ASIAN JOURNAL OF FORESTRY
Volume 10, Number 1, June 2026
Pages: 10

E-ISSN: 2580-2844
https://doi.org/10.13057/asianjfor/r100110

Biodiversity patterns in *Acacia* plantations and natural forest remnants in Sabah, Malaysian Borneo

SITI FATIMAH MD-ISA♥, SHI PIN LIM, NORMAH AWANG BESAR, WILSON VUN CHIONG WONG, MUI-HOW PHUA♥♥
Faculty of Tropical Forestry, Universiti Malaysia Sabah (UMS). Jl. UMS, 88400 Kota Kinabalu, Sabah, Malaysia.
Tel.: +60-88-320000, Fax.: +60-88-320876, ♥email: sitifatimahmdisa@ums.edu.my, ♥♥email: pmh@ums.edu.my

Manuscript received: 16 October 2025. Revision accepted: 6 March 2026.

Abstract. *Md-Isa SF, Lim SP, Besar NA, Wong WVC, Phua M-H. 2026. Biodiversity patterns in* Acacia *plantations and natural forest remnants in Sabah, Malaysian Borneo. Asian J For 10 (1): r100110. https://doi.org/10.13057/asianjfor/r100110.* Evaluating biodiversity patterns in tropical plantations is crucial for balancing production and conservation goals. This study assessed plant biodiversity across six forest types within an *Acacia* hybrid plantation landscape in Sook, Keningau, Sabah, Malaysia. Twenty-nine circular plots were established in *Acacia* stands of different ages (13, 15, and 17 years) and adjacent natural forests (secondary, riparian, and heath). A total of 42 tree species from 24 families were recorded across all forest types, of which 39 species were native; tree-based analyses comprised 34 species from 21 families. Species diversity varied markedly among forest types, with secondary and riparian forests exhibiting the highest diversity (Shannon-Wiener H′ up to 2.547; Simpson 1-D up to 0.904), while younger *Acacia* stands showed the lowest values. Among plantations, the 17-year-old stand supported higher native tree species richness (mean ± SD: 4.50±2.38 species per plot) than the 13- and 15-year-old stands. Differences in native tree richness among forest types were statistically significant (Kruskal-Wallis, p=0.002). Beta diversity partitioning between *Acacia* plantations and natural forests showed turnover values from 0.68 to 1.00 and nestedness values from 0.078 to 0.118. *Acacia mangium* and *A. hybrid* were identified as indicator species of plantations. In contrast, the natural forests contained diagnostic native taxa, including Koordersiodendron pinnatum (classified as Vulnerable under the IUCN Red List). These findings highlight the critical role of remnant natural forests as biodiversity reservoirs and the positive influence of stand age on native species recovery in plantation landscapes. Maintaining remnant patches and extending rotation cycles can enhance biodiversity outcomes in *Acacia* production forests.

Keywords: *Acacia* hybrid plantation, beta diversity, conservation set-asides, species diversity, turnover partitioning

Abbreviations: 1-D: Simpson's dominance Index, Analysis of Variance: ANOVA, DBH: Diameter at Breast Height, H': Shannon-Wiener's Diversity Index, HSD test: Honestly Significant Difference test, IUCN: International Union for Conservation of Nature, J': Pielou's Evenness Index, LC: Least Concern, NE: Not Evaluated, VU: Vulnerable

INTRODUCTION

Tropical forests harbor nearly two-thirds of all known species. They are critical for global biodiversity, yet they are increasingly threatened by deforestation driven by commodities such as palm oil, rubber, and timber. In Borneo, approximately 18.7 million hectares of old-growth forest were cleared between 1997 and 2015, largely for oil palm and pulpwood plantations (Gaveau et al. 2016), much of it within biodiversity hotspots and protected areas (Fagan et al. 2022). Industrial tree plantations, particularly monocultures, are often regarded as "green deserts" because of their reduced biodiversity (Liebke et al. 2021; Zhu et al. 2023; Martello et al. 2024). Nevertheless, plantations can retain ecological value if they include natural forest patches, conservation set-asides, or riparian buffers, which provide habitat continuity and enhance landscape connectivity (Irwin et al. 2014; Wang et al. 2022). These global biodiversity concerns are especially relevant to Malaysia, and in Sabah, where large-scale plantation programs reshape forest landscapes.

In Malaysia, plantation forestry plays a key role in reforestation and timber supply, with over 112,000 hectares established under the Forest Plantation Development Programme as of 2016 (Malaysian Timber Council 2016). In Sabah, about 400,000 hectares of degraded forest reserves have been allocated for industrial tree plantations under the Forest Plantation Development Action Plan 2022-2036 (Kugan and Mannan 2022). These plans include conservation set-asides, areas within production landscapes designated for maintaining biodiversity, ecosystem services, or high conservation value forests. However, the effectiveness of such set-asides in safeguarding plant diversity is still poorly documented, particularly in Southeast Asia, where most plantation biodiversity studies focus on fauna or general habitat structure (Bohnett et al. 2022).

Emerging evidence indicates that forest patches embedded within plantation matrices can harbor substantial biodiversity. For instance, remnant forest patches in plantation landscapes support significant insect diversity (van der Mescht et al. 2023) and maintain rich epiphyte assemblages even when small (Einzmann and Zotz 2016).

Long-term monitoring of *Acacia auriculiformis* plantations in the Philippines revealed gradual increases in floristic diversity, though richness and structure remained lower than in adjacent natural forests (Hernandez et al. 2022). Comparative studies of *Alnus subcordata* stands similarly show that natural forests maintain higher species diversity and structural complexity than plantation counterparts (Taleshi 2014). Collectively, these findings suggest that conservation set-asides and forest remnants may mitigate biodiversity loss in plantation landscapes. However, little is known about how such patches affect native woody plant communities in Borneo's *Acacia* plantations.

Acacia hybrids, widely planted for their fast growth and timber yield, dominate much of Sabah's production forest landscape, yet their potential to support native biodiversity remains unclear. Understanding how biodiversity varies across *Acacia* stands of different ages and adjoining natural forest types is therefore essential for guiding biodiversity-oriented plantation management. This study examines plant biodiversity across an *Acacia* hybrid plantation and associated natural forest patches (secondary, riparian, and heath forests) retained within the plantation matrix in Sabah, Malaysia. We evaluate how species richness, diversity, and community composition differ across forest types and how beta diversity components, species turnover and nestedness, contribute to compositional variation. We further identify indicator species of each forest type to understand the ecological distinctiveness of plantation and remnant forests. We hypothesize that (i) older *Acacia* stands support higher native species richness due to successional recovery, providing insights for age-structured plantation management; (ii) remnant forests harbor distinct plant assemblages, including species of conservation concern, highlighting the importance of conservation set-asides; and (iii) species turnover, rather than nestedness, drives beta diversity among forest types, reflecting ecological differentiation between plantation and natural forests. Addressing these hypotheses provides insight into the role of conservation set-asides in sustaining native plant diversity, with implications for biodiversity management in production forest landscapes.

MATERIALS AND METHODS

Study area

The study was conducted in the KM Hybrid Plantation (Figure 1), a 424-hectare site located in Sook, within the Keningau District of Sabah, Malaysia (approximately 5°10'N, 116°20'E). The plantation has gentle topography with an elevation less than 500 meters above sea level in the interior region of Borneo, characterized by a humid tropical climate with annual rainfall exceeding 2,000 mm and minimal seasonal variation. Soils are predominantly alluvium (Sook association) on low terraces and floodplains, affecting *Acacia* productivity and the persistence of native plant species, while nutrient-poor, sandy heath soils support specialized vegetation. The plantation landscape comprises a mosaic of forest types, including *Acacia* hybrid stands aged 13, 15, and 17 years (hereafter *Acacia* 13, *Acacia* 15, and *Acacia* 17), as well as secondary forest patches within the plantation, such as riparian forests along seasonal streams, degraded secondary forests, and heath forests planted with Geronggang (*Cratoxylum arborescens*). The study area is typical of *Acacia* plantations in Sabah, with site-specific variation in species composition and environmental conditions. Thinning was applied to the *Acacia* stands between 2010 and 2012, which likely reduced canopy density, increased understory light, and promoted natural regeneration and recruitment of native species.

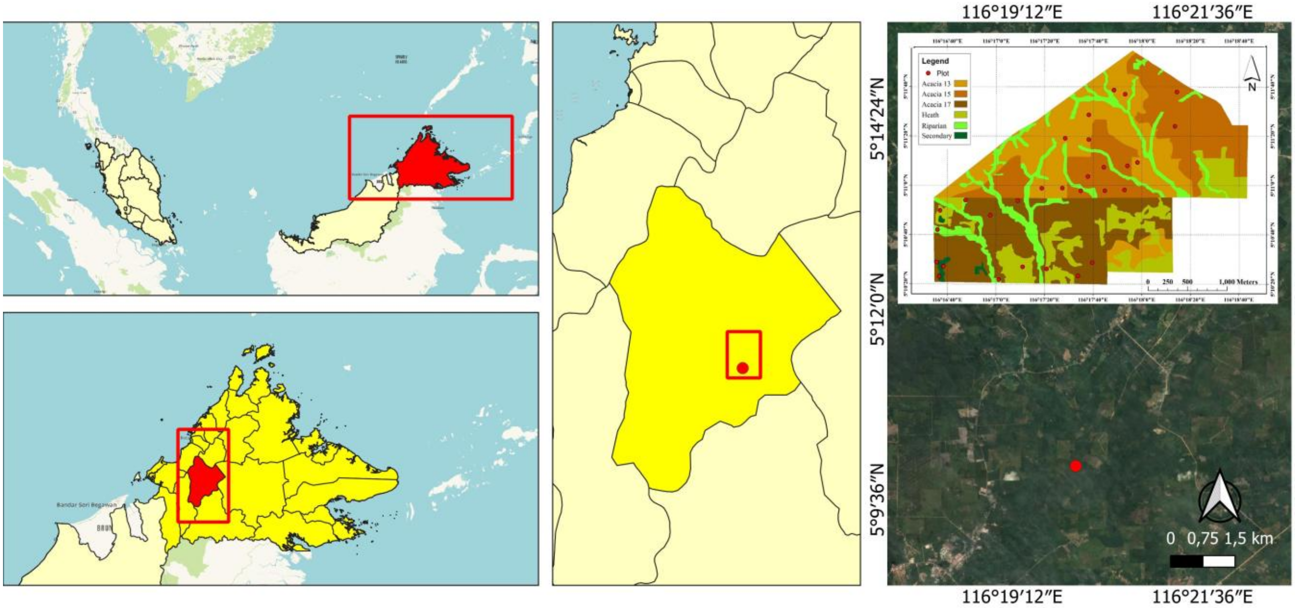

Figure 1. Map of the study area in Sook, Keningau, Sabah, Malaysia, showing 29 sampled plots across six forest types: *Acacia* stands (13, 15, 17 years), secondary forest, riparian forest, and heath forest

Procedures

A systematic sampling approach was employed, stratified by forest type. A 250×250 m grid was generated using the plantation map, and one point was systematically placed within each grid cell. Inaccessible points were excluded. When a point coincided with a road, stream, or recently disturbed area (e.g., logging), the plot was shifted by up to 150 m to minimize edge effects while maintaining comparable site conditions; while this approach preserves overall representativeness, it may introduce some sampling bias by avoiding extreme disturbances. Eight plots were established in both *Acacia* 13 and *Acacia* 15, and four plots in *Acacia* 17 due to extensive clear-felling before the study. Three plots were sampled in each natural forest type (secondary, heath, and riparian), reflecting their limited spatial extent. Given this unavoidable imbalance in plot numbers, non-parametric tests were used and results were interpreted conservatively. During field surveys, some dead trees were observed in the *Acacia* stands in varying numbers. In the case of secondary forest, three patches were present, but two were very small; therefore, all three plots were established in the largest patch. In total, 29 plots were surveyed across all forest types.

Tree species occurrences were recorded in all plots across forest types. For all forests except the heath forest, tree species with a Diameter at Breast Height (DBH) greater than 5 cm were identified and recorded. In the heath forest, a lower DBH threshold (>4 cm) was applied because most trees rarely exceeded 5 cm DBH; this adjustment was made to better reflect the dominant vegetation structure while maintaining comparability across forest types. Although this difference may affect direct comparability, analyses focused on relative patterns of richness and composition, and non-parametric tests were applied to mitigate potential bias. Nevertheless, we acknowledged a potential bias due to the differences in DBH threshold between forest types.

Photographs were taken for all observed species, and voucher specimens were collected for taxa not identifiable in the field. Species identification was conducted at Universiti Malaysia Sabah (UMS), Malaysia, and verified by the Forest Research Centre Herbarium in Sandakan, Sabah. Each species was classified by plant type (tree or non-tree) and by origin status (native or exotic to Sabah).

Data analysis

Only tree species with Diameter at Breast Height (DBH) above the minimum required threshold were included in all analyses, while species with DBH below the threshold were excluded. Tree alpha diversity within each forest type was quantified using Shannon-Wiener (H′), Simpson (1-D), and Pielou's Evenness (J′) indices, capturing species richness, dominance, and evenness to provide a comprehensive measure of community structure in forest ecosystems (Magurran and McGill 2011). All calculations were based on species abundance data expressed as individual counts per species. These abundance-based indices incorporate the number of individuals per species, allowing more sensitive detection of differences in community composition than presence–absence metrics.

Moreover, differences in native tree species richness among forest types were tested using the Kruskal–Wallis test because the Shapiro–Wilk tests indicated significant deviations from normality in tree richness for all forest types, except for the secondary and *Acacia* 17 forests. Native tree richness per plot was used as the response variable, and forest type as the grouping factor. The Kruskal-Wallis test was followed by Dunn's post-hoc pairwise comparisons with Bonferroni correction to identify significant differences among forest types (α=0.05).

To assess compositional heterogeneity, tree species presence–absence per plot was used to partition total beta diversity into turnover and nestedness components using the Jaccard dissimilarity index (Baselga 2010). Pairwise dissimilarities were averaged to obtain mean within- and between-habitat values, indicating whether differences among forest types are mainly driven by species turnover or nestedness due to richness gradients (Guclu et al. 2024). A total beta diversity value of zero indicates identical species composition across plots within a given habitat.

Indicator species analysis was performed to identify tree species that are strongly associated with the forest types. The analysis was based on tree species presence-absence per plot rather than abundance-based IndVal to avoid bias from unbalanced plot numbers and variable stem densities across forest types. Because the number of plots per forest type was unbalanced (ranging from three to eight), statistical power to detect significant indicators was reduced in forest types with fewer plots, increasing the likelihood that some true associations were not identified. Therefore, results were interpreted cautiously, and species restricted to a single forest type but not statistically significant were reported as exclusive species to provide additional ecological context (Habel et al. 2021). The conservation status of these species was determined according to the International Union for Conservation of Nature (IUCN) Red List.

All statistical analyses were conducted using Python (v3.13) and R (v4.3) (R Core Team 2023). In Python, Kruskal–Wallis and Dunn's post-hoc tests were performed using the scipy (Virtanen et al. 2020) and scikit-posthocs (Terpilowski 2019) packages. In R, diversity indices, beta diversity partitioning, and indicator species analysis were computed using vegan (Oksanen et al. 2022), betapart (Baselga and Orme 2012), and indicspecies (De Cáceres and Legendre 2009).

RESULTS AND DISCUSSION

A total of 42 tree species from 24 families, were recorded across six forest types. Of these, 34 tree species had Diameter at Breast Height (DBH) above the minimum required threshold, while 8 species were classified as below the threshold (Table S1). Native taxa dominated the assemblages (39 species), with only a few exotics and one hybrid species. Notable exotic tree species included *Acacia mangium* and *Hevea brasiliensis.*

Tree species richness, varied markedly across forest types. The secondary forest harboured the highest richness (22 species), while the heath forest exhibited the lowest (5 species). Among the *Acacia* stands, the 17-year-old stand (*Acacia* 17) had the highest richness (15 species), followed by the 15-year-old (*Acacia* 15; 5 species) and 13-year-old (*Acacia* 13; 3 species) stands, whereas the riparian forest recorded an intermediate richness of 15 species. The Kruskal–Wallis test revealed significant differences in native tree species richness among forest types (H=16.62, *p*=0.002; Table 1). Post-hoc comparisons indicated that *Acacia* 13 contained significantly fewer native species than the riparian (*p*=0.018) and secondary forests (*p* = 0.003). Similarly, *Acacia* 15 had significantly lower richness than the secondary forest (*p*=0.018). No significant differences were detected among *Acacia* stands or between the heath, riparian, and secondary forests.

Differences in species composition were reflected in the diversity indices (Figure 2). The secondary forest exhibited the highest Shannon-Wiener and Simpson Diversity (H′=2.143; 1-D=0.856) across all forest types, while the riparian forest showed the highest evenness (J′ = 0.924). Heath forest displayed moderate diversity (H′=0.647; 1-D=0.383), whereas the *Acacia* stands had lower overall values. *Acacia* 13 exhibited slightly higher Shannon and Simpson diversity (H′=0.498; 1-D=0.326) and relatively high evenness (J′=0.718). *Acacia* 17 recorded the highest Shannon and Simpson indices among the *Acacia* stands (H′=0.847; 1-D=0.408), comparable to the heath forest.

Patterns of beta diversity further underscored strong community differentiation among forest types (Figure 3 and Table S2). Species turnover was the dominant component of beta diversity (0.68±0.05-1.00±0.00), while nestedness contributed minimally. Total beta diversity of 1.00 occurred in comparisons where forest types shared no species, such as *Acacia* 13 versus riparian forest (Turnover=1.00; Nestedness=0.00). Comparisons among *Acacia* stands showed lower total beta diversity (0.30-0.65) with moderate nestedness. Within-habitat variation was lowest in *Acacia* 13 (β=0.00), moderate in the 15- and 17-year-old stands (0.46-0.57), and highest in natural forests (0.64-0.71), primarily driven by species turnover.

Table 1. Comparison of the number of native tree species across six forest types using the Kruskal-Wallis test with Dunn's Post-hoc test. Mean (± SD) species richness per forest type is also presented

Source	Degree of freedom	*F* statistic	*p*-value
Forest types	5	35.285	<0.001
Residual	23		

Dunn's Post-hoc Test (Bonferroni-corrected):

Group 1	Group 2	*p*-value
Acacia 13	Riparian forest	0.018
Acacia 13	Secondary forest	0.003
Acacia 15	Secondary forest	0.018

Mean ± SD species richness per forest type:

Forest types	Mean ± SD species richness
Acacia 13	2.00±0.00
Acacia 15	1.88±0.64
Acacia 17	4.50±2.38
Heath forest	2.33±1.15
Riparian forest	7.00±1.73
Secondary forest	11.67±3.06

Note: Analysis based on native tree species only. The number of plots (n) was as follows: *Acacia* 13 (n=8), *Acacia* 15 (n=8), *Acacia* 17 (n=4), Heath forest (n=3), Riparian forest (n=3), and Secondary forest (n=3)

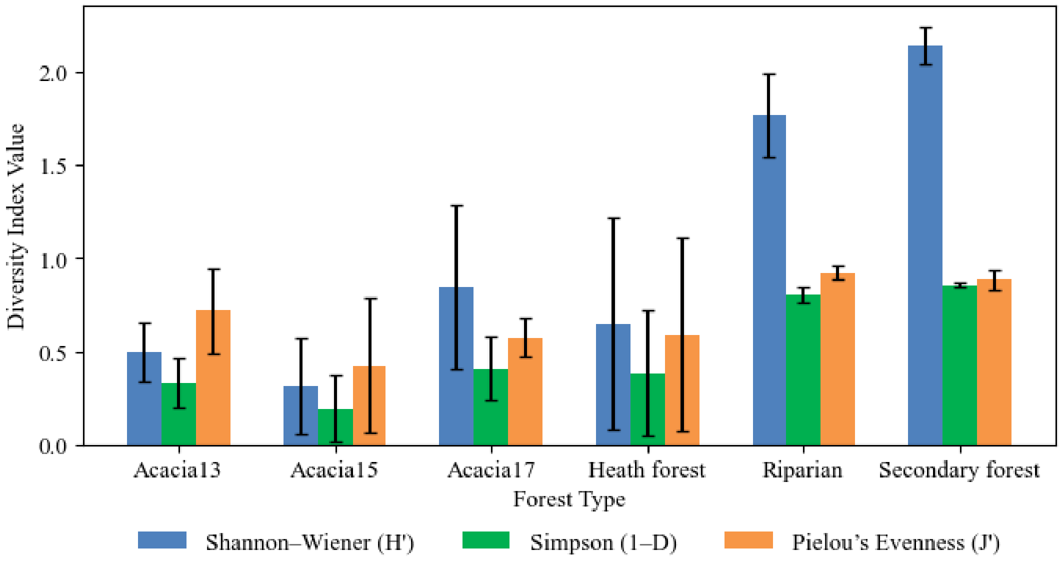

Figure 2. Biodiversity indices across forest types. Shannon-Wiener (H′), Simpson (1-D), and Pielou's Evenness (J′) were calculated for each plot. Diversity values are shown for *Acacia* stands of different ages (13, 15, 17 years) and natural forests (secondary, riparian, heath)

Indicator species analysis supported these compositional distinctions (Table 2). The 13- and 15-year-old *Acacia* plantations were represented solely by their planted species, *A. mangium* and *A. hybrid*, respectively. No significant indicator taxa were identified for *Acacia* 17, as both *Acacia* species occurred across all plantation ages, reducing exclusivity, and because of the smaller sample size and higher compositional heterogeneity among AC17 plots. Several native and understorey species were recorded only in *Acacia* 17 plots, including *Adenanthera pavonina*, *Mallotus paniculatus*, *Garcinia* sp., and *Polyalthia bullata*, which were all below the minimum DBH threshold. The heath forest was defined by *C. arborescens* (IndVal=1.000, *p*=0.002), riparian forest by *Bridelia insulana* and *Cinnamomum* sp., and secondary forest by *Macaranga indica*, *Dyera costulata*, and *Diospyros* sp..

Discussion

Species composition and diversity varied across forest types, reflecting the combined influence of stand age, habitat heterogeneity, and prior land-use history on community assembly within plantation landscapes. Diversity patterns among *Acacia* stands suggest that relative dominance between the two planted species influences overall diversity indices. *Acacia mangium* and *A. hybrid* were identified as indicator species in the younger stands (*Acacia* 13 and *Acacia* 15), reflecting plantation history rather than ecological differentiation. The Kruskal-Wallis results confirmed that native tree richness in the 13- and 15-year-old *Acacia* stands was significantly lower than in riparian and secondary forests, with no significant differences among *Acacia* stands. This indicates that while stand age contributes to recovery processes, compositional differences between planted and natural forests remain substantial.

Table 2. Significant indicator species with p-value<0.05 across different forest types

Forest types	Species	Indicator values	*p*-value	IUCN status
Acacia 13	*Acacia mangium* Willd.	0.586	0.003	LC
Acacia 15	*Acacia hybrid*	0.548	0.001	NE
Heath forest	*Cratoxylum arborescens* (Vahl) Blume	1.000	0.002	LC
Riparian forest	*Bridelia insulana* Hance	0.816	0.028	LC
Secondary forest	*Cinnamomum* sp.	0.866	0.006	-
	Campnosperma auriculatum (Blume) Hook.fil.	0.696	0.049	LC
	Chassalia curviflora (Wall.) Thwaites	0.816	0.018	NE
	Diospyros sp.	0.816	0.018	-
	Koordersiodendron pinnatum (Blanco) Merr.	0.816	0.027	VU
	Macaranga indica Wight	0.866	0.006	LC
	Utania cuspidata (Blume) K.M.Wong, Sugumaran & Sugau	0.816	0.018	LC

Note: IUCN conservation status follows the IUCN Red List of Threatened Species, Version 2025-2 (accessed 22 October 2025). LC: Least Concern, VU: Vulnerable, EN: Endangered, NE: Not Evaluated, -: Absent. The number of plots (n) was as follows: *Acacia* 13 (n=8), *Acacia* 15 (n=8), *Acacia* 17 (n=4), Heath forest (n=3), Riparian (n=3), and Secondary forest (n=3)

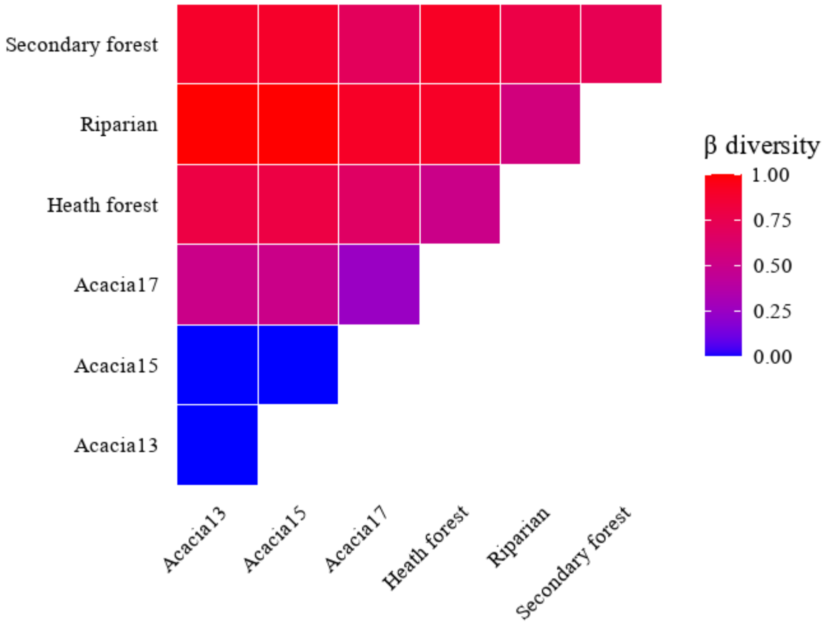

Figure 3. Heatmap of total beta diversity across forest types. Blue indicates low compositional dissimilarity, red indicates high; turnover and nestedness components are shown to illustrate species composition differences

The absence of significant indicator species in the 17-year-old *Acacia* stand (*Acacia* 17) reflects a gradual shift toward a more mixed and transitional community, potentially driven by early natural colonization under reduced management intensity. This pattern is consistent with observations from older tropical plantations where regeneration increases as silvicultural inputs decline (Meli et al. 2017; Hernandez et al. 2022; Ouyang et al. 2023). In Sabah, *Acacia* plantations are typically established on previously degraded or cleared sites and harvested on short rotations; thus, *Acacia* 17 stands in this study represent extended rotations beyond the typical ~10-12 years. Prolonged stand retention allows longer periods for natural recruitment and understorey development, facilitating compositional change through passive recovery (Chen et al. 2024; Zanin et al. 2025). However, recovery in these older stands remains partial and context-dependent, as constraints such as past soil degradation or management intensity may limit recovery potential (Karyati et al. 2018).

The pronounced differences between natural and planted forests highlight the ecological constraints imposed by monoculture management and the ecological value of remnant forest patches in sustaining native diversity (Taleshi 2014). The dominance of native taxa within secondary and riparian forests suggests strong resistance against exotic invasion, potentially driven by competitive interactions, soil feedbacks, and canopy closure that limit the establishment of invasive species (Waddell et al. 2023). These remnant forest types function as key biodiversity reservoirs within plantation landscapes, supporting native species assemblages that are largely absent from *Acacia* stands. Similar successional dynamics have been reported in other tropical production forests, including older *A. auriculiformis* stands in the Philippines and *Eucalyptus* plantations on Hainan Island, where reduced management disturbance was associated with higher native richness and more developed understorey structure (Hernandez et al. 2022; Chen et al. 2024). Collectively, these findings reinforce the importance of remnant forest retention and extended rotations in enabling partial restoration within plantation mosaics (Mang and Brodie 2015; Meli et al. 2017).

Beta diversity analyses showed that species turnover dominated community differentiation among forest types. Complete dissimilarity between the youngest *Acacia* stand and natural forests, such as riparian forest (Total β=1.00), reflects the absence of shared species, while moderate nestedness among *Acacia* stands indicates partial similarity due to shared planted taxa. The predominance of turnover indicates that habitat heterogeneity, rather than species loss alone, drives compositional differentiation across the landscape. Each forest type supports distinct species assemblages that collectively enhance landscape-level biodiversity, and remnant native vegetation within corridors contributes to maintaining regional diversity in fragmented plantation landscapes (Keppel et al. 2016; Socolar et al. 2016; Samways et al. 2025).

From a management perspective, the dominance of turnover-driven beta diversity underscores the importance of maintaining habitat heterogeneity within plantation landscapes. Retaining remnant forest patches and extending *Acacia* rotation cycles can enhance biodiversity outcomes, while riparian and secondary forests function as vital refugia and dispersal corridors that sustain native flora and ecological connectivity (Kugan and Mannan 2022; Wang et al. 2022). Key recommendations include: (i) managing riparian and secondary set-asides to preserve compositional heterogeneity; (ii) promoting longer rotation or mixed-age plantation stands to increase opportunities for natural regeneration; and (iii) implementing targeted native enrichment planting in older stands to accelerate ecological recovery where passive regeneration is constrained. These strategies align with Sabah’s Forest Plantation Development Action Plan, which emphasizes multifunctionality and ecological resilience in production landscapes.

Limitations of this study include unbalanced sample sizes among forest types, particularly for natural forests that are small, narrow, or partially disturbed, limited taxonomic resolution for some taxa, and the absence of environmental covariates such as canopy cover or soil properties. Caution is therefore warranted when interpreting recovery in older Acacia stands, as observed patterns may reflect site-specific legacies rather than generalized recovery trajectories. Future studies incorporating structural and environmental variables, alongside more extensive sampling in underrepresented habitats, would improve understanding of the mechanisms shaping biodiversity recovery across plantation mosaics.

Overall, this study provides new empirical evidence from Sabah demonstrating that stand age and habitat heterogeneity jointly structure alpha and beta diversity in *Acacia* plantation landscapes. While extended rotations and reduced management intensity can facilitate partial recovery of native tree assemblages, remnant forest patches remain essential for maintaining unique species assemblages and overall landscape biodiversity. Integrating stand-age management with remnant forest conservation is therefore critical for developing multifunctional and ecologically resilient production forests.

In conclusion, plant biodiversity varied markedly across forest types within the Acacia plantation landscape in Sabah, with a total of 42 species recorded, 92.9% of which were native. Species diversity indices showed consistently higher values in natural forests, particularly secondary and riparian forests (Shannon-Wiener H′ up to 2.547; Simpson 1-D up to 0.904), while *Acacia* plantations exhibited lower diversity, especially in younger stands. Among plantations, *Acacia* 17 supported higher native species richness (mean ± SD: 4.50±2.38 species per plot) than *Acacia* 13 and *Acacia* 15, indicating partial recovery of native flora with increasing stand age. Differences in native tree species richness among forest types were statistically significant (Kruskal–Wallis, p=0.002), with younger *Acacia* stands containing significantly fewer native species than riparian and secondary forests.

Beta-diversity analyses further revealed strong compositional differentiation among forest types, with species turnover being the dominant component (0.68-1.00) and nestedness contributing minimally (0.078-0.118).

Complete dissimilarity (total β=1.00) between the youngest *Acacia* stand and riparian forest underscores the distinctiveness of natural forest assemblages. Indicator species analysis confirmed that plantations were primarily characterized by planted *Acacia* species, whereas natural forests supported diagnostic native taxa, including *K. pinnatum* (IUCN Vulnerable), emphasizing the conservation value of remnant forest patches. These findings provide a basis for adaptive plantation management that integrates biodiversity conservation within sustainability certification and landscape-level planning frameworks.

ACKNOWLEDGEMENTS

This research was funded by the Japan International Forestry Promotion and Cooperation Center (JIFPRO) (Grant No. LPA2308). The authors gratefully acknowledge Koshii & Co. Ltd. for facilitating the funding application, and special thanks go to Mr. Yutaka Sato for his assistance in field survey. We also extend our appreciation to the anonymous reviewers for their constructive comments and suggestions, which have substantially improved the quality of this manuscript.

REFERENCES

Baselga A, Orme CDL. 2012. Betapart: An R package for the study of beta diversity. Methods Ecol Evol 3 (5): 808-812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19: 134-143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Bohnett E, Goossens B, Bakar MS, Abidin TR, Lim HY, Hulse DW, Ahmad B, Hoctor TM, Gardner PC. 2022. Examining diversity of terrestrial mammal communities across forest reserves in Sabah, Borneo. Biodivers Conserv 31: 1709-1734. https://doi.org/10.1007/s10531-022-02423-8.

Chen H, Du S, Huang H, Tian L, Zhou H, Wu J, Yu X. 2024. Plant diversity in the understory of eucalyptus plantations on Hainan Island and its response to environmental factors. Front Ecol Evol 12: 1366094. https://doi.org/10.3389/fevo.2024.1366094.

De Cáceres M, Legendre P. 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90: 3566-3574. https://doi.org/10.1890/08-1823.1.

Einzmann HJR, Zotz G. 2016. How diverse are epiphyte assemblages in plantations and secondary forests in tropical lowlands? Trop Conserv Sci 9 (2): 629-647. https://doi.org/10.1177/194008291600900205.

Fagan ME, Kim DH, Settle W, Ferry L, Drew J, Carlson H, Slaughter J, Schaferbien J, Tyukavina A, Harris NL, Goldman E, Ordway EM. 2022. The expansion of tree plantations across tropical biomes. Nat Sustain 5: 681-688. https://doi.org/10.1038/s41893-022-00904-w.

Gaveau DLA, Sheil D, Husnayen, Salim MA, Arjasakusuma S, Ancrenaz M, Pacheco P, Meijaard E. 2016. Rapid conversions and avoided deforestation: Examining four decades of industrial plantation expansion in Borneo. Sci Rep 6: 32017. https://doi.org/10.1038/srep32017.

Guclu C, Luk CL, Ashton LA, Abbas S, Boyle MJW. 2024. Beta diversity subcomponents of plant species turnover and nestedness reveal drivers of community assembly in a regenerating subtropical forest. Ecol Evol 14 (9): e70233. https://doi.org/10.1002/ece3.70233.

Habel JC, Zamora C, Rödder D, Fischer M, Lens L, Kotze DJ. 2021. Using indicator species to detect high-quality habitats in an East African Forest biodiversity hotspot. Biodivers Conserv 30: 903-915. https://doi.org/10.1007/s10531-021-02124-8.

Hernandez JO, Ata JP, Combalicer MS. 2022. Long-term changes in floristic diversity, composition, and stand structure in *Acacia auriculiformis* plantation in Mount Makiling Forest Reserve, Philippines. Biodiversitas 23 (7): 3630-3637. https://doi.org/10.13057/biodiv/d230740.

Irwin S, Pedley SM, Coote L, Dietzsch AC, Wilson MW, Oxbrough A, Sweeney O, Moore KM, Martin RD, Kelly DL, Mitchell FJG, Kelly TC, O'Halloran J. 2014. The value of plantation forests for plant, invertebrate, and bird diversity and the potential for cross-taxon surrogacy. Biodivers Conserv 23: 697-714. https://doi.org/10.1007/s10531-014-0627-4.

Karyati, Ipor IB, Jusoh I, Wasli ME. 2018. Tree stand floristic dynamics in secondary forests of different ages in Sarawak, Malaysia. Biodiversitas 19 (3): 717-723. https://doi.org/10.13057/biodiv/d190302.

Keppel G, Gillespie TW, Ormerod P, Fricker GA. 2016. Habitat diversity predicts orchid diversity in the tropical South Pacific. J Biogeogr 43 (12): 2332-2342. https://doi.org/10.1111/jbi.12805.

Kugan F, Mannan S. 2022. Action Plan on Forest Plantation Development (2022-2036). Sabah Forestry Department, Sandakan.

Liebke DF, Harms D, Widyastuti R, Scheu S, Potapov AM. 2021. Impact of rainforest conversion into monoculture plantation systems on pseudoscorpion density, diversity, and trophic niches. Soil Org 93: 83-96. https://doi.org/10.25674/SO93ISS2ID147.

Magurran AE, McGill BJ. 2011. Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford.

Malaysian Timber Council. 2016. Forest Plantations in Malaysia. https://mtc.com.my.

Mang S, Brodie JF. 2015. Impacts of non-oil tree plantations on biodiversity in Southeast Asia. Biodivers Conserv 24: 3431-3447. https://doi.org/10.1007/s10531-015-1022-5.

Martello F, Dáttilo W, Souza-Campana DR, Medeiros HR, Silva RR, Ribeiro MC, Morini MSC. 2024. *Eucalyptus* plantation reduces diversity and disrupts predator-prey correlations of soil invertebrates within the Atlantic Forest. For Ecol Manag 553: 121592. https://doi.org/10.1016/j.foreco.2023.121592.

Meli P, Holl KD, Rey Benayas JM, Jones HP, Jones PC, Montoya D, Mateos DM. 2017. A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. PLoS One 12 (2): e0171368. https://doi.org/10.1371/journal.pone.0171368.

Oksanen J, Simpson GL, Blanchet FG et al. 2022. Vegan: Community Ecology Package. R Package Version 2.6-2. https://cran.r-project.org.

Ouyang S, Tie L, Rao X, Cai X, Liu S, Vitali V, Wei L, Yu Q, Sun D, Lin Y, Bose AK, Gessler A, Shen W. 2023. Mixed-species *Acacia* plantation decreases soil organic carbon and total nitrogen concentrations but favors species regeneration and tree growth over monoculture: A thirty-three-year field experiment in Southern China. Forests 14 (5): 968. https://doi.org/10.3390/f14050968.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.r-project.org.

Samways MJ, Gaigher R, Deacon C, Pryke, JS. 2025. Heterogeneous conservation corridors of remnant vegetation protect biodiversity in South African timber mosaics. Biodivers Conserv 34: 357-379. https://doi.org/10.1007/s10531-024-02993-9.

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP. 2016. How should beta-diversity inform biodiversity conservation?. Trends Ecol Evol 31 (1): 67-80. https://doi.org/10.1016/j.tree.2015.11.005.

Taleshi SAR. 2014. A comparative study on plant diversity in alder (*Alnus subcordata*) stands of natural and plantation areas. Biodiversitas 15 (1): 39-47. https://doi.org/10.13057/biodiv/d150106.

Terpilowski M. 2019. Scikit-posthocs: Pairwise multiple comparison tests in Python. J Open Source softw 4 (36): 1169. https://doi.org/10.21105/joss.01169.

Van der Mescht AC, Pryke JS, Gaigher R, Samways MJ. 2023. Remnant habitat patches provide high value for a wide range of insect species in a timber plantation mosaic. Biodivers Conserv 32 (5): 1755-1775. https://doi.org/10.1007/s10531-023-02574-2.

Virtanen P, Gommers R, Oliphant TE et al. 2020. SciPy 1.0: Fundamental algorithms for scientific computing in Python. Nat Methods 17: 261-272. https://doi.org/10.1038/s41592-019-0686-2.

Waddell EH, Chapman DS, Hill JC, Hughes M, Bin Sailim A, Tangah J, Banin LF. 2023. Evidence of biotic resistance to exotic plant invasion in degraded Bornean Forests. Biotropica 55: 767-778. https://doi.org/10.1111/btp.13227.

Wang C, Zhang W, Li X, Wu J. 2022. A global meta-analysis of the impacts of tree plantations on biodiversity. Glob Ecol Biogeogr 31 (3): 576-587. https://doi.org/10.1111/geb.13440.

Zanin G, DesRochers A, Fenton NJ. 2025. Impact of the origin of sites planted with hybrid poplar on plant community composition and diversity. New For 56: 12. https://doi.org/10.1007/s11056-024-10080-8.

Zhu HH, Zhang J, Cheuk ML, Hau BCH, Fischer GA, Gale SW. 2023. Monoculture plantations impede forest recovery: Evidence from the regeneration of lowland subtropical forest in Hong Kong. Front For Glob Chang 6: 1098666. https://doi.org/10.3389/ffgc.2023.1098666.

Table S1. Tree species abundance above and below minimum DBH across forest types in KM Hybrid Plantation, Sabah, Malaysia. Values indicate the number of individuals of each species

Species	**Forest types**					
	***Acacia* 13**	***Acacia* 15**	***Acacia* 17**	**Heath forest**	**Riparian forest**	**Secondary forest**
Above minimum DBH						
Acacia hybrid	253	174	73	7	0	0
Acacia mangium Willd.	128	64	5	2	0	1
Aquilaria malaccensis Lam.	0	0	0	0	0	6
Aralidium pinnatifidum (Jungh. & de Vriese) Miq.	0	0	2	0	0	0
Artocarpus integer (Thunb.) Merr.	0	0	1	0	0	0
Artocarpus nitidus Trécul	0	0	0	0	0	2
Artocarpus odoratissimus Blanco	0	0	4	0	0	0
Bridelia insulana Hance	0	0	0	0	3	0
Campnosperma auriculatum (Blume) Hook.fil.	0	0	2	0	0	6
Chassalia curviflora (Wall.) Thwaites	0	0	0	0	0	4
Cinnamomum sp.	0	0	0	0	5	1
Cratoxylum sp.	0	0	0	0	4	0
Cratoxylum arborescens (Vahl) Blume	0	0	0	22	0	0
Diospyros sp.	0	0	0	0	0	6
Dyera costulata (Miq.) Hook.fil.	0	1	0	0	0	17
Ficus macrocarpa L.f.	0	0	0	0	1	0
Glochidion littorale Blume	0	0	0	0	2	0
Gluta speciosa (Ridl.) Ding Hou	0	0	0	0	0	1
Koordersiodendron pinnatum (Blanco) Merr.	0	0	0	0	0	5
Lophopetalum javanicum (Zoll.) Turcz.	0	0	0	0	2	0
Macaranga indica Wight	0	0	0	0	5	10
Myristica maxima Warb.	0	0	0	0	0	2
Neolamarckia cadamba (Roxb.) Bosser	0	0	0	0	1	9
Polyalthia lateriflora (Blume) Kurz	0	0	0	0	1	0
Pouteria obovata (R.Br.) Baehni	0	0	1	0	0	0
Sandoricum koetjape (Burm.fil.) Merr.	0	0	0	0	3	3
Schefflera sp.	0	0	0	0	0	1
Sterculia macrophylla Vent.	0	0	1	0	0	8
Syzygium borneense (Miq.) Miq.	0	0	0	0	0	1
Syzygium grande (Wight) N.P.Balakr.	0	0	0	0	0	1
Syzygium lineatum (DC.) Merr. & L.M.Perry	0	1	8	6	5	25
Terminalia catappa L.	0	0	0	0	4	1
Utania cuspidata (Blume) K.M.Wong, Sugumaran & Sugau	0	0	0	0	0	8
Vitex pinnata L.	0	1	4	2	5	34
Below minimum DBH						
**Adenanthera pavonina* L.	0	0	1	0	0	0
**Beilschmiedia sp.*	0	0	0	0	1	0
**Derris sp.*	0	0	1	0	0	0
**Garcinia sp.*	0	0	1	0	0	0
**Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.	0	0	0	0	1	0
**Homalanthus* sp.	1	0	0	0	0	0
**Mallotus paniculatus* (Lam.) Müll.Arg.	0	0	1	0	0	0
**Polyalthia bullata* King	0	0	1	0	0	0
Total	382	241	105	107	43	152

Note: Tree species abundance based on individuals with DBH ≥5 cm (≥ 4 cm in Heath forest). Number of plots (n): *Acacia* 13=8, *Acacia* 15=8, *Acacia* 17=4, Heath forest=3, Riparian=3, and Secondary forest=3

Table S2. Partitioning of beta diversity (Total, Turnover, Nestedness) between and within forest types, with the values ranging from 0 to 1

Comparison	**Total beta diversity**	**Turnover**	**Nestedness**
Between habitats			
Between *Acacia* 13-*Acacia* 15	0.302±0.039	0.167±0.036	0.135±0.027
Between *Acacia* 13-*Acacia* 17	0.583±0.032	0.167±0.052	0.417±0.044
Between *Acacia* 13-Heath forest	0.867±0.020	0.778±0.033	0.089±0.013
Between *Acacia* 13-Riparian forest	1.000±0.000	1.000±0.000	0.000±0.000
Between *Acacia* 13-Secondary forest	0.967±0.010	0.889±0.033	0.078±0.023
Between *Acacia* 15-*Acacia* 17	0.646±0.029	0.214±0.054	0.432±0.052
Between *Acacia* 15-Heath forest	0.881±0.024	0.763±0.059	0.118±0.042
Between *Acacia* 15-Riparian forest	0.966±0.018	0.938±0.034	0.029±0.017
Between *Acacia* 15-Secondary forest	0.956±0.013	0.854±0.041	0.102±0.028
Between *Acacia* 17-Heath forest	0.846±0.046	0.805±0.057	0.042±0.016
Between *Acacia* 17-Riparian forest	0.875±0.008	0.818±0.010	0.057±0.011
Between *Acacia* 17-Secondary forest	0.866±0.022	0.728±0.040	0.139±0.026
Between Heath Forest-Riparian forest	0.930±0.018	0.905±0.024	0.025±0.008
Between Heath forest-Secondary forest	0.942±0.019	0.884±0.036	0.059±0.017
Between Riparian-Secondary forest	0.800±0.023	0.684±0.049	0.115±0.032
Within habitats			
Within *Acacia* 13	0.000±0.000	0.000±0.000	0.000±0.000
Within *Acacia* 15	0.455±0.054	0.214±0.060	0.241±0.049
Within *Acacia* 17	0.570±0.074	0.317±0.101	0.253±0.087
Within Heath forest	0.556±0.056	0.222±0.222	0.333±0.167
Within Riparian forest	0.620±0.044	0.502±0.099	0.118±0.064
Within the Secondary forest	0.681±0.063	0.586±0.084	0.095±0.030

Note: Values represent 95% confidence interval of pairwise beta diversity components, calculated using Baselga's (2010) partitioning framework. The number of plots (n) was as follows: *Acacia* 13 (n=8), *Acacia* 15 (n=8), *Acacia* 17 (n=4), Heath forest (n=3), Riparian forest (n=3), and Secondary forest (n=3)