungle rubber, with no significant difference between forest and oil palm systems. Moths have comparable high functional compositions in both forest and jungle rubber environments, with the least in oil palm plantations. The statistical analysis via the Kruskal-Wallis test supports these observations, with bees (p=0.002), beetles (p<0.0011), and moths (p=0.023) showing significant differences in functional composition across the land-use (Fig. 6).

Bat, bird, and wind pollination syndrome

The functional composition of bat and bird pollination is consistent across all land-use systems—forest, jungle rubber, rubber, and oil palm plantations—showing no statistically significant differences, which is illustrated by the same grouping letter 'a' in the respective boxplots. However, wind pollination varies markedly, with the highest functional composition observed in oil palm plantations, followed by rubber plantations, and the lowest in forest systems. The statistical analysis reinforces these observations with non-significant p-values for bats (0.1129) and birds (0.05), and a highly significant p-value for wind pollination (0.0001), suggesting that while bat and bird pollination patterns are relatively unaffected by land-use type, wind pollination is significantly influenced by the environment (Fig. 7).

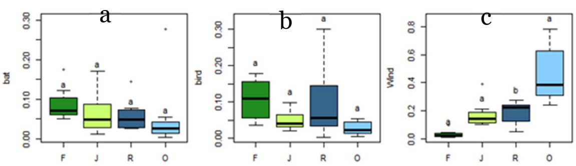

Fig. 7. Ecological plant traits pollination (a), bat (b), bird and (c), wind in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed significance level of differences; (a), p=0.1129 (b), 0.05 (c), p=0.0001

Dispersal syndrome

Anemochorous (wind) dispersal was significantly more pronounced in forests (F) than in other land uses, exhibiting the highest median value (p<2.2e-16. Autochorous (self) dispersal exhibited a notable peak in rubber (R) monocultures (p<0.0002), supporting the suggested predominance in monocultures. Hydrochorous (water) dispersal presented no significant difference between forest (F) and jungle rubber (J), yet it was significantly more common in monocultures (p<2.2e-16), contrary to the equal functional composition purported between systems. Lastly, zoochorous (animal) dispersal differed significantly across the systems, with jungle rubber (J) manifesting the highest functional composition (p<0.0003), which refutes the assertion of non-differential dispersal rates in forest and monoculture systems (Fig. 8).

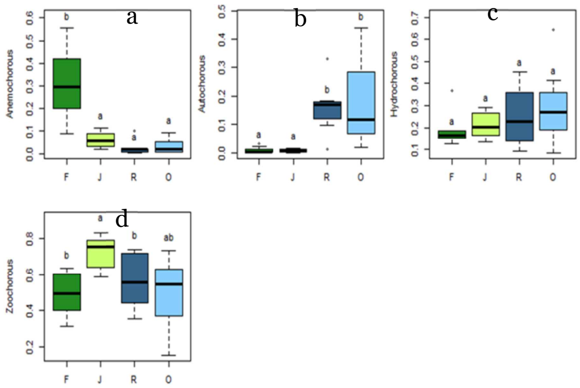

Fig. 8. Ecological plant traits: dispersal syndrome (a), anemochorous (b), autochorous (c), hydrochorous (d), zoochorous in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed significance level of differences (a), p<2.2e-16 (b), p>0.0002 (c), p>2.2e-16 and d), p>0.0003

Functional composition of plant traits at individual level in different land-use systems

The trait composition at individual plant levels was assessed to estimate the comparisons among the ecologically most important traits across land-use systems. Some traits such as woodiness, pollination syndrome i.e. insect (bee, beetle, fly, and moth), bat, bird, and wind and seed dispersal syndrome or mechanisms i.e. autochorous, anemochorous, hypochlorous, and zoochorous seed dispersions of individual plants were compared with the species occurred in four land-use systems.

Pollination syndrome

Insect pollination

Within the context of land-use systems, significant disparities were uncovered in the functional composition of insect pollination. Bees (p=0.001) demonstrated substantial variability, with the most pronounced pollination activity occurring within rubber plantations, a finding that diverges from the earlier narrative of uniformity across systems. Beetles (p=0.0025) upheld the anticipated pattern, showcasing a peak in functional composition within forested areas and diminishing presence in oil palm plantations. In contrast, flies presented a consistent functional composition across all landscapes, contradicting claims of differential activity. Remarkably, moths (p=0.0001) exhibited a higher functional composition in jungle rubber systems, starkly contrasting with the previously asserted dominance in forested systems. These results highlight the nuanced influence of land-use types on the pollination dynamics of these insects at the individual level (Fig. 9).

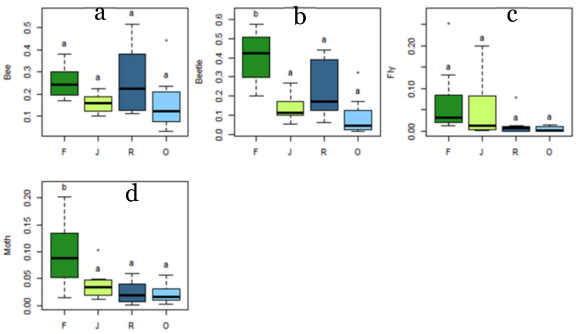

Fig. 9. Ecological plant traits at individual level: insect pollination (a), bee (b), beetle (c), fly and (d), moth in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed significance level of differences (a), p=0.001 (b), p=0.0025 (c), p=0.0001 (d), p=0.0001

Bat, bird, and wind pollination

Bats displayed a pronounced functional composition within jungle rubber (J) plantations, the highest among the studied systems, and a notably lower presence in oil palm (O) plantations (p<0.0001). Bird pollination did not exhibit a preference for monoculture plantations; rather, the analysis revealed no significant variance across the land-use types (p>0.003). Wind pollination was markedly more prevalent in oil palm (O) plantations, surpassing other systems significantly (p<2.2e-16), corroborating the suggested affinity for agro-based monoculture environments. These findings highlight the influence of land-use system on pollinator activity, underscoring the complexity of pollination dynamics within varied ecological contexts (Fig. 10).

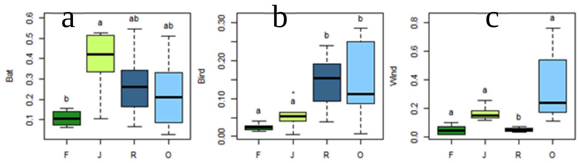

Fig. 10. Ecological plant traits at the individual level: insect pollination (a), bee (b), beetle (c), fly and (d), moth in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed a significant level of differences (a), p<0.0001 (b), p>0.003 and (c), p>2.2e-16

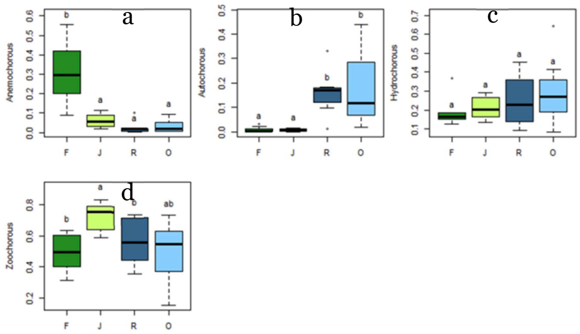

Fig. 11. Ecological plant traits at individual level: seed dispersal syndrome (a), anemochorous (b), autochorous (c), hydrochorous and (d), zoochorous in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed significance level of differences (a), p<2.2e-16 (b), p>0.0002 (c), p>2.2e-16 and d), p>0.0003

Dispersal syndrome

Anemochorous (wind) seed dispersal predominated in forest systems (p<2.2e-16. Autochorous (self) seed dispersal revealed a heightened presence in rubber monocultures (p=0.0002. Hydrochorous (water) seed dispersal did not favor forest or jungle rubber over monocultures, with the latter showing significantly increased functional composition (p<2.2e-16). Zoochorous (animal) seed dispersal was most prevalent in jungle rubber and rubber monocultures (p=0.0003.

Functional dissimilarity

Multi-dimensional scaling of functional plant traits

We observed the non-metric multidimensional scaling (NMDS) ordination-based dissimilarity of ecological plant traits across four land-use systems and visualized the significant variations in the compositional dissimilarity. The NMDS ordination revealed the distinct plant trait groups for forest and jungle rubber (Fig. 12) but two monoculture plantations performed higher compositional similarity to each other. The monoculture plantations i.e. rubber and oil palm plantations showed similarities based on the higher degree of overlap in the confidence area. On the other hand, the trait composition in jungle rubber and forest systems were clear separations from the other systems. Forest and jungle rubber plots resulted in a significant amount of higher trait composition. It appeared outside the confidence area and also within the forest confidence area indicating a higher trait composition similarity to jungle rubber plots than to other monoculture plantations.

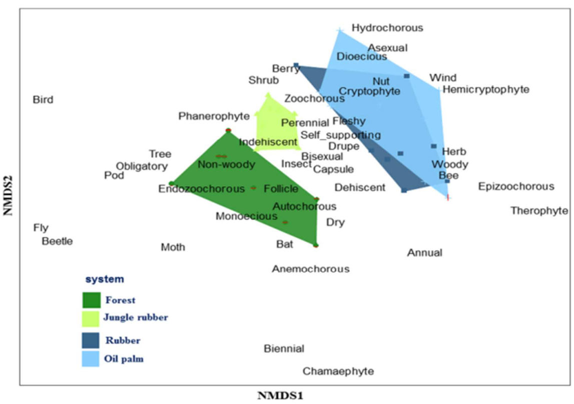

Fig. 4. Functional traits composition of the four land-use systems as produced by the non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity of traits between plots (n=8 plots per system). The polygon shows the core part of the corresponding system of ecological plant traits.

Relationships between functional diversity indices and taxonomic diversity at the individual level

This is a vital component of biodiversity which encompasses the wide range of functional ecological traits of plants that can be measured by the functional diversity indices i.e. functional richness, evenness, dispersion, etc. Functional diversity is an assessment of functional traits that influence the multiple aspects of distribution patterns and functional roles for ecosystem functioning in a particular ecological community. On the other hand, the taxonomic diversity of plants evaluates the various pairs of species and individuals in different land-use systems based on the already collected data set from experimental plots and illustrated in the form of functional diversity indices.

Functional diversity indices assemblage the linking of multiple aspects of species dominancy and the numbers of individuals and their functional distinctness.

The relationship between functional diversity and taxonomic diversity showed a correlation (R2 =0.9854 and confidence interval 95%) and the significance test of functional diversity indices with taxonomic diversity in species level did not show significant variations at p>0.001 (Fig. 13a). Similarly, in individual level, it showed the correlation at R2 = 0.5711 with significance test at p>0.0035 (Fig. 13b). The correlation between species level functional diversity and taxonomic diversity showed higher correlation than individual levels as produced in the results. The species-level relationships did not show a linear correlation.

The individual level also showed a non-linear correlation between functional diversity and taxonomic diversity. The species level had a higher correlation than the individual plant level and found that the higher correlation in species level led to better functional diversity as shown in the trend line (Fig. 13a) but the individual level estimated the declining trend of functional diversity after reaching the maximum level (Fig. 13b).

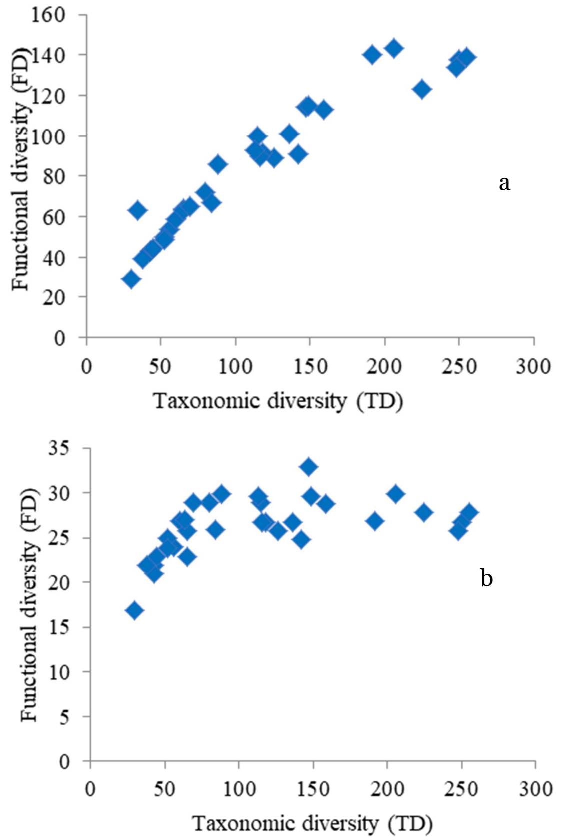

Fig. 13. Relationship between functional diversity (FD) and taxonomic diversity (TD) at a) species and b) at individual levels. The significance between FD and TD: significant at p>0.05, n=32 plots)

Effects of land-use change on functional diversity indices in species and individual level

At the species level, forests (F) show the highest species richness, significantly differing from other land-use types (p=0.0001), while jungle rubber (J) has the highest functional richness, challenging the correlation with species richness (p>0.0001). Functional evenness is lowest in rubber plantations with observed significance (p>0.037). Functional dispersion and RaoQ exhibit no significant differences across land uses. At the individual level, jungle rubber also presents the highest functional richness, distinctly more than forests, and an increase in functional evenness from forests to oil palm plantations is noted (p>0.0745), which also contrasts with the earlier interpretation. Both functional dispersion and RaoQ remain consistent across land-use types at the individual level as well (p>0.00197 and p<0.106), reflecting the resilience of these indices to land-use changes. These findings elucidate the intricate response of functional diversity to land-use alteration, emphasizing the complex interplay between biodiversity components and environmental context.

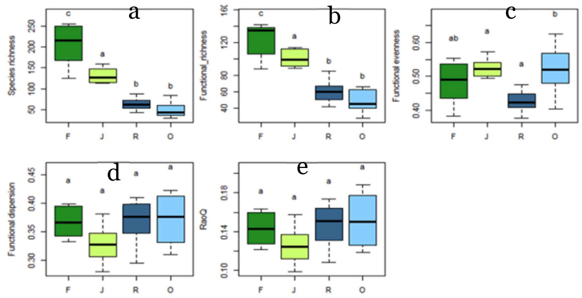

Fig. 14. Functional diversity indices species level (a), species richness (b), functional richness (c), functional evenness (d), functional dispersion and (e), quadratic entropy in four different land-use systems (n= 8 plots per system). Kruskal-Wallis one-way analysis of variance showed significance level of differences (a), p=0.0001 (b), p>0.0001 (c), p>0.002 (d), p>0.037 and (e), p<0.006

Discussion

Land-use change and biodiversity

The study's observation of greater species richness and trait diversity in natural forests and jungle rubber systems compared to monoculture plantations aligns with the previous findings, which noted significant biodiversity loss due to deforestation and land-use change field (Gibbs *et al.*, 2010; Wilcove *et al.*, 2013). The decline in biodiversity within monocultures raises concerns about these systems' sustainability and ecological balance, a phenomenon also highlighted by (Claudino-Sales, 2019; Murdjoko *et al.*, 2021), which stresses the crucial function of diverse ecosystems in biodiversity preservation.

Ecological plant trait composition in different land-use systems

The study emphasizes significant differences in plant characteristics among various land-use systems, with forests displaying a greater abundance of woody vegetation, indicating complex ecological processes. This corresponds to the findings of (Soliveres *et al.*, 2014), highlighting the ecological significance of woody vegetation. The sexual reproduction characteristics, such as the presence of both male and female reproductive organs in plants, known as monoecious and bisexual plants, show variations across different land-use systems. These variations can impact ecosystem functioning and diversity (Neuschulz *et al.*, 2016; Winsa *et al.*, 2017). The widespread occurrence of insect pollinators such as bees and beetles in various land-use regimes highlights their essential contribution to the agreement on pollination processes (Nicholls and Altieri, 2013). The pollination habits of bats and birds show a preference for more diversified plant communities, suggesting a strong connection between the behavior of pollinators and the complexity of their habitat (Neuschulz *et al.*, 2016; Quesada *et al.*, 2011).

Functional composition of plant traits in different land-use systems

Different functional compositions of plant features, particularly in growth forms and reproductive mechanisms, are evident across various land-use systems. The forest and jungle rubber systems exhibit a more excellent functional composition, indicating a more comprehensive range of ecological roles. The prevalence of insect pollination in these systems, mainly by bees and beetles, underscores the significance of these pollinators in upholding species diversity and ecosystem functioning (Neuschulz *et al.*, 2016). Monoculture plantations, on the other hand, have a unique structure characterized by a more significant occurrence of wind pollination and self-dispersion mechanisms, which indicates a less complex ecological network.

Dissimilarity in functional features

The dissimilarity analysis based on NMDS ordination reveals considerable variations in the composition of plant features among the different land-use systems. The more excellent proximity of features in forests and jungle rubber suggests a more complex and integrated ecological network than monoculture plantations, which display a more dispersed distribution of traits. Conversion from forest to monoculture plantations may result in simplifying ecological networks and a potential decline in ecosystem functioning (Aranzana *et al.*, 2005; Zhu and Yu, 2009).

Variation in functional diversity among different land-use systems

Functional diversity, an essential element of how ecosystems work, experiences a notable decrease in jungle rubber and monoculture plantations compared to forests. This is consistent with the concept that changes in land use might result in the decline of functional groups and the ecological activities they support (Goswami *et al.*, 2017; Midgley, 2012). The study finds that monoculture plantations, although they have less variety of species, show more functional dispersion and Rao's quadratic entropy. This indicates that they are influenced by widespread ecological filtering (Mumme *et al.*, 2015).

Relationships between functional and taxonomic diversity

The relationship between functional and taxonomic diversity is intricate and not straightforward, highlighting that ecosystem functioning is influenced by the number of species and the functions and interactions of species within the community (Edie *et al.*, 2018). The correlation between functional richness and taxonomic diversity indicates that ecosystems with higher diversity tend to possess a broader range of functional traits, which enhances the stability and resilience of the ecosystem on both macro-ecological and evolutionary levels (Novack-Gottshall, 2007).

Conclusion

Preserving biodiversity and ecosystem services requires the urgent implementation of sustainable land-use practices. The study's findings align with an expanding body of literature that emphasizes the ecological impacts of changes in land use. This highlights the need for policies combining ecological preservation and economic development, focusing on the significance of preserving the multiple functions of ecosystems for the well-being of both the environment and human societies. Future research should focus on the long-term ecological and socio-economic impacts of biodiversity loss and functional homogenization. Investigations into the socio-economic impacts of land-use change could provide a more comprehensive understanding of these environmental changes.

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