Diverse Paths to Restoration: Assessing biodiversity responses to enrichment planting in Sabah's tropical forests

A 27-year comparison of line and gap-cluster planting in the INIKEA restoration project

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Adrien Lamodière

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Swedish University of Agricultural Sciences, SLU
Department of Forest Ecology and Management
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Adrien Lamodière

Supervisor:	**Ulrik Ilstedt, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management**
Assistant supervisors:	Petter Axelsson, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management
	Arvid Lindh, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management
Examiner:	Maja Sundqvist, Swedish University of Agricultural Sciences, Department of Forest Ecology and Management

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Swedish University of Agricultural Sciences
Faculty of Forestry
Department of Forest Ecology and Management

Abstract

Tropical forest restoration initiatives increasingly aim to enhance biodiversity recovery, yet long-term data remains scarce, particularly on how different enrichment strategies influence naturally regenerating communities. This study assesses the biodiversity outcomes of line planting and gap-cluster planting 27 years after implementation in the INIKEA Sow-a-Seed project in Sabah, Malaysian Borneo. Focusing exclusively on naturally regenerated trees, I evaluated tree species richness, composition, and successional status across 38 plots, including enriched and control sites, while accounting for a degradation gradient based on remnant tree structure.

Generalized linear models revealed that both enrichment treatments significantly increased species richness compared to control plots, regardless of initial degradation level. NMDS and PERMANOVA analyses confirmed distinct community compositions between treatments, showing that enrichment planting not only increases the number of species but also steers regeneration toward compositionally different forest communities. In contrast, Shannon and Simpson indices showed no significant differences between treatments, indicating similar species evenness. Likewise, the proportion of late-successional species among naturally regenerated individuals did not differ significantly, likely reflecting the slow functional recovery typical of these species.

These findings suggest that enrichment planting can effectively steer regeneration toward more diverse and compositionally distinct communities, but that full ecological recovery remains a long-term process shaped by both intervention and initial site conditions.

Keywords: Tropical forest restoration, enrichment planting, natural regeneration, tree species diversity, degradation gradient.

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Abbreviations

Abbreviation	Description
DBH	Diameter at Breast Height
GLM	Generalized Linear Model
NMDS	Non-metric Multidimensional Scaling
PERMANOVA	Permutational Multivariate Analysis of Variance
SLU	Swedish University of Agricultural Sciences
PVC	Polyvinyl Chloride (for plot marking)
GPS	Global Positioning System

1. Introduction

1.1 Context and background

Tropical rainforests, despite covering only a small fraction of the Earth's surface, harbor an astonishing part of global biodiversity (Myers et al., 2000). In Southeast Asia, the lowland dipterocarp forests are among the most biologically rich ecosystems on the planet, supporting thousands of tree species and a vast diversity of associated fauna (Gibson et al., 2011). Yet, they are also some of the most threatened. In Borneo, decades of unsustainable logging, repeated forest fires, and widespread land conversion for agriculture have drastically altered these ecosystems (Curran et al., 2004; Gaveau et al., 2016; Miettinen et al., 2011). The result is a mosaic of degraded landscapes, where natural regeneration alone often struggles to bring back the diversity and structural complexity of the original forest (Suding, 2011; Bartholomew et al., 2024; Axelsson et al., 2024).

In response to these widespread ecological disturbances, large-scale forest restoration efforts have gained attention worldwide. Global initiatives such as the Bonn Challenge and the UN Decade on Ecosystem Restoration aim to restore millions of hectares of degraded land to improve biodiversity conservation, enhance carbon sequestration, and support ecosystem services (Bastin et al., 2019; UNEP & FAO, 2020). However, the long-term ecological effectiveness of these efforts remains uncertain, particularly in tropical regions. Many restoration projects still focus on early indicators such as seedling survival or biomass accumulation, with relatively little attention given to how species composition and biodiversity recover over decades (Crouzeilles et al., 2017; Rozendaal et al., 2019).

One key limitation is the lack of long-term studies comparing different reforestation strategies in similar environmental conditions. This gap restricts our understanding of how different approaches, such as enrichment planting or assisted natural regeneration, shape forest composition, community assembly, and ecological function over time (Chazdon, 2008; Brancalion et al., 2016). Furthermore, most monitoring frameworks emphasize planted individuals, even though the recruitment of naturally regenerated trees plays a central role in determining whether restored forests are truly self-sustaining and ecologically resilient (Holl and Aide, 2011; Chazdon et al., 2016).

This study addresses these challenges by focusing on naturally regenerated trees within restored forest stands, using them as indicators of biodiversity recovery beyond the initial planting phase. In doing so, it explicitly emphasizes biodiversity outcomes, such as species richness, composition, and successional dynamics, as indicators of long-term recovery, beyond structural regeneration alone. The analysis draws on one of the few large-scale, long-term tropical restoration programs currently available for such research. Located in eastern Sabah, Malaysian Borneo, the study site offers a unique opportunity to examine how different enrichment planting designs have influenced tree community development over a 27-year period.

1.2 Challenges in Forest Restoration

While forest restoration has gained international attention as a tool to reverse land degradation and biodiversity loss, implementing it successfully in tropical ecosystems remains a major ecological challenge. In these diverse landscapes, where hundreds of tree species may coexist within a single hectare, simply planting trees is not enough. The complexity lies not only in what species to plant, but also where, how, and under what initial conditions. Understanding forest recovery demands long-term monitoring, ecological sensitivity, and a recognition that restoration is as much about re-establishing ecological interactions as it is about structural cover (Chazdon, 2008; Lamb et al., 2005; Axelsson et al., 2022).

One key challenge is the pronounced heterogeneity of degraded forest sites. Historical land use, fire intensity, soil conditions, and remnant vegetation all interact to shape regeneration trajectories. In Borneo, extensive forest fires linked to the 1982-83 El Niño event, combined with decades of logging, left many areas with few or no seed trees, making natural regeneration slow or even unlikely without intervention (Woods, 1989; Axelsson et al., 2024). In such contexts, active restoration becomes not just beneficial, but essential (Crouzeilles et al., 2017; Brancalion et al., 2016). Yet, selecting the right technique, whether line planting, gap-cluster enrichment, or assisted natural regeneration, requires a careful understanding of site conditions and expected outcomes.

Another persistent limitation in tropical restoration is the lack of long-term ecological data. While early monitoring may capture seedling survival, growth rates, or canopy development, it often fails to reflect the gradual return of species interactions or native community structure (Rozendaal et al., 2019; Bartholomew et al., 2024). Moreover, relatively few studies directly compare different restoration strategies under similar environmental conditions, making it difficult to draw conclusions about their relative biodiversity outcomes (Reid et al., 2018; Holl & Aide, 2011).

A critical part of understanding biodiversity recovery is assessing not just the planted trees, but the naturally regenerating individuals that colonize restored sites over time. These spontaneous recruits provide insight into whether ecological processes such as seed dispersal, regeneration, and species filtering are functioning again (Chazdon et al., 2016). For this reason, focusing on non-planted trees can offer a clearer picture of long-term forest recovery and resilience.

Although few large-scale projects currently provide long-term data, some tropical restoration efforts have maintained consistent biodiversity monitoring over extended periods. These rare examples offer important opportunities to investigate how planting design and site conditions influence natural regeneration and community composition over time.

As global restoration efforts continue to scale up, these practical and ecological challenges must be addressed. Restoration is not a one-size-fits-all solution, and in the tropics, context-specific knowledge remains essential. There is a growing need for empirical studies that not only report biodiversity outcomes but help explain the processes behind them, to support more effective and resilient restoration practices in the decades ahead.

1.3 Purpose of This Study

The INIKEA Sow-a-Seed project in Sabah, Malaysia, began its first phase of planting in 1998. Now, 27 years later, this early reforestation effort presents a rare and timely opportunity to evaluate how tropical forest landscapes evolve over the long term. While many restoration projects are constrained by short funding cycles or limited monitoring, this site offers a unique window into what forest recovery can look like when given time, protection, and consistent follow-up care. The trees planted here are no longer seedlings, they are now entering mid-succession, forming closed canopies, producing fruit and seeds, and shaping the ecological character of their sites. At this stage, questions about forest composition and biodiversity become especially relevant: which species have persisted? How has the tree community evolved? Are planted individuals coexisting with, or outcompeting, naturally regenerating species? Equally important are questions related to overall biodiversity: how many species have colonized these plots? How even their abundances are? and whether species composition reflects long-term ecological differentiation across treatments.

This study focuses on two enrichment planting strategies implemented during Phase 1 of the INIKEA project (1998–2003): line planting and gap-cluster planting. These methods were applied to sites that had been heavily degraded by logging and fire, and they represent contrasting approaches to reforestation. In addition to planting, both treatments were implemented alongside silvicultural interventions such as climber cutting, selective thinning, and weeding, which aimed to facilitate natural regeneration by improving light availability and reducing competition (Axelsson et al., 2024). Line planting involves clearing linear strips and planting trees in rows, a method that offers consistency and ease of implementation. In contrast, gap-cluster planting mimics natural regeneration by planting small groups of seedlings in canopy gaps, potentially supporting more heterogeneous forest development (Figure 1). Line planting is more commonly used in other tropical restoration contexts, while gap-cluster planting remains less widespread and has rarely been evaluated over such a long time span.

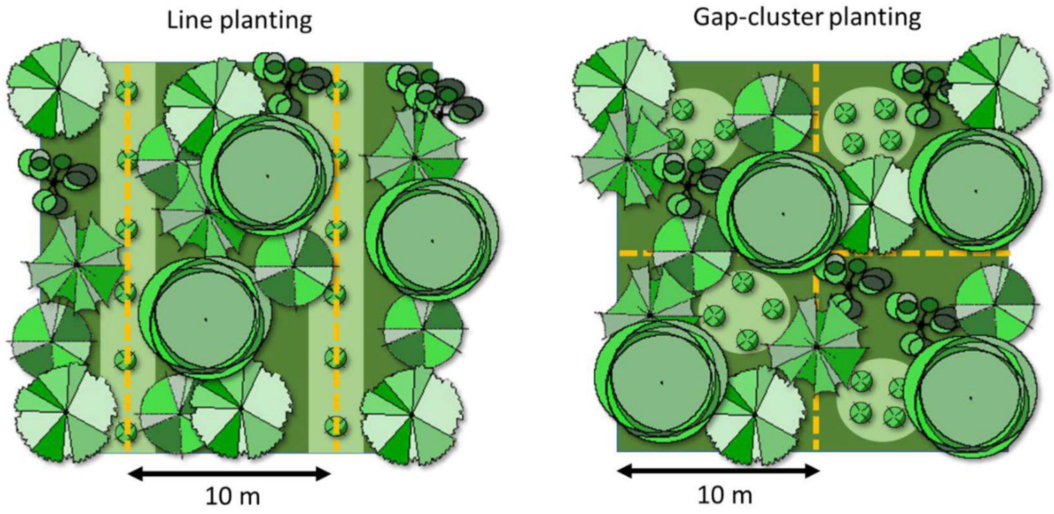

Figure 1. On the left, the line planting method is depicted, where 2-meter-wide linear corridors are cleared of existing vegetation at 10-meter intervals across the landscape. Within these corridors, native tree seedlings are planted at 3-meter spacing. Yellow dashed lines represent the planting transects, and the planted seedlings are marked by green circles with an "X". Surrounding unmarked circles represent the remaining competing or protecting vegetation, depending on the species and structure. On the right, the gap-cluster planting method is illustrated. In this approach, one naturally occurring or manually created canopy gap is selected within each 10 x 10-meter subplot. Four seedlings are planted within each gap, where increased light availability supports growth. These planting zones are shaded in light green, and the planted trees are again indicated by green circles with an "X" (Axelsson et al., 2024).

By comparing these two planting approaches, this study seeks to assess their influence on the composition and diversity of tree communities after 27 years. While planting strategies are central to the study design, the analysis focuses specifically on the naturally regenerated individuals that have established in each plot. These trees are considered key indicators of both regeneration processes and biodiversity recovery, offering insights into species richness, community composition, and successional development across treatments**.** In addition, I will incorporate a degradation gradient based on the basal area of remnant trees, those that survived initial disturbances, as a way to explore how initial site conditions interact with planting design to shape long-term outcomes.

Ultimately, the goal is not only to compare restoration treatments, but also to inform future practice in tropical forest restoration. As global reforestation initiatives expand, there is a growing need for empirical evidence that links restoration design with biodiversity outcomes. This study contributes to that evidence base, grounded in a real-world landscape where restoration has already been underway for more than two decades.

1.4 Research Objectives & Rationale

This thesis aims to evaluate the long-term effects of two enrichment planting methods on forest recovery in Sabah, Malaysia. The study focuses specifically on the naturally regenerated tree communities that have established within these restored plots, using them as indicators of long-term biodiversity outcomes. These outcomes include not only the number of species present (richness), but also how species abundances are distributed (evenness), and whether forest communities differ functionally and compositionally across treatments. By examining species composition and structural characteristics in mature enrichment plots, the research explores how planting strategy and site history interact to influence ecological recovery.

To better understand how reforestation outcomes are influenced by initial site conditions, the analysis incorporates a degradation gradient. Rather than relying on a single proxy, I used three complementary indicators: the basal area of remnant trees, the proportion of pioneer species, and the richness of remnant individuals. These legacy trees, those that survived the initial disturbance events, are not merely structural remnants; they may play key ecological roles in regeneration by providing seeds, stabilizing microsites, or shaping competitive dynamics. Including these variables provides a more nuanced view of how degradation intensity influences recovery trajectories.

In addition to the enriched plots, control sites were included to provide a baseline for passive regeneration. Although these controls were not part of the original Phase 1 reforestation, they are located within unplanted areas of the broader INIKEA project that experienced similar disturbance histories. As such, they offer a useful reference point for comparing actively restored and naturally recovering forest stands within the same landscape.

Specifically, I will address the following research questions:

1. How do line planting and gap-cluster planting differ in terms of tree species composition and diversity after 27 years?
2. How does the degradation gradient, based on remnant tree structure and composition, influence current biodiversity in enriched plots?
3. How do enriched plots compare to nearby control plots in terms of diversity and structural development among naturally regenerated trees?
4. To what extent do patterns observed in non-planted tree communities reflect restoration success across treatments?

The rationale for these questions lies in their combined scientific and practical relevance. From a restoration planning perspective, understanding how different planting designs influence biodiversity over the long term is essential for selecting methods that are both cost-effective and ecologically robust. Scientifically, this study contributes to a longstanding gap in tropical forest restoration research by linking early reforestation decisions with long-term outcomes in forest composition and structure.

By grounding these questions in one of the world's longest-running operational-scale tropical restoration projects, this thesis offers a rare, real-world perspective on forest recovery. The findings aim to support future restoration initiatives, not as a rigid template, but as evidence-based guidance shaped by experience, monitoring, and time.

2. Materials and Methods

2.1 Plot selection

This study was conducted in the lowland dipterocarp forests of eastern Sabah, Malaysian Borneo. These forests are part of one of the most diverse terrestrial ecosystems in the world but have been heavily impacted by decades of logging, recurring fires, and agricultural expansion (Curran et al., 2004; Gaveau et al., 2014; Miettinen et al., 2011). The resulting landscapes are highly degraded, with varying levels of remnant canopy cover, biomass loss, and altered successional pathways.

The research took place within the INIKEA Sow-a-Seed project, a large-scale forest restoration initiative launched in 1998 through a partnership between Yayasan Sabah, IKEA, and the Swedish University of Agricultural Sciences (SLU) (Figure 2). Spanning over 18,000 hectares of previously logged and fire-affected forest, the project represents one of the most extensive operational-scale restoration programs in Southeast Asia (Axelsson et al., 2024). Its long-term commitment to monitoring and adaptive management provides a rare opportunity to assess the effectiveness of restoration strategies over time.

Figure 2. This map shows the island of Borneo within the broader Southeast Asian region (inset), highlighting its political divisions among three countries: Malaysia (Sabah and Sarawak, shown in dark green), Brunei (blue), and Indonesia (Kalimantan, in light green). The INIKEA project area is marked with a red dot in eastern Sabah, Malaysian Borneo (Engström, 2023).

To evaluate the long-term effects of enrichment planting on forest recovery, I established a total of 28 research plots within Phase 1 of the INIKEA project, corresponding to the earliest restored areas (1998 - 2003). These plots were evenly split between two restoration treatments: 14 plots in areas restored with line planting and 14 with gap-cluster planting. In addition, 10 control plots were selected from Phase 4 (2015 - 2020), where reforestation was intentionally omitted to allow for natural regeneration. Although these areas are more recent in project timeline, they share comparable disturbance histories, mainly logging and the 1983 fire event, and therefore offer a meaningful baseline for comparison. Importantly, the control plots were never planted, serving as references for passive recovery trajectories. The number of control plots (10) was lower than for the enriched treatments (14 each), due to limited availability of accessible, ecologically comparable unplanted sites in the project area. While this imbalance was not statistically corrected for, it was mitigated by the use of generalized linear models with robust standard errors (quasi-Poisson), and group comparisons were interpreted with appropriate caution.

Each phase of the project is divided into operational blocks, with each block typically representing a specific treatment. I aimed to sample two plots per block wherever feasible, balancing ecological coverage with logistical constraints. Plots were located at least 150 meters apart to minimize spatial autocorrelation and at least 120 meters from the nearest road to avoid edge effects. These distances were estimated using handheld GPS devices in the field rather than pre-planned from maps. While this method allowed flexible navigation in rugged terrain, occasional deviations occurred due to limited GPS accuracy under canopy cover. In such cases, the experience of local rangers, familiar with the forest's restoration history and spatial layout, was invaluable in guiding final placement decisions. It is worth noting that control plots tended to be more spatially clustered and located closer to the edge of unplanted forest areas than treatment plots. This spatial layout may have influenced dispersal patterns or edge-related dynamics, which are discussed as potential confounding factors in the interpretation of results (Section 4.3).

The selection of plots also considered the need to evaluate biodiversity responses along a degradation gradient. Sites were intentionally chosen to ensure some overlap in degradation levels across reforestation treatments, thereby enabling comparative analyses across similar ecological baselines. This sampling strategy was essential for separating the effects of planting method from those of initial site conditions (Chazdon, 2003; Letcher & Chazdon, 2009).

Each plot measured 40 x 40 meters and was established in accessible areas, either adjacent to forest trails or after short off-trail walks. Local field teams played a crucial role in locating viable sites and supporting field logistics. The spatial distribution of all selected plots, along with operational block layout and treatment types (Figure 3).

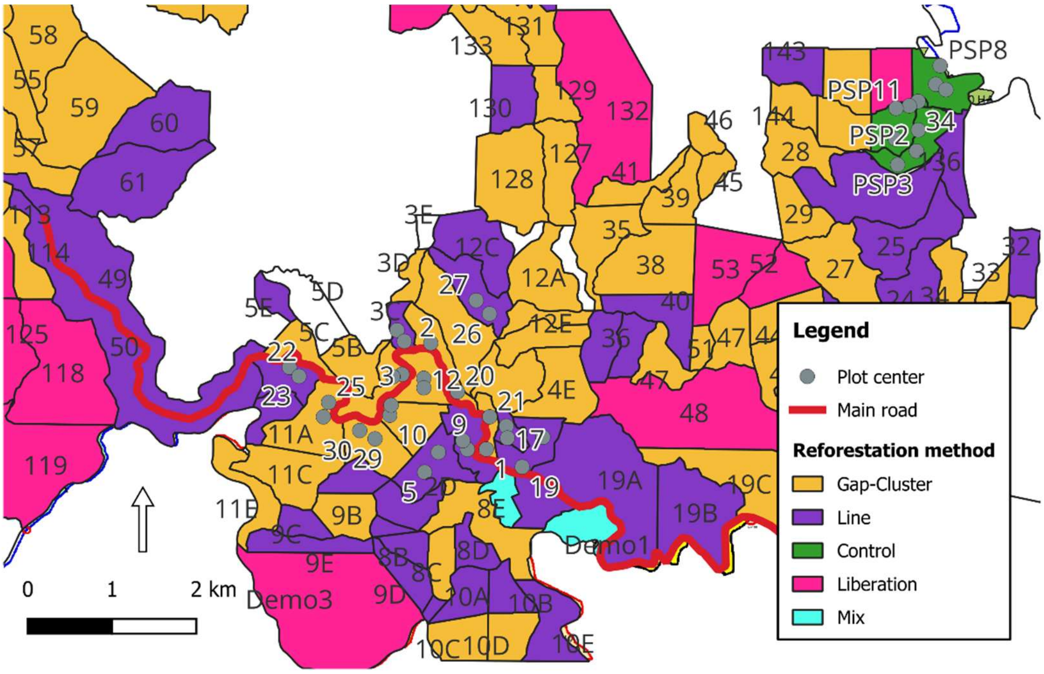

Figure 3. Spatial distribution of operational blocks and associated reforestation treatments in the INIKEA Sow-a-Seed restoration project area, Sabah, Malaysian Borneo. Each coloured polygon represents a block treated with one of five reforestation methods: gap-cluster planting (orange), line planting (purple), control (no treatment, green), liberation (pink), or mixed treatment (light blue). The main access road is shown in red. Dots indicate the centres of the plots surveyed in this study, including several permanent sample plots (PSPs) located within control blocks. All plots were used for biodiversity and forest structure monitoring.

2.2 Plot Layout and Data Collection Strategy

Once a suitable location was identified, we marked the center of each 40 x 40 m plot with a PVC pipe, leaving about one meter exposed above the ground for visibility. To aid future relocation, the top of the pipe was painted blue. At this central point, GPS coordinates were recorded using a Garmin 64S handheld unit, referenced in WGS84 format.

With the assistance of local rangers and a compass, we divided each plot into four subplots, labelled A, B, C, and D, laid out in clockwise order. Four 20-meter strings were extended in the cardinal directions from the central pipe to mark boundaries. This approach delineated four 20 x 20 m subplots: subplot A in the northwest, B in the northeast, C in the southeast, and D in the southwest. Each corner of the larger plot was marked with a secondary, unpainted PVC pipe approximately 50 cm tall to facilitate future relocation (Figure 4).

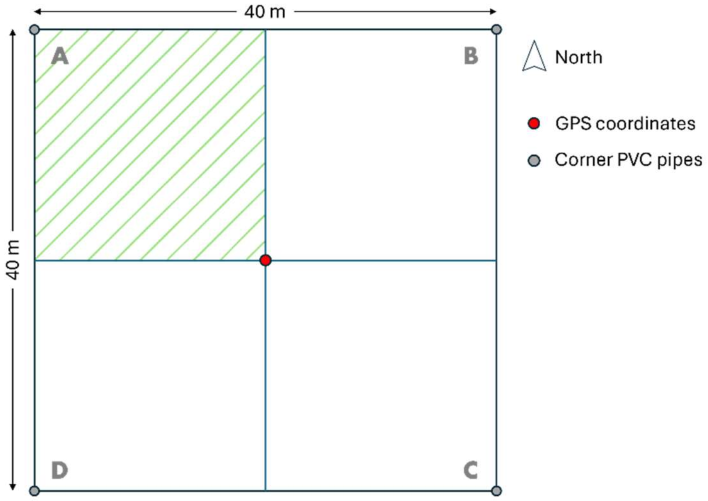

Figure 4. Schematic layout of a 40 x 40 m plot divided into four subplots (A-D), each measuring 20 x 20 m. The central red dot indicates the PVC pipe marking the plot centre, where GPS coordinates were recorded. A blue PVC pipe was installed and painted for visibility. Subplots were laid out clockwise from the northwest (A) using cardinal orientation. Subplot A (green diagonal hatching) was used for detailed inventory of all trees taller than 1,3 m, regardless of DBH. Corner pipes were also installed (grey dots) to facilitate future relocation and remeasurement.

In each plot, subplot A, always located in the northwest quadrant, was used for a more detailed inventory. There, we recorded all naturally regenerated trees taller than 1.3 meters, regardless of DBH. This finer-scale sampling allowed for the inclusion of younger, smaller individuals that would otherwise be missed with a 10 cm DBH threshold, providing a more comprehensive view of regeneration patterns and species composition.

Across all four subplots, we recorded all trees with a DBH greater than 10 cm. In addition, every planted tree was inventoried, regardless of its size or DBH. Planted individuals were identified based on planting layout, visible planting rows or clusters, and field knowledge provided by local rangers familiar with the site's restoration history. While these individuals were documented, they were excluded from the biodiversity analyses. The rationale behind this decision was to isolate the effects of enrichment planting on spontaneous, naturally regenerated communities. Including planted trees - whose species identity, density, and survival reflect initial design decisions rather than ecological processes - would have confounded this objective.

To aid remeasurement, trees over 10 cm DBH and all planted individuals were marked with a blue paint dot facing the central pipe. Smaller, non-planted individuals in subplot A were temporarily marked with hemp string to avoid double-counting during identification.

To increase efficiency, data collection was conducted in parallel. One team measured all planted trees and those exceeding 10 cm DBH across all subplots. At the same time, the other team worked with two other rangers to identify and measure the smaller, non-planted individuals in subplot A. This division of tasks allowed us to complete each plot in a coordinated and timely manner.

Data collection began in late February and continued through March. I completed my fieldwork in approximately five weeks.

2.3 Data analysis

All statistical analyses were conducted in R (R Core Team, 2023), based on widely used methods for studying biodiversity and species communities in tropical forests. Data cleaning and structuring were performed using the *tidyverse* (Wickham et al., 2019), *janitor* (Firke, 2023), and *readxl* (Wickham & Bryan, 2023) packages. Column names were standardized, and variables were transformed into appropriate formats to ensure consistency across analytical steps. Biodiversity analyses focused exclusively on naturally regenerated individuals in subplot A, with planted trees excluded to isolate patterns of spontaneous recovery. This decision aligns with the study's aim to understand how enrichment planting influences natural regeneration processes, rather than merely documenting species initially introduced through planting. However, this choice also limits the assessment of total woody species richness, which is addressed in the Discussion.

To quantify degradation, I calculated three complementary indicators for each plot: (1) the basal area of unplanted remnant trees with a diameter at breast height (DBH) > 40 cm, used as a structural indicator of disturbance and biomass recovery (Chazdon, 2003; Poorter et al., 2016); (2) the ratio of basal area from pioneer species among all naturally regenerated individuals, reflecting successional status and the legacy of past disturbance (Letcher & Chazdon, 2009); and (3) remnant tree species richness, capturing the taxonomic memory retained at each site (Arroyo-Rodríguez et al., 2017). For each plot, the basal area of large remnant trees was calculated using the standard geometric formula and normalised to a per-hectare basis based on the actual plot surface area. To derive the composite degradation score, the remnant basal area was rescaled to a 0-1 range and then multiplied by one minus the pioneer basal area ratio. This final score integrates both structural and successional maturity, with higher values indicating less degraded conditions. The remnant species richness metric was retained separately as an alternative proxy, offering a taxonomic complement to the structural and functional indicators.

Tree diversity was quantified using species richness, Shannon index, and Simpson index. Diversity metrics were calculated from abundance matrices using the *vegan* package (Oksanen et al., 2022), based on unplanted individuals in subplot A. Species richness was modelled with generalised linear models (GLMs) using a quasi-Poisson distribution to account for mild overdispersion (dispersion parameter ≈1.49), a standard correction in ecological count data (Zuur et al., 2009). In each GLM, *reforestation method* was included as a fixed factor, and one of three *degradation proxies* (remnant basal area, composite degradation score, or remnant species richness) was added as a covariate. Interaction terms between method and degradation were tested to assess whether the effect of planting strategy varied along degradation gradients. None of the interaction terms were statistically significant and were therefore not retained in the final model. No random effects were included. Shannon and Simpson indices were analysed via Kruskal-Wallis tests due to non-normal residuals and heteroscedasticity. For all GLMs, global effects were tested with Type II ANOVA using the *car* package (Fox & Weisberg, 2019), and estimated marginal means with Tukey-adjusted pairwise comparisons were computed using *emmeans* (Lenth, 2023).

Further analyses were conducted to explore differences in species composition and determine whether reforestation methods influenced current tree community structure. This was explored using non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA), both based on Bray-Curtis dissimilarity. NMDS ordination plots were generated to visualise compositional patterns, using species abundance matrices filtered to exclude planted individuals. PERMANOVA models tested whether species composition varied significantly between reforestation methods and along degradation gradients (Anderson, 2001), with 999 permutations used to assess statistical significance. To confirm that PERMANOVA assumptions were met, homogeneity of group dispersions was tested using the *betadisper* function in the *vegan* package. Finally, a complementary analysis based on presence-absence data used Jaccard dissimilarity to evaluate species turnover, capturing differences in community identity across treatments.

Finally, to evaluate successional trajectories, I computed the proportion of late-successional trees among unplanted individuals in subplot A and analysed treatment-level differences using a quasibinomial GLM. This metric serves as a functional indicator of ecological maturity, commonly used in secondary forest research (Chazdon, 2003; Letcher & Chazdon, 2009).

3. Results

3.1 Degradation proxies across reforestation methods

Degradation levels were broadly similar across the three reforestation methods, with no strong differences in any of the assessed indicators. This consistency supports the comparability of treatments across a shared baseline of disturbance.

The assessment of site-level degradation included the three complementary proxies: (1) the basal area of large unplanted remnant trees, (2) a composite degradation index integrating basal area and pioneer dominance, and (3) the richness of remnant tree species. These proxies were calculated at the whole-plot level using all remnant trees present, independent of subplot designation.

Remnant basal area (DBH > 40 cm) ranged from 3.91 to 29.83 m^2/ha. The mean basal area was 15.0 ± 7.9 m^2/ha in control plots, 14.5 ± 7.6 m^2/ha in gap-planted plots, and 15.2 ± 6.5 m^2/ha in line-planted plots. The composite degradation score ranged from 0.01 to 0.90, with mean values of 0.37 ± 0.28 for control, 0.34 ± 0.27 for gap, and 0.35 ± 0.23 for line treatments. Remnant species richness varied between 2 and 13 species per plot, with averages of 6.7 ± 2.8 species in control plots, 6.6 ± 2.5 in gap plots, and 6.8 ± 2.3 in line plots.

3.2 Effects of degradation on biodiversity across reforestation methods

No significant relationships were found between any of the degradation proxies and biodiversity indices. All associated linear models returned non-significant results ($p > 0.05$), with low R^2 values, indicating that the influence of degradation on biodiversity did not vary between planting treatments.

For **species richness**, the number of species ranged approximately from 18 to 46 across all plots. In control plots, species richness tended to decrease with increasing basal area, composite score, and remnant species richness. In gap and line plots, richness values remained relatively stable across the degradation gradients, with slight upward or flat trends. Linear regression fits are shown for each treatment group (Figure 5).

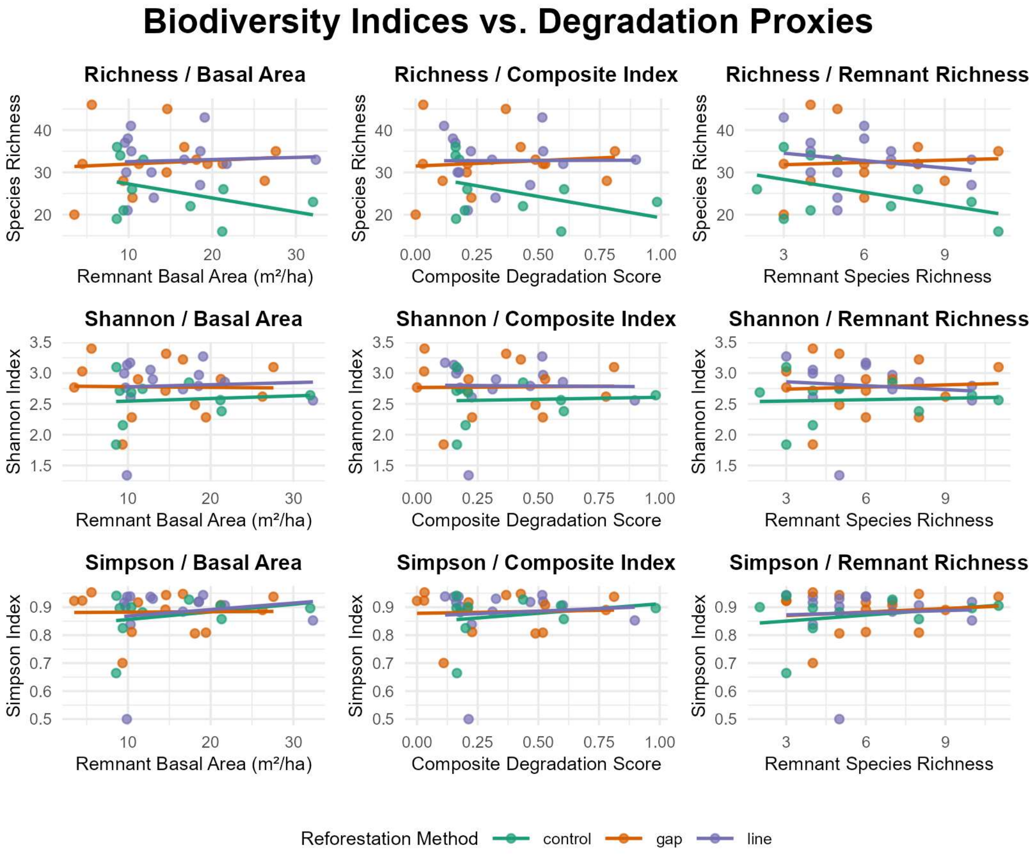

Figure 5. Relationships between tree biodiversity indices (species richness, Shannon, and Simpson) and three degradation proxies: basal area of large remnant trees (DBH > 40 cm), composite degradation score, and remnant species richness. Each point represents a subplot A, with biodiversity calculated from naturally regenerated (non-planted) trees only. Reforestation treatments are color-coded as follows: control (green), gap-cluster planting (orange), and line planting (purple). Linear regression lines are fitted separately for each treatment to visualize trends across the degradation gradient.

Shannon index values ranged from approximately 1.5 to 3.3. These values showed little variation across the degradation proxies, with fitted lines for all three treatments remaining close to horizontal. Across the proxies, gap and line plots generally showed higher or comparable values to control plots.

Simpson index values ranged from around 0.5 to 0.93. Across all degradation gradients, Simpson values remained within a narrow band. Linear fits for each treatment showed little to no slope, indicating weak or no directional patterns.

When comparing biodiversity indices between reforestation methods without considering degradation gradients, non-parametric Kruskal-Wallis rank sum tests were performed. For species richness, the test returned a chi-squared value of 5.75 with a p-value of 0.0576. This result suggests that richness values were not distributed identically across treatments. For the Shannon index, the chi-squared value was 3.94 ($p = 0.1386$), and for the Simpson index, 1.47 ($p = 0.4805$), indicating more even distributions of these diversity indices across reforestation methods. All indices were computed from unplanted trees in subplot A, and tests were conducted independently for each index.

3.3 Generalized linear modelling of species richness

This subsection presents the results of formal model-based inference using Generalized Linear Models (GLMs), which were applied to test the **effects of reforestation method and degradation proxies on species richness**, building on the exploratory analyses presented in 3.2.

Reforestation method had a significant effect on species richness across all models, regardless of the degradation proxy used.

Generalized Linear Models (GLMs) with a quasi-Poisson distribution were used to assess the influence of reforestation method and degradation level on species richness. Three separate models were fitted using distinct proxies of site-level degradation: (1) the basal area of large unplanted remnant trees (***degradation level***), (2) a composite degradation score integrating structural and successional maturity (***degradation score***), and (3) the richness of remnant tree species (***remnant richness***). Each model included an interaction term between the degradation proxy and reforestation method (control, gap, line).

Model summaries revealed no statistically significant effect of degradation level ($p = 0.216$), composite degradation score ($p = 0.178$), or remnant species richness ($p = 0.127$) on tree species richness. Similarly, none of the interaction terms between degradation and reforestation method reached statistical significance (all $p > 0.19$). However, Type II ANOVA tests performed on the GLMs indicated a significant main effect of reforestation method across all three models. For the model using degradation level, the reforestation method term explained 12.14 units of deviance ($F = 4.06$; $p = 0.027$). This effect was consistent when using degradation score ($F = 4.04$; $p = 0.027$) and remnant species richness ($F = 4.44$; $p = 0.020$). None of the degradation proxies themselves nor their interactions with method were statistically significant (all $p > 0.25$).

Estimated marginal means (emmeans) were computed from each model to compare back-transformed species richness estimates, that is, predicted values converted back to the original species count scale, for each treatment. When adjusting for the basal area of remnant trees (degradation level), estimated species richness was approximately 25.5 species in control plots, 32.5 in gap plots, and 32.8 in line plots. Using the composite degradation score, the estimates were similar: 25.7 in control, 32.5 in gap, and 32.8 in line plots. With remnant species richness as a covariate, control plots were estimated at approximately 25.3 species, gap plots at approximately 32.5, and line plots at approximately 32.9.

These estimates are shown in the model predictions with 95% confidence intervals (Figure 6). Across all three models, pairwise comparisons indicated significantly lower species richness in control plots compared to both gap and line plots ($p < 0.05$), while gap and line plots did not differ significantly from one another.

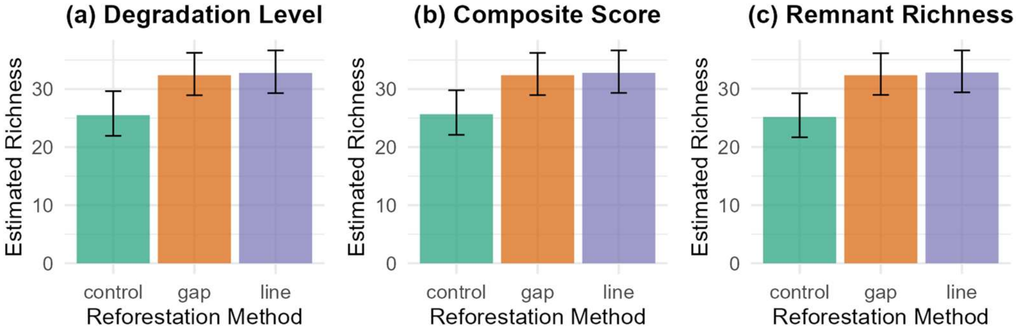

Figure 6. Estimated species richness across reforestation methods (control, gap, and line planting) based on quasi-Poisson generalized linear models (GLMs), adjusted for three degradation proxies: (a) basal area of large remnant trees (DBH > 40 cm), (b) composite degradation score, and (c) remnant species richness. Bars represent back-transformed model estimates with 95% confidence intervals (n = 38 plots). In all three models, richness was significantly lower in control plots compared to gap and line planting (p < 0.05), while no significant difference was found between gap and line treatments.

3.4 Species Composition and Turnover

As in other analyses, only naturally regenerated individuals were included to assess the recovery of spontaneously assembling communities. All data were drawn from subplot A of each plot.

3.4.1 NMDS Ordination Based on Species Abundance (Bray-Curtis)

Non-metric multidimensional scaling (NMDS) was performed using Bray-Curtis dissimilarities calculated from the abundance of non-planted trees in subplot A of each plot. The resulting ordination had a stress value of 0.232, indicating a fair but usable two-dimensional representation of community dissimilarities. Each point corresponds to a plot, and ellipses represent 95% confidence regions around reforestation method centroids (Figure 7).

In the ordination space, some visual separation is observable between reforestation methods. Control plots tend to cluster away from gap and line plots, although a considerable degree of overlap remains between all three treatment groups. This overlap suggests that while species composition differs between treatments, the separation is not complete.

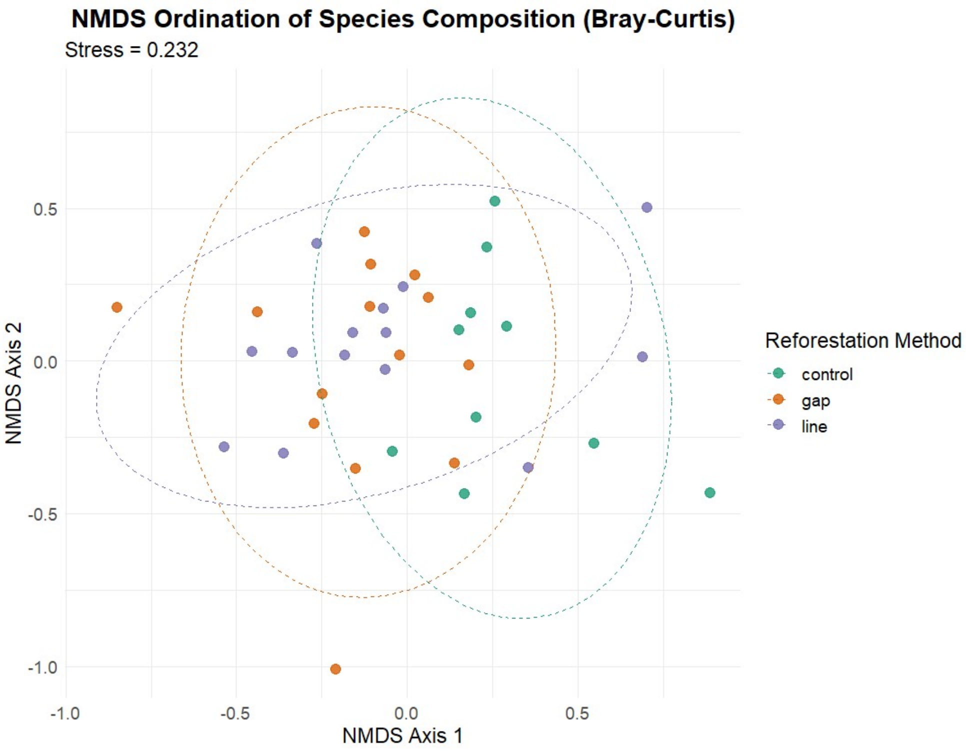

Figure 7. Non-metric multidimensional scaling (NMDS) ordination of species composition based on Bray-Curtis dissimilarities among non-planted trees in subplot A (n = 38 plots). Each point represents a single plot, color-coded by reforestation treatment: control (green), gap-cluster (orange), and line planting (purple). Ellipses indicate 95% confidence intervals around the centroid of each treatment group. The ordination has a stress value of 0.232, indicating a fair but interpretable two-dimensional representation of community dissimilarity.

3.4.2 NMDS Ordination Based on Species Presence/Absence (Jaccard)

To assess species turnover independent of abundance, NMDS was repeated using the Jaccard dissimilarity index applied to presence-absence data, again based only on non-planted individuals in subplot A of each plot. The resulting ordination had a stress value of 0.228, again falling within the fair range for interpretation (Figure 8).

As in the Bray-Curtis analysis, some separation is observable between control plots and enriched plots (gap and line), though group boundaries overlap. This pattern supports the existence of compositional differences in community structure across reforestation methods, based solely on species identity.

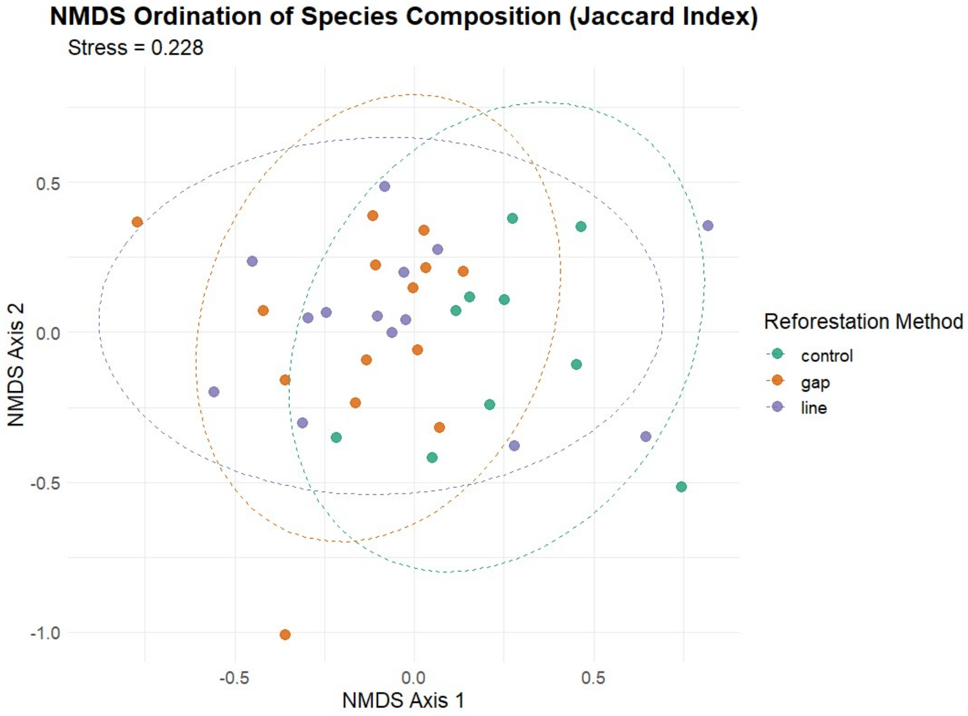

Figure 8. Non-metric multidimensional scaling (NMDS) ordination of species composition based on Jaccard dissimilarities calculated from presence-absence data of non-planted trees in subplot A (n = 38 plots). Each point represents a plot, color-coded by reforestation treatment: control (green), gap-cluster (orange), and line planting (purple). Ellipses indicate 95% confidence intervals around the centroid of each treatment group. The stress value of 0.228 indicates a fair but interpretable two-dimensional representation of community dissimilarity. The ordination suggests compositional differences between treatments based on species identity, though substantial overlap remains among groups.

3.4.3 PERMANOVA: Community Composition Differences

To test for statistical differences in species composition across treatments, permutational multivariate analysis of variance (PERMANOVA) was applied using Bray-Curtis dissimilarities with three models, each incorporating one degradation proxy and its interaction with reforestation method.

The model using the basal area of remnant trees (degradation level) returned a significant result ($F = 1.48$; $p = 0.003$; $R^2 = 18.8\%$). The model using the composite degradation score also showed significance ($F = 1.55$; $p = 0.001$; $R^2 = 19.5\%$). Similarly, the model using remnant species richness was significant ($F = 1.46$; $p = 0.002$; $R^2 = 18.5\%$). These results indicate that both reforestation method and degradation gradients contribute to shaping current species composition.

To examine whether these differences were driven by unequal group dispersion, a beta-dispersion test was conducted. ANOVA on distances to group centroids revealed no significant differences in dispersion among the three reforestation methods ($F = 0.443$; $p = 0.646$). A permutation test confirmed this result ($p = 0.633$), suggesting that group composition differences found in PERMANOVA were not confounded by differences in within-group heterogeneity.

3.4.4 Species Turnover Based on Jaccard Index

A final PERMANOVA was performed using the Jaccard dissimilarity matrix, again using presence-absence data from non-planted individuals in subplot A of each plot. This model gave a significant result ($F = 1.57$; $p = 0.002$), with reforestation method explaining 8.2% of the total variation in species identity. These results suggest that species turnover also varies significantly between reforestation strategies, complementing the Bray-Curtis-based findings.

3.4.5 Successional Composition of Naturally Regenerating Trees

This analysis complements the previous diversity and composition results by examining the functional characteristics of regenerating communities, specifically the proportion of late-successional species.

The proportion of late-successional individuals was calculated for each plot as the number of unplanted late-successional trees divided by the total number of naturally regenerated individuals in subplot A. Only naturally regenerated individuals were included, consistent with previous analyses.

The distribution of late-successional ratios across the three reforestation methods (control, gap, line) was visualized using boxplots (Figure 9).

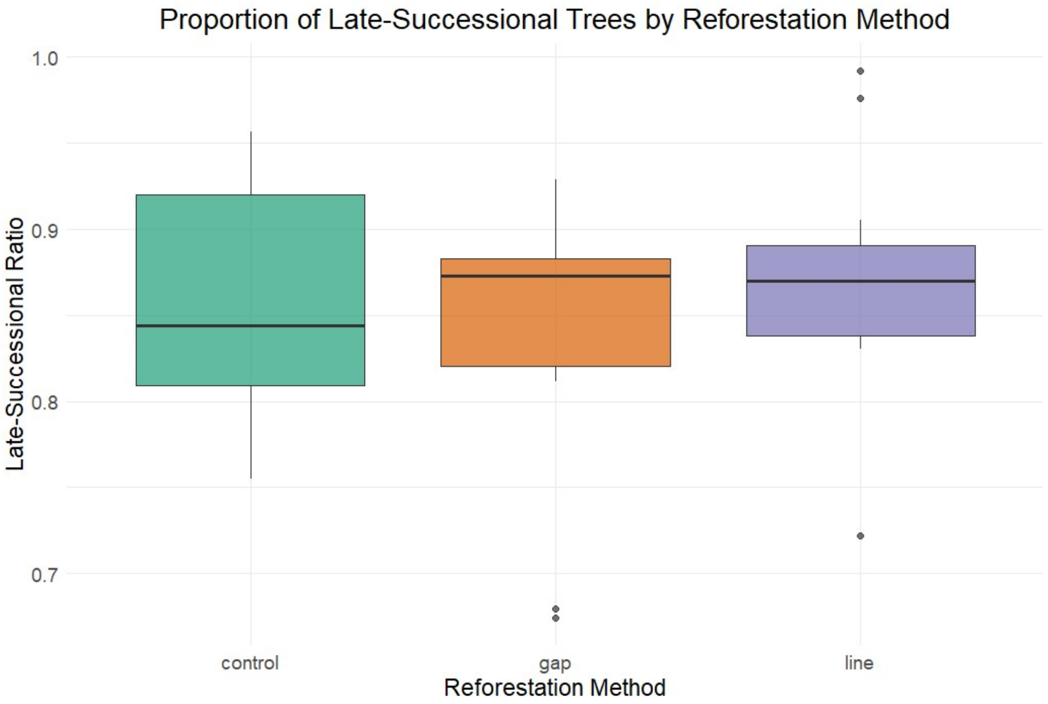

Figure 9. Proportion of late-successional trees among naturally regenerated (unplanted) individuals in subplot A, grouped by reforestation method (control, gap, line). The ratio for each plot was computed as the number of unplanted late-successional individuals divided by the total number of non-planted individuals. Boxes show interquartile ranges and medians; outliers are indicated as individual points. These distributions were analysed using a Kruskal-Wallis test and a Generalized Linear Model (GLM) with a quasibinomial error structure, neither of which detected significant differences among treatments.

A Kruskal-Wallis test was applied to compare the late-successional ratios between reforestation methods. The test returned a chi-squared value of 0.595 with 2 degrees of freedom and a p-value of 0.742.

A Generalized Linear Model (GLM) with a quasibinomial error structure was also used to model the ratio of late-successional individuals. In this model, the intercept (control) estimate was 1.933 (SE = 0.183), with gap and line treatments showing non-significant estimates of -0.171 (p = 0.468) and 0.068 (p = 0.779), respectively. A Type II ANOVA on the GLM showed no significant global effect of reforestation method (F = 0.671; p = 0.518).

4. Discussion

Before interpreting the results in depth, it is useful to revisit the four research questions that guided this study. These addressed: (1) the comparative effects of line and gap-cluster planting on species diversity and composition after 27 years; (2) the influence of degradation, measured through remnant tree structure and composition, on biodiversity outcomes within enriched plots; (3) the differences in tree diversity between enriched and passively regenerating control plots; and (4) the extent to which patterns in naturally regenerated trees reflect broader restoration success. Together, these questions aimed to clarify how planting strategy and site conditions interact to shape forest recovery, and to assess whether spontaneous recruitment in enriched plots supports meaningful biodiversity gains over the long term.

4.1 Interpretation of key results

This study revealed consistent differences in biodiversity outcomes between the three treatments: control, gap planting, and line planting. Among the diversity metrics analyzed, species richness showed the clearest pattern, with both enrichment methods supporting significantly more species than the control plots. Importantly, this result held when excluding planted individuals, which were omitted to isolate the effect of enrichment planting on spontaneous forest recovery. This suggests that planting interventions may contribute to increased species richness by creating conditions that enhance natural recruitment. Although the specific mechanisms behind this effect were not directly tested, it may reflect improved microhabitats, better light conditions, or reduced competition from aggressive ground vegetation. These effects were likely reinforced by additional silvicultural interventions such as climber cutting, girdling of remnant trees, and regular weeding. These interventions were applied in enriched plots but absent in controls. Such maintenance actions, which have been linked to restoration success in similar contexts (Engström, 2023; Axelsson et al., 2022), may have amplified the biodiversity benefits of planting beyond the establishment of trees alone.

The results offer partial but consistent support for the research questions. Both gap and line planting treatments supported significantly higher species richness than control plots, even when planted individuals were excluded. NMDS and PERMANOVA analyses confirmed distinct community compositions across treatments, showing that enrichment planting not only increases the number of species, but also steers regeneration toward compositionally different forest communities. These outcomes directly support the first and third research questions, reinforcing the role of enrichment planting in shaping both richness and identity of naturally regenerating species.

In contrast, the Shannon and Simpson indices did not differ significantly between treatments. These indices incorporate both species richness and the relative abundance of each species, making them more sensitive to dominance patterns. The lack of significant differences suggests that, while enriched plots had more species overall, the distribution of individuals across species remained relatively even in all treatments. In other words, enrichment planting increased richness but did not substantially alter species evenness.

Patterns in species composition further support this interpretation. Both NMDS ordinations and PERMANOVA analyses revealed significant differences in species identity between treatments. This means that enrichment planting not only increases the number of species present but also changes which species are present. The additional species in enriched plots are not simply more of the same, they contribute to distinct community structures. This implies that enrichment planting can actively shape the ecological trajectory of naturally regenerating communities, potentially steering them toward more diverse and compositionally distinct endpoints. However, the full impact on overall forest diversity, including planted individuals, remains beyond the scope of this study.

The analysis of successional composition, measured as the proportion of late-successional species among naturally regenerated individuals, did not show significant differences between treatments. This likely reflects the slow growth and late emergence of these species, particularly dipterocarps, which dominate mature forest canopies in Borneo. These results align with other long-term studies in the region, which show that late-successional species often require decades to influence forest structure and diversity in measurable ways (Philipson et al., 2020; Engström, 2023).

A more nuanced result concerns degradation history. Although visual trends hinted that plots with more remnant basal area might support slightly higher richness, none of the degradation proxies showed a statistically significant relationship with biodiversity indices. This suggests that, within the scope of this study, structural legacies such as remnant trees did not strongly influence current patterns of species richness. Although previous research has emphasized the role of site history in shaping recovery trajectories, our findings indicate that planting strategy had a more consistent impact on biodiversity than initial degradation levels. The partial overlap of degradation levels across treatments further limited the ability to isolate degradation effects but reinforces the importance of treatment design over site condition. These findings offer weaker support for the second research question.

The fourth research question, whether patterns in non-planted tree communities reflect restoration success, was supported by the observation that enriched plots supported more diverse and distinct naturally regenerating communities than controls. This finding indicates that enrichment planting creates ecological conditions that facilitate spontaneous recovery. However, it also highlights that such recovery is shaped by both planting strategy and initial site conditions, particularly the presence of remnant trees.

In summary, the results show that enrichment planting has a clear and measurable effect on tree diversity and species composition after 27 years, even when planted individuals are excluded. These findings support research questions 1 and 3 by demonstrating higher species richness and distinct species composition among naturally regenerating trees in enriched plots compared to controls. The second research question received weaker support, as degradation gradients showed limited influence on diversity. However, changes in dominance patterns and successional trajectories might be less apparent at this stage. While these findings point to the effectiveness of enrichment methods in enhancing diversity and shaping community structure, they also suggest that full ecosystem recovery, including the return of late-successional traits, may still be in progress. This aligns with research question 4, which expected that naturally regenerating communities would differ by treatment but remain incomplete in functional recovery. Future studies could benefit from incorporating the “liberation” treatment, where maintenance is conducted without planting, as a useful comparison to better isolate the role of post-planting interventions in driving biodiversity outcomes. Continued monitoring will be essential to understand how these patterns evolve over longer timescales.

4.2 Ecological Mechanisms and Successional Dynamics

The biodiversity differences observed between treatments suggest that enrichment planting may alter ecological conditions in ways that promote a broader range of natural tree recruitment. By opening the canopy and reducing competition from dense ferns and climbers, enrichment likely facilitates colonization by species that otherwise struggle to establish in heavily degraded sites. In the INIKEA project, these ecological shifts were further supported by targeted silvicultural actions such as climber cutting, selective weeding, and girdling of competing vegetation, all of which were applied alongside planting to enhance light availability and reduce suppression (Axelsson et al., 2024). Though not directly measured in this study, such facilitative mechanisms have been well documented in related restoration efforts within the same project area (Axelsson et al., 2022).

The design of the planting treatments may have influenced the patterns observed. Gap planting introduces concentrated canopy openings, while line planting creates more linear gaps, both of which likely modify light conditions and microsite availability. While I did not measure these factors directly, the treatments resulted in significantly higher species richness compared to control plots and led to distinct species compositions, as shown by NMDS and PERMANOVA analyses. These findings suggest that the spatial arrangement of enrichment planting could influence which species are able to regenerate, potentially steering forest recovery along different compositional paths. However, the lack of significant differences between gap and line plots suggests that these spatial arrangements may converge over time, particularly if maintenance activities and planted canopy development homogenize conditions across treatments.

Nevertheless, planting method is only part of the story. While the treatments were implemented in different project phases, Phase 1 for the enrichment plots and Phase 4 for the controls, all sites were affected by the same major disturbance: the 1982-1983 El Niño event, which caused widespread drought and fire damage. This means that, despite differences in when plots were established within the project timeline, their degradation occurred during the same period and under similar climatic conditions. As such, the control plots offer a valid point of comparison, representing areas where no active restoration took place following the disturbance. What remains uncertain, however, is the precise severity and nature of degradation across plots. Degradation in tropical forests is shaped by complex factors, including past fire intensity, logging practices, and ecological resilience, which are rarely documented in detail. To address this, I used three complementary proxies of site degradation: the basal area of large remnant trees, the proportion of pioneer species, and the richness of remnant species. These indicators varied across plots but showed no consistent differences between reforestation treatments. By incorporating each proxy into the statistical models as a covariate, the analysis adjusted for variation in site degradation. This allowed the biodiversity effects of enrichment planting to be evaluated more confidently, independent of underlying differences in initial site condition.

Within the enriched plots, the original project strategy assumed that line planting would be applied to the most heavily degraded areas, while gap planting would be used in less degraded sites. However, the data from this study do not fully support that assumption. In several cases, gap plots showed lower remnant basal area than line plots, indicating higher degradation than initially expected. This inconsistency highlights the importance of using field-based indicators, rather than relying solely on planning documents, to understand site conditions. It also complicates the interpretation of treatment effects, as planting method and degradation intensity are not cleanly separated. This overlap makes it difficult to attribute differences in richness and composition solely to planting method, since they may also reflect underlying variation in site quality.

Another key observation is the consistent positive relationship between species richness and remnant basal area across all treatments. This suggests that forest structure remaining from pre-logging conditions continues to influence recovery, even decades later. Remnant trees may act as sources of seed, shade, or structural complexity, providing ecological memory that shapes regeneration. This legacy effect is one of the most consistent patterns observed in the data, underscoring the long-term influence of pre-disturbance structure on forest regeneration. In this context, enrichment planting may accelerate recovery, but it builds on whatever ecological foundation remains, making site history a critical component of restoration outcomes. Structural legacies such as remnant trees have been shown to significantly influence regeneration dynamics in tropical systems (Goosem & Tucker, 2013).

Finally, the lack of a significant increase in late-successional species, despite the planting of many dipterocarps, likely reflects their slow growth and the early stage of recovery. Most dipterocarp species are shade-tolerant and slow-growing, and although planted individuals were excluded from the analysis, many may still be relatively small and not yet contributing meaningfully to canopy structure or competitive dynamics. As a result, the influence of late-successional traits may remain limited at this stage. This pattern is consistent with findings from other studies in the region, which report that the structural and ecological impacts of planted dipterocarps only become more evident after several decades (Philipson et al., 2020; Engström, 2023).

Taken together, these findings suggest that enrichment planting can steer regeneration toward more diverse and distinct forest communities, but that its effectiveness is shaped by a combination of planting design and the ecological context in which it is applied. Restoration is not a reset button, it is a process of working with what remains, and the long-term outcome depends as much on initial site conditions as on the interventions themselves.

4.3 Limitations and Confounding Factors

While the results of this study provide meaningful insights into the biodiversity effects of enrichment planting, several limitations should be acknowledged when interpreting the findings.

First, although the exclusion of planted individuals helped focus the analysis on natural regeneration, it also removed a significant part of the vegetation structure from the dataset, particularly in enriched plots where planted dipterocarps and other species likely make up a substantial portion of the stand. This approach was necessary to isolate the effects of enrichment on spontaneous recruitment, but it may underrepresent the total diversity and successional dynamics currently present in the plots.

Second, biodiversity metrics were calculated from a single subplot (subplot A of each plot). While this allowed for a standardized comparison, it does not fully capture the spatial variation that may exist across each site. Tree recruitment can be highly patchy, particularly in regenerating forests where microsite conditions vary at small scales. As such, patterns observed in subplot A may not always reflect conditions across the full plot. Similarly, degradation metrics were calculated at the plot level, which may not perfectly align with conditions within the subplots used for biodiversity assessment. This scale mismatch could introduce some noise into the relationship between degradation and diversity.

A further complication lies in the partial overlap between planting method and site condition. As discussed earlier, restoration design intended for line planting to be implemented in more degraded areas, while gap planting was aimed at sites with more residual forest structure. However, the actual degradation levels recorded in the field did not always follow this logic. In practice, some gap plots were more degraded than line plots, and control plots showed the lowest structural legacies overall. This partial confounding between treatment and degradation makes it difficult to attribute observed biodiversity patterns to planting method alone. The statistical models attempted to separate these effects by including degradation as a continuous variable, but the combined influence of site history and intervention design remains difficult to fully untangle. Additionally, control plots were slightly more remote, up to 6 km away from the enriched blocks, and more spatially clustered, often located along the edges of unplanted forest blocks. While this distance is relatively short, it could still introduce subtle differences in topography, seed rain, microclimate, or edaphic factors. The clustered layout may also have reduced variability within the control group and potentially limited seed dispersal diversity or exposed these sites to shared microclimatic or edge-related conditions. The spatial clustering and peripheral location of control plots may have influenced species dispersal, reduced heterogeneity in control group composition, or exposed these sites to consistent microclimatic or edaphic conditions, potentially confounding comparisons with more heterogeneously distributed treatment plots. These limitations should be kept in mind when interpreting contrasts between control and enriched sites.

Another potential source of uncertainty comes from the realities of fieldwork. All data collection and sampling design were carried out collaboratively in the field and had to be adapted to conditions on the ground. Plans were adjusted as vehicles broke down, roads became impracticable due to heavy rain, and a critical bridge collapsed before arrival, cutting off access to the RRE zone, which had initially been selected for study. This zone includes well-established and frequently monitored plots and was chosen for its potential to offer a more controlled sampling environment.

With that option no longer available, we had to revise our field design upon arrival and continue adjusting as conditions changed. These adaptations have probably introduced some inconsistencies compared to the initial plan. In addition, because we worked with different rangers across multiple visits, species identification was not always fully consistent. While many uncertainties were discussed and corrected on-site, often with input from multiple rangers, there remains a possibility of minor identification errors. Later, after plotting GPS points in QGIS, we also realized that a few plots were closer to the forest edge than we had intended, which may have introduced edge effects. While these issues are not uncommon in field-based studies, they nonetheless represent sources of potential variation. Throughout the fieldwork, all key decisions were made with efforts focused on maintaining consistency and transparency in methods, even as on-the-ground conditions required ongoing adaptation.

Finally, while species composition and richness were thoroughly assessed, this study did not consider other important aspects of forest recovery, such as vegetation structure, functional traits, soil conditions, or faunal return. All these elements are essential for understanding ecosystem-level resilience and long-term restoration success. Including these variables in future research would offer a more complete picture of how different reforestation strategies shape forest recovery.

Despite these limitations, the patterns observed are robust enough to draw meaningful conclusions. They demonstrate that enrichment planting can influence biodiversity outcomes over the long term, while also highlighting the importance of initial site conditions and the need for careful interpretation when treatment effects and degradation levels are not perfectly independent.

4.4 Implications for Forest and Landscape Restoration

The results of this study offer valuable insights for forest and landscape restoration efforts, particularly in the context of biodiversity recovery. The clear increase in species richness and the shifts in species composition observed in both gap and line planting treatments suggest that enrichment planting can be an effective strategy for restoring tree diversity in degraded tropical forests. Even when excluding planted individuals, enriched plots supported more naturally recruiting species than control plots, indicating that these interventions help re-establish ecological conditions that support broader regeneration processes. This supports the growing body of evidence showing that assisted natural regeneration, when combined with targeted planting, can promote diverse and compositionally distinct forest communities (Strassburg et al., 2020).

For biodiversity-focused restoration, these findings underscore the importance of combining planting interventions with careful attention to site conditions. The strong influence of remnant basal area on species richness across all treatments highlights the value of retaining structural forest elements, such as large trees or patches of less disturbed vegetation, during and after logging operations. This echoes earlier findings from Neotropical forests, including the Atlantic Forest and lowland tropical regions like Costa Rica, where structural legacies were found to boost both biodiversity and ecosystem function decades after disturbance (Letcher & Chazdon, 2009; Melo et al., 2013). Enrichment alone is not a silver bullet, it performs best when applied in areas where some ecological memory remains, enabling the re-establishment of biotic interactions and successional dynamics.

That said, there are important trade-offs to consider. Enrichment planting is more resource-intensive than passive restoration. It requires labour, nursery infrastructure, and long-term maintenance, including activities such as climber cutting or girdling. From a cost-efficiency standpoint, this raises the question of where and when enrichment planting is justified. If natural regeneration can deliver comparable outcomes over the long term in less degraded areas, passive approaches may be more appropriate in some contexts. This aligns with findings from Crouzeilles et al. (2017) and Holl & Aide (2011), which show that passive restoration often performs surprisingly well in areas with moderate disturbance, particularly in terms of cost-effectiveness and species accumulation rates.

Conversely, in severely degraded sites with limited natural seed sources or persistent barriers to regeneration, active planting appears to offer clear benefits. This has been shown in multiple regions, including Southeast Asia and Latin America, where active restoration outperforms passive strategies, especially in structurally simplified or highly degraded landscapes (Suding et al., 2015; Reid et al., 2018). Such cases highlight the importance of tailoring restoration strategies to degradation context, recognizing that intervention intensity should scale with site limitation.

Another dimension of this trade-off lies in the relationship between biodiversity and biomass or carbon goals. In the INIKEA project, enrichment planting has been shown to accelerate aboveground carbon recovery (Engström, 2023). Similar patterns have been reported in other tropical contexts where active planting increased biomass and carbon storage (Poorter et al., 2016). However, the results of this study suggest that biodiversity may not track carbon gains in the same way, particularly in early and mid-successional stages. These results support growing evidence that biodiversity and carbon recovery may follow different trajectories (Lamb et al., 2005; Meli et al., 2017). This underlines the need for integrated planning frameworks that consider multiple indicators, functional diversity, community composition, and ecosystem services, rather than relying on carbon alone as a proxy for restoration success.

In practical terms, this study supports the inclusion of enrichment planting in restoration toolkits, especially in areas with moderate to high degradation. While this study found no strong differences between gap and line methods, site-specific conditions and logistical constraints may still influence which strategy is more appropriate. Restoration is not a one-size-fits-all intervention, it is context-dependent, and success hinges on matching strategies to site conditions, long-term objectives, and available resources. Adaptive management approaches, supported by long-term monitoring, will be essential for refining and improving restoration outcomes (Brancalion & Holl, 2020).

4.5 Future Research Directions and Conclusion

While enrichment planting supported significantly greater species richness and distinct species composition among naturally regenerating trees, these findings also point to key knowledge gaps and long-term uncertainties, opening several directions for future research. First, the lack of a clear increase in late-successional species in enriched plots likely reflects the slow growth rates and delayed canopy emergence of these species. In particular, many dipterocarps planted decades ago may not yet exert a strong influence on stand structure or diversity, despite successful establishment. Long-term monitoring will be essential to determine when and how these species begin to contribute meaningfully to biodiversity, carbon storage, and canopy dynamics.

Second, expanding biodiversity assessments to include trait-based metrics could help track more subtle changes in ecosystem function. Traits such as wood density, shade tolerance, or dispersal mode could offer insight into functional shifts that are not captured by species richness alone. These approaches have been applied in successional studies to reveal how community assembly mechanisms evolve over time (Chazdon et al., 2010). Similarly, incorporating structural metrics like canopy openness, understory complexity, and soil characteristics could clarify how environmental changes mediate recruitment patterns.

Finally, future research should look beyond the tree community to assess broader ecological recovery. Studies on fauna, such as pollinators, frugivores, or birds, could help evaluate whether key biotic interactions are returning. Faunal recovery often lags behind vegetation and may take decades to resemble that of intact forests (Suganuma & Durigan, 2015), yet anecdotal observations from rangers and residents suggest that animal diversity has begun to return in several restored areas. Verifying and monitoring this more systematically would strengthen understanding of restoration effectiveness at the ecosystem level.

Overall, this study contributes to a growing body of work emphasizing the importance of long-term, integrative approaches to restoration monitoring. Tracking both planted and spontaneously regenerating components, in combination with site history and functional traits, will be key to understanding how different reforestation strategies shape the trajectory and resilience of tropical forest ecosystems.

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Popular science summary

Tropical rainforests are home to an incredible variety of life, but many have been heavily degraded by logging, fires, and land conversion. In the Malaysian state of Sabah, on the island of Borneo, large areas of forest have been lost or damaged. To reverse this trend, one of Southeast Asia's biggest restoration efforts, the INIKEA Sow-a-Seed project, was launched over 27 years ago. It aims to bring back native forest ecosystems by planting millions of trees in areas that were once logged or burned.

This study looked at what happens in these restored areas over the long term. Specifically, it focused on trees that have grown naturally, without being planted, in order to understand whether restored forests are really coming back to life on their own. The research compared two types of planting strategies: line planting, where trees are planted in straight rows, and gap-cluster planting, where trees are planted in small groups in natural openings. It also included nearby areas where no planting was done, to see how the forest would recover without intervention.

The study found that planted areas supported significantly more naturally regenerated tree species than unplanted ones, even decades later. These enriched plots also developed distinct tree communities, not just more species but different ones, suggesting that restoration planting actively shapes how forests recover. Importantly, this effect was observed even without including the planted trees in the analysis, showing that enrichment planting improves conditions for natural forest regrowth. In contrast, areas left to recover on their own had lower diversity and less distinct species composition. The type of planting (line vs. gap) made less of a difference, and initial site conditions, like the presence of surviving large trees, also played a role in shaping recovery.

These findings show that active restoration efforts like enrichment planting can boost biodiversity and help tropical forests recover, especially when combined with favourable site conditions, such as existing remnant trees. However, they also highlight that full ecological recovery takes time. Long-term monitoring is essential to understand what works best and to adapt strategies accordingly. As global attention turns to reforestation as a climate and biodiversity solution, this kind of research can help guide for more effective restoration practices.

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Thanks also to my co-supervisors, Petter Axelsson and Arvid Lindh, for their valuable support and feedback throughout the project. When the original study site became inaccessible due to a bridge collapse, they played a key role in helping me quickly adapt and find alternative solutions. With their prior familiarity with the site and the project, they stayed longer to assist during the early stages of fieldwork, and their presence was a great help in adjusting our plans and logistics on the ground.

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Appendix

Table 1 : List of Naturally Regenerating Tree Species Observed Across All Plots.

Species name	Latin name
Bawing	*Adinandra spp.*
Kopi Kopi	*Aglaia argentea*
Lentupak jambu	*Aglaia elliptica*
Kondolon	*Alangium javanicum*
Pulai bukit	*Alstonia angustiloba*
Pulai basung	*Alstonia spatulata*
Karai	*Annonaceae*
Tandoropis	*Antidesma ghaesembilla*
Penatan	*Aporusa elmeri*
Galang-galang	*Aporusa grandistipula*
Bagil	*Aporusa nitida*
Jaring	*Archidendron jiringa*
Surusop	*Ardisia elliptica*
Terap Ikal	*Artocarpus anisophyllus*
Terap ikal	*Artocarpus anisophyllus*
Terap togop	*Artocarpus elasticus*
Terap Togop	*Artocarpus elasticus*
Belimbing hutan	*Baccaurea angulata*
Tampoi kuning	*Baccaurea latifolia*
Kunau-Kunau	*Baccaurea parviflora or Baccaurea stipulata*
Kunau-kunau	*Baccaurea parviflora or Baccaurea stipulata*
Tampalang	*Barringtonia macrostachya*
Medang wangi	*Beilschmiedia micrantha*
Biko biko	*Bhesa paniculata*
Bintangor	*Calophyllum obliquinervium*
Kedondong	*Canarium, Dacryodes & other Burseraceae*
Garu-garu	*Cleistanthus paxii*
Kapas-kapas	*Croton argyratus*
Rambai-rambai	*Crypteronia griffithii*
Katong-Katong	*Cynometra inaequifolia or Cynometra ramiflora*
Kedondong bulu	*Dacryodes laxa*
Obah merah	*Decaspermum fruticosum or Eugenia cerasiformis*
Anjarapai	*Dendrocnide elliptica*
Simpoh gajah	*Dillenia borneensis*
Simpoh Gajah	*Dillenia borneensis*
Simpoh Laki	*Dillenia excelsa*
Simpoh laki	*Dillenia excelsa*
Mata kucing	*Dimocarpus longan*
Obah Putih	*Dimorphocalyx murinus*
Obah putih	*Dimorphocalyx murinus*
Kayu Malam	*Diospyros spp.*
Kayu malam	*Diospyros spp.*
Nyatoh putih	*Diploknema sebifera*
Keruing putih	*Dipterocarpus caudiferus*
Keruing spp.	*Dipterocarpus spp.*
Kapur gumpait	*Dryobalanops keithii*
Kapur Paji	*Dryobalanops lanceolata*
Kapur paji	*Dryobalanops lanceolata*
Odopon putih	*Drypetes longifolia*
Magas	*Duabanga moluccana*

Durian kuning	*Durio griffithii*
Durian merah	*Durio kutejensis*
Durian spp.	*Durio spp.*
Senduk-senduk mata	*Endospermum diadenum*
Perepat Burung	*Erythroxylum cuneatum*
Perepat burung	*Erythroxylum cuneatum*
Obah	*Eugenia spp.*
Belian	*Eusideroxylon zwageri*
Todopon puok	*Fagraea volubilis & several other Fagraea spp.*
Kayu Ara	*Ficus callosa*
Ficus	*Ficus spp.*
Rukam	*Flacourtia rukam*
Nyatoh king	*Ganua kingiana*
Nyatoh katiau	*Ganua motleyana*
Manggis	*Garcinia mangostana*
Kandis	*Garcinia parvifolia*
Tambong	*Geunsia pentandra*
Obah Nasi	*Glochidion borneensis or Glochidion rubrum*
Obah nasi	*Glochidion borneensis or Glochidion rubrum*
Rengas	*Gluta, Semecarpus, Melanochyla & Swintonia*
Kembang	*Heritiera simplicifolia*
Ludai Susu	*Homalanthus populneus*
Ludai susu	*Homalanthus populneus*
Selangan mata kucing	*Hopea ferruginea*
Selangan jangkang	*Hopea nervosa*
Selangan Jangkang	*Hopea nervosa*
Selangan	*Hopea spp.*
Karpus tulangsai	*Hydnocarpus borneensis*
Merbau	*Intsia palembanica*
Pauh kijang	*Irvingia malayana*
Darah-Darah kerantu	*Knema laurina*
Kilas	*Koilodepas longifolium*
Mengaris	*Koompassia excelsa*
Ranggu	*Koordersiodendron pinnatum*
Medang	*Lauraceae*
Mali-mali	*Leea indica*
Mempening	*Lithocarpus & Quercus*
Sedaman Jari	*Macaranga beccariana*
Sedaman jari	*Macaranga beccariana*
Sedaman Putih	*Macaranga hypoleuca*
Sedaman putih	*Macaranga hypoleuca*
Sedaman	*Macaranga spp.*
Nyatoh	*Madhuca Madhuca sp.*
Mallotus	*Mallotus spp.*
Mallotus Segar-Segar	*Mallotus wrayi*
Mallotus segar-segar	*Mallotus wrayi*
Mangga wangi	*Mangifera odorata*
Pauh-pauh	*Melicope luna-akenda*
Nipis kulit	*Memecylon laevigatum*
Cempaka hutan	*Michelia montana*
Kerodong Damak-Damak	*Microcos crassifolia*
Kerodong damak-damak	*Microcos crassifolia*
Darah-Darah	*Myristicaceae*
Darah-darah	*Myristicaceae*
Bangkal kuning	*Nauclea subdita*
Bangkal	*Nauclea subdita or Neonauclea bernardoi*
Laran	*Neolamarckia cadamba*
Bangkal merah	*Neonauclea bernardoi*

Meritam	*Nephelium mutabile*
Karai Hitam	*Orophea myriantha*
Nyatoh Bulu	*Palaquium beccarianum*
Nyatoh taban merah	*Palaquium gutta*
Nyatoh sidang	*Palaquium rostratum*
Kepayang	*Pangium edule*
Membuakat	*Paranephelium xestophyllum*
Terap	*Parartocarpus or Artocarpus*
Urat mata daun licin	*Parashorea malaanonan*
Urat mata batu	*Parashorea smythiesii*
Urat mata beludu	*Parashorea tomentella*
Torog	*Parinari costata (Kunth)*
Layang-layang	*Parishia insignis*
Nyatoh taban putih	*Payena acuminata*
Takalis daun bulat	*Pentace adenophora*
Takalis Daun Halus	*Pentace laxiflora*
Takalis daun halus	*Pentace laxiflora*
Buluh-Buluh	*Pleiocarpidia sandakanica*
Buluh-buluh	*Pleiocarpidia sandakanica*
Karai putih	*Polyalthia sumatrana*
Sirih-Sirih	*Pternandra coerulescens*
Sirih-sirih	*Pternandra coerulescens*
Gapis	*Saraca declinata*
Sukung-Sukung	*Saurauia ferox*
Kembang semangkuk jantan	*Scaphium longipetiolatum*
Melapi agama	*Shorea agamii*
Seraya daun mas	*Shorea argentifolia*
Selangan batu hitam	*Shorea atrinervosa*
Seraya langgai	*Shorea beccariana*
Seraya	*Shorea curtisii*
Seraya kuning	*Shorea faguetoides*
Seraya Kuning	*Shorea faguetoides*
Selangan batu laut	*Shorea falciferoides*
Seraya daun kasar	*Shorea fallax*
Seraya kuning gajah	*Shorea gibbosa*
Seraya majau	*Shorea johorensis*
Seraya tembaga	*Shorea leprosula*
Seraya Tembaga	*Shorea leprosula*
Selangan batu biabas	*Shorea leptoderma*
Kawang jantung	*Shorea macrophylla*
Seraya melantai	*Shorea macroptera*
Kawang burung	*Shorea mecistopteryx*
Seraya Kepong	*Shorea ovalis*
Seraya Punai	*Shorea parvifolia*
Seraya punai	*Shorea parvifolia*
Seraya lupa	*Shorea parvistipulata*
Oba suluk	*Shorea pauciflora*
Selangan batu terendak	*Shorea seminis*
Seraya Timbau	*Shorea smithiana*
Seraya timbau	*Shorea smithiana*
Selangan batu daun halus	*Shorea superba*
Seraya kuning barun	*Shorea xanthophylla*
Sepetir	*Sindora beccariana Baker or Sindora irpicina*
Katok	*Stemonurus scorpioides*
Jiak	*Symplocos fasciculata*
Buak-Buak Batu	*Teijsmanniodendron holophyllum*
Ranggau	*Toona sp.*
Pelawan-pelawan	*Tristaniopsis merguensis*

Resak putih	*Vatica albiramis*
Resak Bukit	*Vatica dulitensis*
Resak daun merah	*Vatica maingayi*
Resak sarawak	*Vatica sarawakensis*
Resak	*Vatica spp.*
Karai jangkang	*Xylopia ferruginea*

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