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Dipterocarp Diversity and Regeneration in Mengilan Forest Reserve, Sabah, Malaysia, Near the Sabah–Kalimantan Border

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ABSTRACT

Mengilan Forest Reserve, a class I protected forest in Southern Sabah adjacent to Kalimantan, was previously logged and is now managed for biodiversity under the Heart of Borneo Initiative. Despite its strategic location within a transboundary conservation landscape, information on dipterocarp diversity and regeneration remains limited. This study established a baseline assessment of dipterocarp diversity, species composition, and regeneration patterns following historical logging across an elevational gradient. A rapid survey of dipterocarp trees and seedlings was conducted along three transects spanning upland mixed dipterocarp and lower montane kerangas forests across an elevational gradient. Adult dipterocarps were inventoried along line transects, and seedling regeneration was quantified using systematically distributed 1 m × 1 m quadrats. Species diversity and community composition were evaluated using diversity indices, Jaccard dissimilarity, ANOSIM, and NMDS. A total of 31 dipterocarp species representing six genera and 41 adult individuals were recorded. Of these, 19 species (61.30%) were globally threatened, and 14 species (45.20%) were endemic, including the Sabah endemic *Shorea symingtonii*. Species richness and diversity were highest in the lower-elevation transect (15 species; H′ = 2.69; 1−D = 0.93) and lowest in the upper transect (5 species; H′ = 1.61; 1−D = 0.80). Species composition differed significantly among transects (ANOSIM R = 0.72, $p < 0.01$), with high turnover (Jaccard dissimilarity = 0.89–0.95). A total of 131 seedlings representing 14 species were recorded, with regeneration highest in upland mixed dipterocarp forest and lowest in lower montane kerangas forest. These findings demonstrate the lasting influence of historical logging and elevation on dipterocarp communities. Mengilan FR therefore represents an important refuge for threatened and endemic dipterocarps while providing a baseline for long-term monitoring and transboundary conservation management within the Heart of Borneo landscape.

1. Introduction

Over the past decades, the timber industry has played a key role in Sabah's economic growth. In 1953, forests covered about 86% of the state, mainly consisting of dipterocarp forests distributed across lowland to montane areas. However, extensive logging and subsequent conversion to oil palm plantations have caused severe forest degradation (Gaveau et al. 2016; Ng et al. 2022).

Between 1973 and 2015, Sabah lost around 25% of its land area (1.86 million ha). Despite this, forests still covered 53% of the state in 2015 (3.97 million ha), although much of it was no longer intact; only 22% remained undisturbed, while 31% had been logged or was regenerating (Gaveau et al. 2016; Khoo et al. 2023; Ng et al. 2022).

Conventional mechanized logging was among the causes of forest degradation. It typically removed 8–15 trees per hectare and damaged 40–70% of the remaining trees. It also disturbed up to 40% of the forest floor (Bartholomew et al. 2024; Ewers et al. 2024; Hayward et al. 2021). These impacts changed forest structure, reduced canopy cover, and limited natural regeneration, especially for dipterocarps that rely on mature seed trees. Concerns about these impacts led to the adoption of sustainable forest management (SFM), including reduced impact logging (RIL) and the expansion of protected areas. Long-term studies in Sabah show that better management can help maintain forest structure and support regeneration (Hayward et al. 2021; Pang et al. 2024).

As management practices changed, the Sabah Forestry Department reclassified several logged production forests as class I protection forests to protect biodiversity. Mengilan forest reserve (FR), re-gazetted in 2012 from the former Serudong FR, is one example. Unlike nearby forests managed under reduced impact logging (RIL), Mengilan was logged using conventional methods. As a result, it now consists of mixed secondary forest, with uneven canopy structure and varying regeneration. Recent reports show road upgrades and border development in the nearby Serudong area as part of cross-border connectivity plans (Bernama 2025; Malay Mail 2024; New Straits Times 2025a). In July 2025, about 23 ha of the neighboring Serudong FR was degazetted for border security infrastructure. Replacement forest land was gazetted elsewhere to maintain the total forest reserve area (New Straits Times 2025b).

Despite growing attention to dipterocarp conservation, ecological data from forest reserves along international borders remain limited. Mengilan forest reserve offers a useful case study given its history of conventional logging, elevation variation, and increasing development pressure. In this study, we assess how the availability and distribution of reproductive trees influence dipterocarp regeneration. Regeneration may also be affected by broader landscape factors and increased access in this border area, reflecting wider patterns of biodiversity loss in Southeast Asia (Hayward et al. 2021; Pang et al. 2024; Zheng et al. 2025). Mengilan also lies within the Heart of Borneo (HoB) conservation landscape, where maintaining forest integrity and connectivity is a key priority (Suis et al. 2023).

Here, we provide a baseline assessment of dipterocarp diversity, composition, and regeneration in a logged protection forest. By examining patterns across elevation and topography, we can better understand forest recovery processes. We hypothesize that dipterocarp species composition, diversity, and regeneration vary along the elevational gradient in response to environmental variation and past logging disturbance. These findings provide a baseline for future monitoring and support forest management in this transboundary forest landscape.

2. Materials and Methods

2.1. Study Area

Mengilan FR, in Southern Sabah, Malaysia, covers approximately 6,684 ha and comprises two forest blocks, one bordering Kalimantan, Indonesia (**Fig. 1**). Elevation within the reserve ranges from ~450 to 1,300 m a.s.l., placing it among the higher hill formations of the former Serudong forest landscape. Climatic data were obtained from the nearest station at Sungai

Serudong (DOPA 2020; **Fig. 2**), which shows a mean annual rainfall of ~2,317 mm (monthly mean 193 mm) and mean monthly temperatures of 26.40–27.60°C (max 31.80°C in May; min 22.30°C in January). In early August 2020, the Sabah Forestry Department organized a scientific expedition to assess flora and fauna in Mengilan FR. We documented forest condition and regeneration as part of this survey.

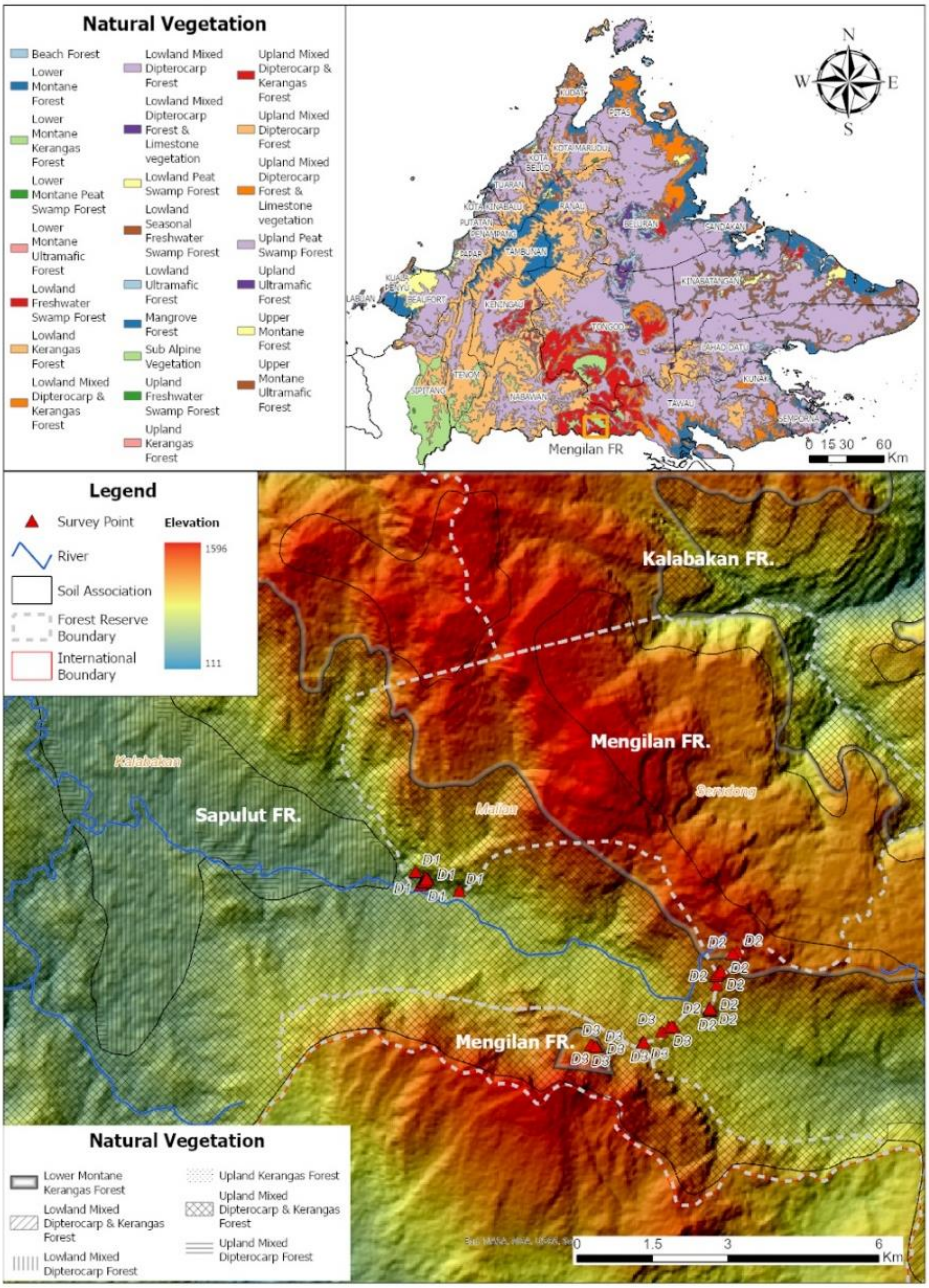

Fig. 1. Upper: Natural vegetation map of Sabah (Sabah Forestry Department). Lower: Topography of Mengilan FR derived from SRTM DEM (30 m resolution), processed in ArcGIS Pro with hillshade and relief. Reserve boundaries (dashed line), soil associations, vegetation types, river networks (blue) and survey points (D1–D3) are shown.

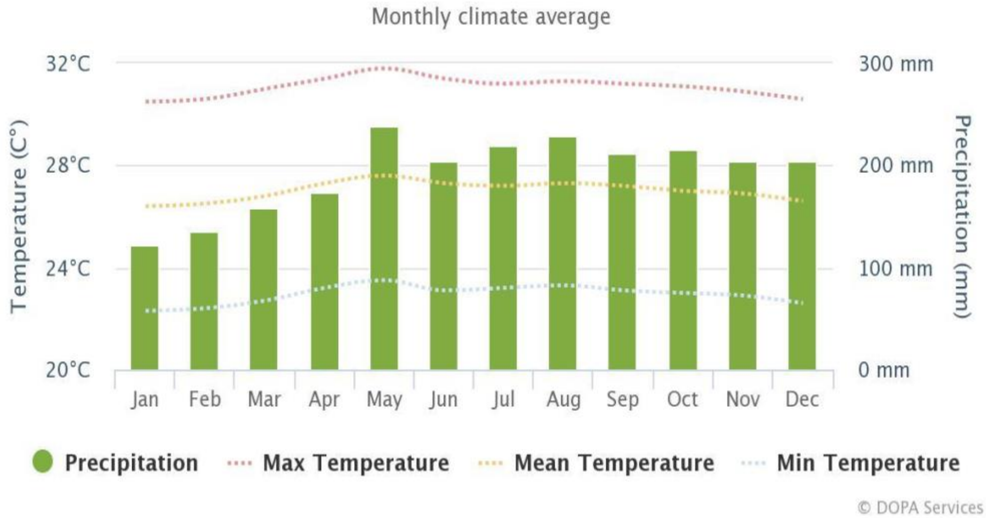

Fig. 2. Climatic data for Sg. Serudong (DOPA 2020).

2.2. Geology, Soil and Vegetation

Mengilan FR is underlain predominantly by the Neogene sedimentary Kapilit Formation, which is geologically similar to the Maliau Basin (Hisham and Zainal 2023; Sabah Forestry Department 2025). The Kapilit Formation consists mainly of sandstone and mudstone with minor conglomerate, limestone, and coal deposits (Hisham and Zainal 2023; Sabah Forestry Department 2025). Weathering of these substrates produces nutrient-poor, sandy soils that are characteristic of kerangas (heath) forest habitats.

Based on the survey observations, upland mixed dipterocarp forest predominated at the lower elevations (490–578 m a.s.l.), whereas kerangas (heath) forest and lower montane kerangas forest were more evident at the higher elevations surveyed (807–1,166 m a.s.l.). However, the transition between these forest types was gradual rather than abrupt, with some areas showing characteristics of more than one vegetation type along the elevational gradient.

2.3. Field Equipment and Data Recording

Field surveys were conducted using a handheld GPS receiver (Garmin GPSmap 62st) to record coordinates, a diameter tape to measure diameter at breast height (DBH), binoculars for canopy observation and a digital camera for photographic documentation. Species identity, location, DBH measurements and field observations were systematically recorded and compiled after the survey.

Transects were established to capture variation in forest composition and regeneration across the elevational gradient within Mengilan FR during the expedition; new access trails were created where necessary to reach representative forest habitats. Transect orientation was guided primarily by accessibility and terrain conditions, particularly along ridges and existing topographic features, rather than following riverbanks, contour lines, or other predetermined landscape alignments. This approach enabled sampling across a range of elevations and vegetation types encountered within the reserve. The surveyed transects spanned elevations from 490 to 1,166 m a.s.l. (**Table 1**), representing the accessible portion of the elevational gradient, while the highest peak of Mengilan Hill reaches approximately 1,300 m a.s.l.

Table 1. Summary of transect surveys and regeneration quadrat sampling conducted in Mengilan FR, Sabah

Survey Unit	Forest Block	Elevation (m a.s.l.)	Transect Start Point (lat; long)	Transect Length (km)	Estimated Covered Area (km²)	No. of Regeneration Quadrats (1 m²)	Dominant Vegetation Type
D1	Primary block	490–576	N4.39409; E116.9193	1.60	0.09	51 (1 km)	UMDF & KF
D2	Primary block	969–1,166	N4.37774; E116.9721	1.79	0.09	51 (1 km)	UMDF & KF; LMKF
D3	Secondary block (near Kalimantan border)	807–981	N4.36864; E116.9646	1.19	0.09	51 (1 km)	UMDF & KF; LMKF

Notes: LMKF = Lower montane kerangas forest, UMDF = Upland mixed dipterocarp forest, KF = Kerangas forest. Geographic coordinates for transects are referenced to the WGS 1984 datum.

2.4. Shuttle Radar Topography Mission (SRTM) - Digital Elevation Model (DEM)

The Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) at 1 arc-second (30 m) resolution was obtained from the USGS EarthExplorer repository, clipped to the Mengilan FR boundary, and further analyzed in ArcGIS Pro. Terrain visualization layers, including hillshade and relief, were generated to support interpretation of topographic variation across the study area. Reserve boundaries, river networks and survey points were overlaid on the DEM, and vertical exaggeration was applied where necessary to enhance three-dimensional visualization. This approach follows common applications of DEMs for representing terrain gradients and supporting ecological interpretation in forested landscapes (Guth et al. 2024; Li et al. 2022; Sulebak 2000).

2.5. Dipterocarp Species Inventory and Diversity Analysis

The survey was conducted as a rapid floristic assessment to establish a baseline inventory of dipterocarp diversity and regeneration during a short-duration scientific expedition, following an approach similar to that used in the Sungai Rawog Conservation Area, Segaliud Lokan Forest Reserve, Sabah (Tsen et al. 2019). Dipterocarp surveys were carried out along 10-m-wide line transects (**Table 1**), during which all individuals encountered were recorded and identified, where possible, including mature trees, poles, and saplings. Individuals were classified according to standard tropical forest inventory criteria as saplings (DBH < 10 cm), poles (DBH 10–29.90 cm), and trees (DBH ≥ 30 cm), following Wyatt-Smith (1963) and Sabah Forestry Department Forest inventory guidelines. Diameter at breast height (DBH) was measured at 1.3 m above ground level. Voucher specimens were collected from individuals that could not be confidently identified in the field and were subsequently verified at the SAN Herbarium, Forest Research Centre, Sandakan. Despite these verification efforts, two *Hopea* specimens could not be confidently identified to the species level and were therefore excluded from subsequent diversity and compositional analyses. Species diversity and richness were quantified using Shannon–Wiener diversity (H′), Simpson's diversity (1−D), Margalef's richness index and Shannon-derived evenness (E = eH′/S) (Magurran 2004; Margalef 1958; Shannon and Weaver 1963; Simpson 1949).

2.6. Species Composition

Species composition among transects was analyzed using a species-by-transect presence–absence matrix. Community similarity was assessed using Jaccard similarity and visualized using a Venn diagram and heatmap. Differences in species composition were tested using analysis of similarity (ANOSIM) with 9,999 permutations. Non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity was used to visualize compositional differences among transects, with species scores calculated as weighted averages to aid interpretation of site–species relationships. Ordination analyses were conducted in Python using Google Colab, and results were cross-checked with PAST software by Hammer et al. (2001) to ensure consistency.

2.7. Dipterocarp Seedling Regeneration

Seedling regeneration was assessed as a rapid complement to the adult transect survey. Seedlings were defined as dipterocarp individuals less than 50 cm in height, following the seedling classification adopted for regeneration assessments in tropical dipterocarp forests (Appanah and Manaf 1994). Along each 1,000 m transect, 51 regeneration quadrats (1 m × 1 m) were established systematically at 20 m intervals, including both the starting (0 m) and ending (1,000 m) points. To sample adjacent microhabitats and minimize directional bias, quadrats were positioned alternately 10 m to the left and right of the transect line (Kent 2012) (**Fig. 3**). All dipterocarp seedlings within each quadrat were identified and counted where possible. Seedling abundance and species occurrence were subsequently summarised in 200 m segments along each transect to provide a descriptive representation of regeneration patterns along the elevational gradient.

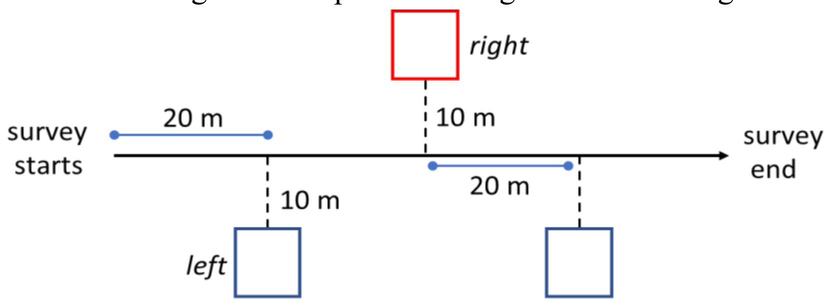

Fig. 3. Schematic showing 1 m × 1 m regeneration quadrats placed along the line transects.

3. Results and Discussion

3.1. Results

3.1.1. Digital elevation model of Mengilan FR

The SRTM-DEM shows that elevation within the reserve ranges from approximately 450 to 1,300 m a.s.l., with higher elevations concentrated toward the central and northern portions of the reserve (**Fig. 1;** lower). The terrain shows undulating to steep slopes with hilly conditions commonly found in the Kapilit Formation within the Maliau Basin. Transect locations were spread across different elevation zones, allowing sampling of upland mixed dipterocarp forest, lower montane forest and kerangas. The elevation changes shown in the DEM help explain the patterns of dipterocarp species distribution and regeneration found along the transects (**Fig. 1**).

3.1.2. Species richness, diversity and checklist of dipterocarps

A total of 31 confirmed dipterocarp species representing six genera were recorded across the three transects and included in subsequent analyses. Diameter at breast height (DBH) of all recorded dipterocarp individuals (n = 41) ranged from 1 to 130 cm (mean ± SD = 45.50 ± 32.20 cm), encompassing sapling, pole, and tree size classes. This broad size distribution indicates a structurally heterogeneous forest with individuals spanning multiple developmental stages (**Table 2**).

Table 2. Alpha diversity indices and structural attributes of dipterocarps across transects in Mengilan FR

Parameter	D1	D2	D3
Species richness	15	12	5
Individuals (n)	16	16	5
Elevation range (m a.s.l.)	490–578	969–1036	807–981
DBH range (cm)	17.50–110	3–70	5–130
Mean DBH (cm)	54.20 ± 26.60	32.90 ± 31.70	54.90 ± 36.90
Dominance (D)	0.07	0.11	0.20
Simpson's diversity (1–D)	0.93	0.89	0.80
Shannon–Wiener index (H′)	2.69	2.36	1.61
Evenness (eH′/S)	0.98	0.88	1.00

Notes: D1–D3 denote transects 1–3; Individuals = Total dipterocarp individuals recorded; DBH = Diameter at breast height.

Species richness and diversity varied among transects. D1 (490–578 m a.s.l.) recorded the highest species richness (15 species) and diversity (H′ = 2.69; 1–D = 0.93), followed by D2 (12 species; H′ = 2.36; 1–D = 0.89), whereas D3 recorded the lowest richness and diversity (5 species; H′ = 1.61; 1–D = 0.80). All transects exhibited low dominance values (D = 0.07–0.20), indicating the absence of strongly dominant species. Evenness (E) remained high across all transects, indicating that individuals were relatively evenly distributed among species despite differences in species richness. Although D2 recorded the lowest mean DBH (32.90 ± 31.70 cm), the high standard deviation indicates substantial variation in tree size, reflecting a heterogeneous stand structure comprising both small and medium-sized individuals.

3.1.3. Species composition

The predominance of site-specific species indicates restricted distribution across transects (**Fig. 4a; Table 3**). A large proportion of species was confined to individual transects, with 11 species unique to D1, nine to D2 and five to D3. Only six species were shared between pairs of transects, comprising three species between D1 and D2 (*Shorea laevis*, *S. ovata*, *S. parvistipulata*), two between D1 and D3 (*S. leprosula*, *S. pauciflora*) and one species between D2 and D3 (*Shorea flaviflora*), while no species occurred across all three transects.

This high degree of site-specificity, including lowland-associated taxa such as *Dipterocarpus hasseltii* and *Vatica sarawakesis* in D1, and elevation-associated taxa such as *Dryobalanops lanceolata* in D2 and *Anisoptera costata* in D3, indicates strong compositional differentiation among transects. This pattern is reflected in high Jaccard dissimilarity values (0.89–0.95; **Fig. 4b**) and is supported by significant differences in species composition (ANOSIM: R = 0.72, $p < 0.01$).

Table 3. Dipterocarp species unique to and shared among transects D1–D3, corresponding to the overlap patterns shown in the Venn diagram (**Fig. 4a**)

Group	Count	Species
D1 only	11	*Dipterocarpus hasseltii*; *Hopea beccariana*; *Hopea semicuneata*; *Shorea bracteolata*; *Shorea hopeifolia*; *Shorea johorensis*; *Shorea macroptera*; *Shorea obscura*; *Shorea parvifolia*; *Shorea symintonii*; *Vatica sarawakesis*
D2 only	9	*Dryobalanops lanceolata*; *Hopea ferruginea*; *Shorea monticola*; *Shorea patoiensis*; *Shorea platyclados*; *Vatica chartacea*; *Vatica granulata*; *Vatica oblongifolia*; *Vatica umbonata*
D3 only	5	*Anisoptera costata*; *Hopea montana*; *Vatica albiramis*; *Vatica coriacea*; *Vatica rassak*
D1 ∩ D2	3	*Shorea laevis*; *Shorea ovata*; *Shorea parvistipulata*
D1 ∩ D3	2	*Shorea leprosula*; *Shorea pauciflora*
D2 ∩ D3	1	*Shorea flaviflora*
D1 ∩ D2 ∩ D3	0	None

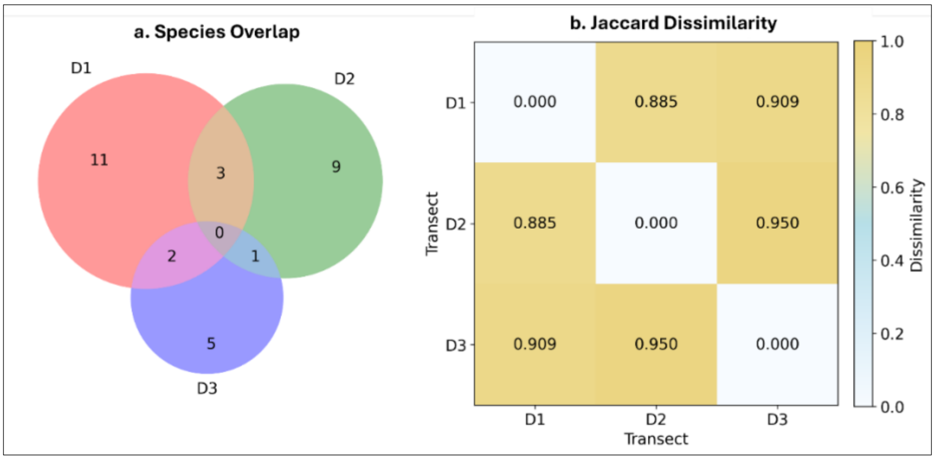

Fig. 4. (a) Venn diagram showing overlap in dipterocarp species composition among transects D1–D3. Numbers indicate species unique to and shared among transects, corresponding to **Table 3**, (b) Pairwise Jaccard dissimilarity heatmap among transects based on species presence–absence data. Higher values indicate greater compositional differences, highlighting strong species turnover along the elevation gradient.

The NMDS ordination based on Bray-Curtis dissimilarity highlighted these differences in species composition (**Fig. 5**). Each transect occupied a distinct position in the ordination, with D3 clearly separated from D1 and D2. This suggests greater compositional differences at intermediate elevations. Species found across multiple transects were positioned between the sites. In contrast, some shared species, such as *Shorea laevis*, *Shorea ovata* and *Shorea parvistipulata*, overlapped in the ordination due to their similar occurrence patterns. The ordination yielded a stress value of 0.11, indicating a good representation of compositional differences among transects. The concordance among Jaccard dissimilarity, ANOSIM, and NMDS analyses suggests consistent patterns of species turnover along the elevational gradient. However, these patterns should be interpreted cautiously given the limited sample size and lack of spatial replication, particularly in D3.

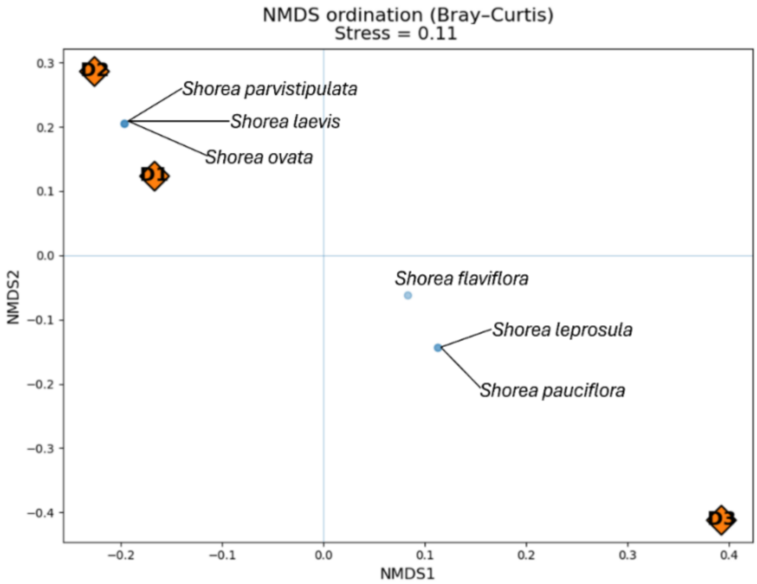

Fig. 5. NMDS ordination of dipterocarp species composition (Bray–Curtis) with selected species labels. Overlapping positions indicate identical occurrence patterns. Stress = 0.11.

3.1.4. Dipterocarp seedling regeneration

A total of 131 dipterocarp seedlings representing 14 species were recorded across the three regeneration transects (**Table 4**).

Table 4. Seedling regeneration of dipterocarp species recorded along regeneration transects (D1–D3) in Mengilan FR

No.	Species	D1	D2	D3	Total seedlings
1	*Shorea laevis*	27	–	3	30
2	*Shorea parvistipulata*	19	5	3	27
3	*Shorea platyclados*	–	13	13	26
4	*Shorea ovata*	15	–	–	15
5	*Shorea obscura*	7	–	–	7
6	*Hopea montana*	–	–	6	6
7	*Shorea hopeifolia*	6	–	–	6
8	*Vatica coriacea*	–	–	6	6
9	*Hopea beccariana*	2	–	–	2
10	*Shorea parvifolia*	2	–	–	2
11	*Hopea ferruginea*	–	1	–	1
12	*Hopea semicuneata*	1	–	–	1
13	*Shorea pauciflora*	1	–	–	1
14	*Vatica albiramis*	–	–	1	1
Total seedlings		80	19	32	131
Total species		9	3	7	

Note: D1–D3 denote transects 1–3.

Seedling abundance varied among transects, with D1 recording the highest number of seedlings (80), followed by D3 (32) and D2 (19) (**Fig. 6d**). Species richness was highest in D1 (nine species), followed by D3 (seven species), while D2 supported only three species. Three species, *Shorea laevis*, *Shorea parvistipulata* and *Shorea platyclados*, were recorded in more than one transect, whereas no species occurred across all three transects. Spatial patterns of seedling distribution differed among transects (**Fig. 6a–c**). In D1, seedlings were distributed along much of the transect, with several localized peaks of abundance. In D2, seedlings were sparse and confined to a limited section. In D3, regeneration was intermittent, with gaps interspersed with localized peaks. The Kruskal–Wallis test approached significance (χ^2 = 4.27, p = 0.07), suggesting a potential trend in regeneration differences among transects. However, this pattern should be interpreted cautiously given the limited replication and unequal sample sizes among transects.

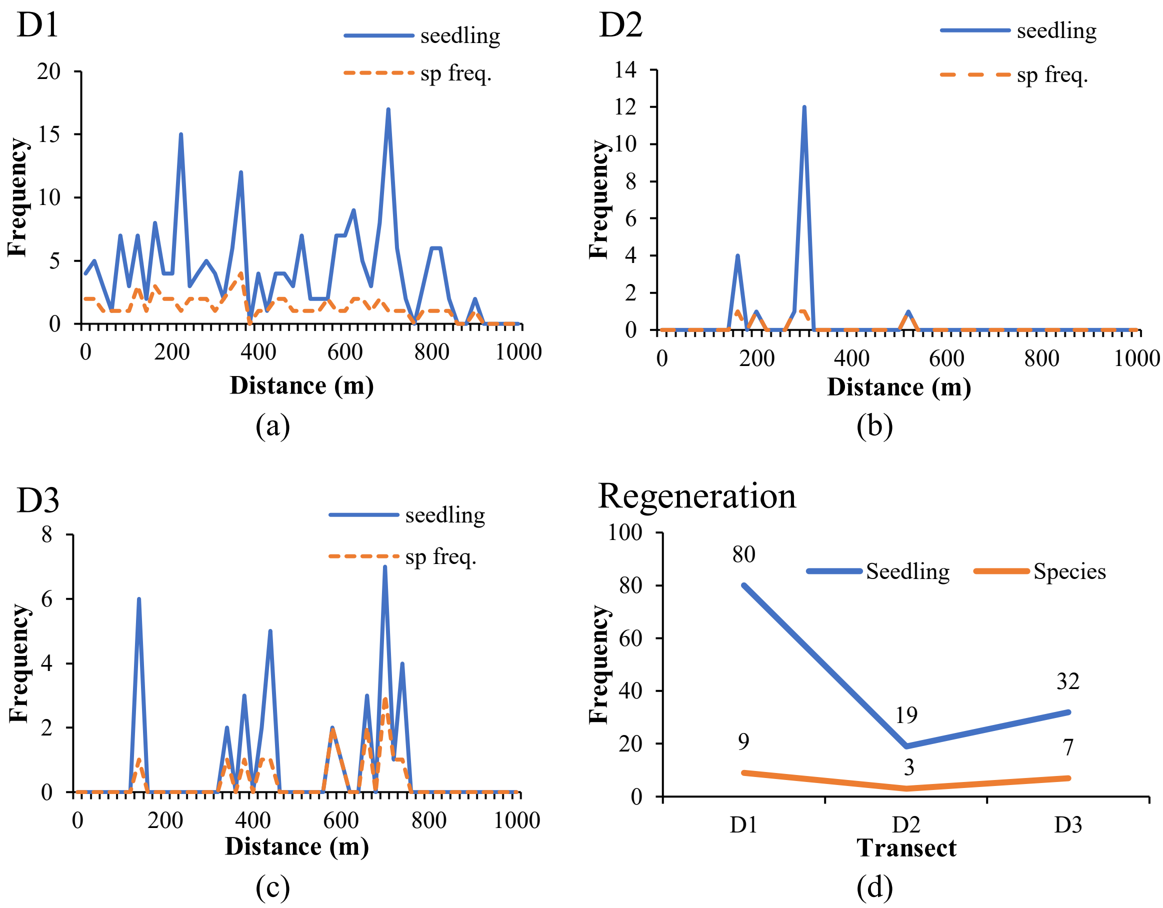

Fig. 6. (a–c) Spatial patterns of dipterocarp seedling regeneration frequency along transects D1–D3, (d) Comparison of total seedling abundance and number of regenerating species among transects. sp. freq. denotes species frequency (number of individuals per sampling point along the transect, m).

3.1.5. Conservation status of recorded dipterocarp species

Based on the global IUCN Red List categories, a high proportion of dipterocarp species recorded in Mengilan FR are of conservation concern. Of the 31 confirmed species, 19 species (61.30%) were classified as threatened, comprising 4 critically endangered (CR), 8 endangered (EN) and 7 vulnerable (VU) species (**Table 5**). The remaining species were listed as near threatened (NT) (3 species) and least concern (LC) (9 species). Endemism among the recorded dipterocarps was notable. 13 species are endemic to Borneo, and 1 species, *Shorea symingtonii*, is endemic to Sabah (Khoo et al. 2023), representing 45.20% of the recorded dipterocarp flora. Several endemic species were also categorized under IUCN threatened categories, highlighting the conservation importance of Mengilan FR for regionally restricted dipterocarp taxa. Several species included in the conservation assessment were recorded only at the seedling stage and not encountered as adult trees during transect surveys; these species are indicated by an asterisk (*) in **Table 5**.

Table 5. The IUCN Red List assessment of dipterocarp species in Mengilan FR.

No	Species	Frequency	Global IUCN
1	*Anisoptera costata*	1	EN
2	*Dipterocarpus hasseltii*	1	EN
3	***Dryobalanops lanceolata***	1	LC
4	*Hopea beccariana*	1	VU
5	*Hopea ferruginea**	1	CR
6	*Hopea montana**	1	CR
7	*Hopea semicuneata**	1	EN
8	*Shorea bracteolata*	1	EN
9	***Shorea flaviflora***	2	VU
10	*Shorea hopeifolia*	1	CR
11	*Shorea johorensis*	1	CR
12	*Shorea laevis*	2	VU
13	*Shorea leprosula*	2	NT
14	***Shorea macroptera***	1	LC
15	***Shorea monticola***	3	LC
16	***Shorea obscura***	1	VU
17	*Shorea ovata*	2	EN
18	*Shorea parvifolia*	1	LC
19	***Shorea parvistipulata***	2	LC
20	***Shorea patoiensis***	1	NT
21	*Shorea pauciflora*	2	EN
22	*Shorea platyclados*	3	EN
23	*Shorea symingtonii***	1	VU
24	***Vatica albiramis****	1	LC
25	***Vatica chartacea***	1	EN
26	***Vatica coriacea****	1	NT
27	***Vatica granulata***	1	LC
28	***Vatica oblongifolia***	1	VU
29	*Vatica rassak*	1	LC
30	***Vatica sarawakesis***	2	VU
31	*Vatica umbonata*	1	LC

Notes: Species marked with an asterisk (*) were recorded only in regeneration quadrats. ** indicates species endemic to Sabah. Bold text indicates Bornean endemic species. IUCN categories: CR = Critically endangered, EN = Endangered, VU = Vulnerable, NT = Near threatened, LC = Least concern, NE = No assessment available.

3.2. Discussion

3.2.1. Species composition pattern

The results show that dipterocarp species change with elevation. The different transects had very distinct species, with most found at only one site and none shared across all three. This suggests that dipterocarp species have preferences for different elevations. The transects showed high species dissimilarity (0.89–0.95), indicating high turnover along the elevation gradient. Consistent with the diversity indices, D1 and D2 exhibited comparatively higher species richness and moderate diversity (H′ = 2.69 and 2.36, respectively), whereas D3 supported fewer species and lower diversity (H′ = 1.61). However, the high evenness values recorded across all transects (0.88–1.00) indicate that individuals were relatively evenly distributed among species, with no strong dominance by any single taxon. Certain species like *Dipterocarpus hasseltii* and *Vatica sarawakensis* were only found in the lowest transect, while *Dryobalanops lanceolata* and *Anisoptera costata* were restricted to the middle and upper transects. This supports the hypothesis that dipterocarp species have habitat preferences related to elevation.

The differences between transects with similar vegetation show that species composition is influenced by local environmental factors, not just vegetation type. This matches what has been recorded in other logged forests in Sabah, where small-scale environmental variation leads to differences in species after logging (Ewers et al. 2024; Hayward et al. 2021). The mix of upland and kerangas species suggests the forest is in a transitional state, likely due to past logging. The inclusion of seedling species also indicates that regeneration may differ from that of the current adult trees, pointing to ongoing recovery processes.

3.2.2. Regeneration and forest condition

Dipterocarp regeneration patterns in Mengilan FR suggest that recruitment is influenced by a combination of elevation, stand structure, and historical disturbance. Regeneration generally mirrored patterns observed in the adult tree community, indicating that the availability of reproductive trees may influence local recruitment. The low overlap of regenerating species among transects further suggests that elevation-associated environmental conditions contribute to differences in both adult and regenerating dipterocarp assemblages.

The comparatively lower regeneration observed in D2 may reflect reduced seed availability associated with fewer large reproductive trees. However, the high DBH variation (32.90 ± 31.70 cm) indicates a heterogeneous stand comprising both small and medium-sized individuals. Similar patterns have been reported in other logged dipterocarp forests in Sabah, where regeneration is shaped by interactions among disturbance history, stand structure, and local environmental conditions (Ewers et al. 2024; Hayward et al. 2021; Pang et al. 2024). The coexistence of upland mixed dipterocarp and kerangas-associated species, together with regenerating taxa not recorded in the adult layer, suggests that Mengilan FR remains in a transitional recovery stage following past logging disturbance, with future forest composition potentially differing from the current canopy assemblage.

3.2.3. Logging legacy and forest structure

The observed differences in species composition and regeneration among transects suggest that forest recovery in Mengilan FR remains influenced by the legacy of past conventional logging. Field observations indicate that much of the reserve consists of secondary forest characterized by pole-sized trees, canopy gaps, and heterogeneous stand structure. Similar conditions have been reported in other logged dipterocarp forests in Sabah and Borneo, where microsite conditions strongly influence regeneration, the availability of remaining seed trees, and the intensity of past disturbance (Axelsson et al. 2024; Bartholomew et al. 2024; Ichie et al. 2023; Malik et al. 2023; Williams et al. 2022).

Legacy effects of logging may persist for decades through soil compaction, skid trails, and altered drainage patterns, which can affect seed dispersal, seedling establishment, and survival (Ewers et al. 2024; Hayward et al. 2021; Jiang et al. 2024). These factors likely contribute to the patchy regeneration observed among transects, including areas where adult dipterocarps remain present but seedling recruitment is limited. The occurrence of several species only at the seedling stage further suggests that recovery is ongoing and that future forest composition may continue to change as succession progresses.

3.2.4. Conservation value of threatened and endemic dipterocarps

Of the 31 species recorded in this study, 61.30% are classified as threatened (Critically Endangered, Endangered, or Vulnerable), indicating that Mengilan FR supports a substantial proportion of Sabah's conservation-priority dipterocarp species. This pattern is consistent with regional trends, where dipterocarp populations have declined due to historical logging and land-use change (Chazdon et al. 2021; IUCN 2023; Pang et al. 2024).

Mengilan FR supports a diverse dipterocarp assemblage that is broadly comparable to those reported from other forest reserves in Sabah, despite differences in survey design and sampling effort among studies. The 31 confirmed dipterocarp species documented in this study exceed those reported from Mensalong FR (19 species) and Mt. Silam (18 species), but are lower than values recorded from Sg. Rawog Conservation Area (40 species), Sg. Imbak Virgin Jungle Reserve (66 species), and Timimbang–Bontitian FR (65 species) (Majapun et al. 2014, 2019; Tsen et al. 2019). These comparative surveys were conducted as part of the Sabah Forestry Department's biodiversity assessments and Heart of Borneo conservation initiatives, providing useful regional context for evaluating the conservation significance of Mengilan FR. Overall, the findings indicate that Mengilan FR retains a moderate to high level of dipterocarp diversity despite its history of logging disturbance. Despite these differences in species richness, the proportion of threatened species in Mengilan FR is comparable to that reported from other conservation areas in Sabah, underscoring its importance as a refuge for threatened dipterocarps within the Heart of Borneo landscape.

Endemism further underscores the reserve's conservation significance. Thirteen species are endemic to Borneo, while *Shorea symingtonii* is endemic to Sabah, representing 45.20% of the recorded dipterocarp flora (Khoo et al. 2023). The presence of threatened and endemic species in both the adult and regeneration layers indicates ongoing recruitment and suggests that natural regeneration contributes to the persistence of these taxa. Several species were recorded only as seedlings, implying that future forest composition may differ from the current canopy assemblage as succession progresses. Similar observations have been reported from other protected forests in Sabah, including Rawog Conservation Area, where regeneration contributes to the long-term persistence of threatened dipterocarp species (Tsen et al. 2019). Therefore, continued monitoring of regeneration and population structure will be essential to evaluate long-term recovery and ensure the persistence of these conservation-priority species.

3.2.5. Landscape context and emerging development pressures

Mengilan FR lies within a key transboundary landscape in Sabah's Heart of Borneo (HoB), connecting to forests in North Kalimantan. This connectivity supports ecological processes across borders but also increases exposure to emerging development pressures and human access. Mammal surveys support the ecological value of the area, with Mengilan recording the highest mammal species richness (36 species) among 15 forest reserves assessed within the HoB region from 2016 to 2020 (Suis et al. 2023). This indicates high species richness and strong ecological connectivity with nearby forests in North Kalimantan within the HoB landscape. Hence, stakeholder engagement with Indonesia through research collaboration can effectively foster the protection of endangered mammal species in Mengilan FR (Novriyanti et al. 2025; Suis et al. 2023).

Bird surveys also show that Mengilan FR is highly biodiverse and ecologically important for forest-dependent species, including endemic Bornean birds, with 75 species from 33 families recorded (Petol et al. 2021). These findings indicate that the habitat is relatively intact and maintains good forest conditions and should therefore be protected to preserve its biodiversity. Hence, agencies and local communities may play an important role in promoting sustainable ecological practices to safeguard this area, particularly in buffer zones around incoming development and by increasing access (Agil et al. 2025).

Despite its status as a class I protection forest, Mengilan FR continues to face anthropogenic pressures. Signs of illegal hunting, including snares, spent cartridges, and temporary camps, have been recorded within the reserve (Suis et al. 2023). This suggests that legal protection alone may be insufficient where road networks and other access routes facilitate human entry into the forest. Similar patterns have been observed in other frontier landscapes, where historical logging roads and infrastructure development increase accessibility and elevate the risk of biodiversity loss (Hayward et al. 2021; Pang et al. 2024; Zheng et al. 2025). In this context, the variation in dipterocarp regeneration observed in this study is important. Increased access can lead to stronger edge effects, higher resource use, and local disturbance. These pressures can affect regeneration even in protected forests. This highlights the importance of having baseline data on species composition and regeneration to track future changes and guide better forest management as development pressures continue.

3.2.6. Conservation implications

The findings of this study have several implications for the conservation and management of Mengilan FR. Given the high proportion of threatened and endemic dipterocarp species recorded, priority should be given to maintaining habitat integrity and protecting mature reproductive trees that serve as seed sources for natural regeneration. Long-term monitoring of seedling density, recruitment into larger size classes, and the regeneration of threatened species should be conducted at regular intervals to assess forest recovery and population persistence. In addition, continued enforcement is required to reduce illegal hunting and other anthropogenic disturbances within the reserve. Where regeneration is limited, particularly in areas affected by past logging, enrichment planting using locally occurring threatened dipterocarp species may be considered to support natural recovery processes.

The baseline information generated by this study will contribute to the forthcoming Conservation Area Management Plan (CAMP) for Mengilan FR and support strategic planning under the HoB initiative. As one of the first documented assessments of dipterocarp diversity and regeneration in the reserve, it provides a benchmark for future monitoring. We aim to repeat a comparable survey within the next decade to assess changes in species composition, regeneration, and forest condition, particularly in relation to increasing accessibility and surrounding development. The findings will also support environmental planning, mitigation measures, and conservation decision-making at the state level. In the longer term, these data may contribute to assessments under internationally recognized frameworks such as the IUCN Green List and FSC standards, thereby strengthening the conservation and management of Mengilan FR and its dipterocarp diversity.

3.2.7. Study Limitations

This study provides a baseline assessment of dipterocarp diversity and regeneration in Mengilan FR, but several limitations should be acknowledged. The use of a single transect within each elevational zone and the lack of spatial replication limit the ability to distinguish elevational effects from local environmental variation, disturbance history, and stand structure. In addition, the relatively small sample size in D3 and the absence of environmental measurements, such as soil properties, nutrient availability, and canopy conditions, may have influenced the observed patterns in species composition and regeneration. Therefore, the results should be interpreted as preliminary trends, and future studies incorporating replicated sampling and environmental variables are recommended to understand better the drivers of dipterocarp diversity and regeneration in the reserve.

4. Conclusions

The results support the hypothesis that dipterocarp species composition and regeneration vary along the elevational gradient in Mengilan FR, forming distinct assemblages with limited overlap among transects. These patterns suggest that both environmental conditions and the legacy of past logging continue to influence forest recovery across the reserve. The occurrence of threatened and endemic species in both the adult and regeneration layers highlights the importance of Mengilan FR as a refuge for dipterocarp diversity within the transboundary Sabah–Kalimantan forest landscape and the wider Heart of Borneo region. To sustain this diversity, management should focus on protecting mature seed-source trees, monitoring the regeneration of threatened species, and strengthening enforcement against illegal activities. The baseline information generated by this study provides an important foundation for the forthcoming Conservation Area Management Plan (CAMP) for Mengilan FR and will support future conservation planning under the Heart of Borneo (HoB) initiative.

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Author Contributions

R.J.M.: Conceptualization, Formal Analysis, Methodology, Software, Investigation, Resources, Data Curation, Writing – Original Draft Preparation; Writing – Review and Editing; J.J.: Resources, Data Curation, Validation, Supervision, Investigation; C.J.W.: Formal Analysis, Software, Validation, Writing – Review and Editing; S.T.T.L.: Writing – Review and Editing, Data Curation; Validation, Methodology, Supervision.

Conflict of Interest

The authors declare no conflict of interest.

Declaration of Generative AI And AI-Assisted Technologies in the Manuscript Preparation

The authors declare that generative AI tools were used to assist with Python coding for data visualization, language refinement and reference formatting. All scientific analyses, interpretations and conclusions were conducted and verified by the authors, who take full responsibility for the content of this manuscript.

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