Evaluating enrichment planting strategies in Borneo

Evidence from a long-term tropical restoration project

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Master's thesis • 60 credits
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Forest Ecology and Management
Examensarbeten / SLU, Institutionen för skogens ekologi och skötsel
2026:17 • 1654-1898
Umeå 2026

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Credits:	60 credits
Level:	Advanced level A2E
Course title:	Master's thesis in Forest Science, A2E - Forest Ecology and Management
Course code:	EX0957
Programme/education:	Forest Ecology and Sustainable Management / Master of Science in Forestry
Course coordinating dept:	Forest Ecology and Sustainable Management
Place of publication:	Umeå
Year of publication:	2026

Title of series:	Examensarbeten / SLU, Institutionen för skogens ekologi och skötsel
Part number:	2026:17
ISSN:	1654:1898

Keywords:	Tropical forest restoration, enrichment planting, assisted natural regeneration, aboveground biomass, long-term monitoring, Borneo

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Abstract

Tropical forest degradation threatens biodiversity and carbon recovery across Southeast Asia, highlighting the need for effective restoration strategies. A key response to this challenge is assisted natural regeneration (ANR) — an active restoration approach for degraded tropical landscapes — which combines selective enrichment planting of native seedlings with maintenance activities to enable and enhance natural regeneration. Yet long-term field evidence on the efficacy of specific enrichment planting strategies within ANR remains scarce, particularly from large-scale restoration projects in degraded tropical forests.

This thesis evaluates 25-year outcomes of gap-cluster and line enrichment planting against untreated control plots at the INIKEA restoration project in Sabah, Malaysian Borneo, using linear mixed-effects models across a gradient of initial site degradation to assess treatment effects on aboveground biomass, seedling performance, and planted stem contribution to stand-level recovery.

Gap-cluster planting produced significantly greater total aboveground biomass than untreated controls ($p = 0.019$; difference: 53.9 ± 18.4 Mg/ha). The line treatment showed a consistent positive trend that did not reach statistical significance, and no significant difference in planted seedling survival or establishment was detected between treatments. Initial site condition, measured as the basal area of pre-disturbance remnant stems exceeding 60 cm DBH, was the dominant predictor of total and natural biomass ($p < 0.001$) but showed no association with post-restoration biomass accumulation, while planted stem contribution to total stand biomass declined significantly with increasing remnant basal area ($p < 0.001$). Biomass differences between treatments were concentrated in larger stem size classes, in line with either the direct contribution of planted material or the growth of naturally regenerating stems benefiting from maintenance activities, or a combination of both. These patterns are consistent with a compensatory dynamic in which natural regeneration offsets reduced planted stem contribution at structurally intact sites, producing post-restoration biomass accumulation broadly comparable across the degradation gradient.

These findings suggest that gap-cluster enrichment planting can meaningfully accelerate biomass recovery in degraded dipterocarp forest, and that initial site degradation level is at least as important a determinant of restoration outcomes as the choice of planting format — affecting not only how enrichment planting is executed but also whether active seedling planting is warranted at all, at least within the 25-year timeframe examined here.

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Abbreviations

Abbreviation	Description
AGB	Aboveground Biomass
AIC	Akaike Information Criterion
ANR	Assisted Natural Regeneration
BA	Basal Area
CI	Confidence Interval
DBH	Diameter at Breast Height
EMM	Estimated Marginal Mean
FAO	Food and Agriculture Organization
LMM	Linear Mixed-Effects Model
GLMM	Generalized Linear Mixed Model
ICC	Intraclass Correlation Coefficient
INIKEA	Sow-A-Seed restoration project, Sabah, Borneo
LRT	Likelihood Ratio Test
Mg/ha	Megagrams per hectare
OLRE	Observation-Level Random Effect
OLS	Ordinary Least Squares
REML	Restricted Maximum Likelihood
SLU	Swedish University of Agricultural Sciences

1. Introduction

1.1 Background

The world's forests are home to 80% of the terrestrial species on Earth and are of immense importance due to the ecological, cultural and economic values they provide (World Bank, 2023; FAO & UNEP 2024). For example, forests sequester approximately 2.6 billion tonnes of CO2 annually (IUCN, 2024), forested watersheds supply approximately 75% of the world's accessible freshwater and around 1.6 billion people rely on forests for their livelihoods (FAO & UNEP, 2024). Spanning across all forest types, the boreal, the temperate and the tropical, these ecosystems are under pressure from a multitude of factors (FAO & UNEP, 2024).

The main driver for both historical and current deforestation is agricultural conversion, and the total figure of deforested forest land is approximately 10 million hectare per year (FAO & UNEP, 2024). While land-use change remains the primary driver of deforestation, forest fires are the second largest contributor to forest loss and degradation. This fire susceptibility is frequently exacerbated by industrial logging, which acts as a precursor to these events. By desiccating the understory and accumulating combustible debris, logging creates the specific microclimatic conditions necessary for fires to take hold (Holdsworth & Uhl, 1997; Cochrane, 2003).

The tropics have been particularly affected and have experienced an intensification of forest fires in recent years (Bourgoin et al., 2025). The resulting landscapes are not only fragmented by land-use change but further ecologically degraded by fire, which depletes seed banks and eliminates the faunal dispersers necessary for natural regeneration (Cochrane, 2003; Edwards et al., 2014; Marsh et al., 2025). In response, major initiatives such as the Bonn Challenge and the UN Decade on Ecosystem Restoration have been launched, underscoring the severity of forest loss and the urgent need to identify effective strategies for restoring these degraded ecosystems (UNEP & FAO, 2021; IUCN, 2011). Despite these ambitious global targets, significant uncertainty remains regarding the most effective silvicultural interventions for accelerating recovery across varying degrees of forest degradation.

1.2 The tropical restoration gap and current practices

Current forest restoration practices in boreal and temperate forests trace their foundations to the transition toward scientific silviculture during the 18th century (Carlowitz, 1713; Fernow, 1911; Lowood, 1990), building centuries of structured, site-specific management knowledge. Tropical forestry presents a stark contrast,

characterized by a significant lack of long-term silvicultural and restoration data despite tropical rainforests being the most biodiverse ecosystems on Earth — harboring two thirds of all terrestrial species while covering only about 7% of the surface (Barlow et al., 2018; Chazdon, 2014).

This knowledge gap reflects the logistical and financial barriers to ground-level tropical research. Remote and demanding environments necessitate specialized transport and equipment, making field-based research far more resource-intensive than comparable work in boreal and temperate forests (Stocks et al., 2008; Amano et al., 2016; Nunez et al., 2019). The extraordinary species richness and complexity of biotic interactions further complicate data collection and monitoring (Gaston, 2000; Schemske et al., 2009). The result is a persistent scarcity of long-term field evidence from operational restoration projects — precisely the evidence base needed to evaluate whether and how active intervention accelerates recovery in heavily degraded tropical landscapes.

Assisted Natural Regeneration (ANR) is a restoration approach that focuses on protecting land from disturbances, such as grazing and fire, while controlling competition to enhance natural regeneration of local tree species, occasionally utilizing support planting of indigenous species if the degradation of the forest is deemed severe enough to necessitate it (FAO, 2019). Research indicates that ANR can be not only more effective than plantation-based approaches at restoring biodiversity and ecosystem function, but also more cost-effective, particularly where natural regeneration capacity is sufficient to drive recovery without active planting (Chazdon, 2014). This is supported by multiple studies including a global meta-analysis finding that naturally regenerating forests outperformed plantations in biodiversity protection and ecosystem services (Hua et al., 2022; Crouzeilles et al., 2017; Shono et al., 2007).

Although studies such as these categorize ANR as a viable ecological and economic alternative, the prevailing global approach remains tilted toward industrial-style monocultures. This preference is not based on ecological merit, but on the simplicity of implementation and rapid biomass production. Such metrics are frequently used as proxies for 'success' to satisfy the reporting requirements of international stakeholders and carbon markets, despite potentially masking a lack of ecosystem function and biodiversity (Hua et al., 2022; Veldman et al., 2019; Brancalion, 2025).

Consequently, the complexity of the tropical ecosystem is often sacrificed for the administrative ease of a uniform plantation. This is well illustrated by an evaluation of the Bonn Challenge by Lewis et al. (2019), in which they analyzed 166 million hectares of restoration pledges and found that 45% was slated for commercial monoculture plantation, 21% for agroforestry, and only 34% for natural restoration. This is despite the fact that the Bonn Challenge explicitly

supports Forest and Landscape Restoration, which is meant to prioritize the ecological functionality of degraded forests (Bonn Challenge, 2020).

Even among proponents of ANR, however, the primary point of contention concerns when to apply the full method, including support planting, when partial intervention suffices, and when passive natural regeneration alone is adequate. A passive approach reduces the risk of over-planting and misallocated resources, while more active intervention reduces the risk of successional stagnation, particularly in landscapes heavily degraded by logging and fire (Chazdon, 2014; Chazdon & Guariguata, 2016; Holl & Aide, 2011). Chazdon et al. (2022) synthesized two decades of research into a framework of site-specific recommendations for navigating this trade-off, though the authors acknowledge that a persistent lack of long-term comparative studies may have led to an overestimation of passive regeneration relative to more active measures (Holl & Aide, 2025). Evidence also suggests that active restoration enhances species composition and accelerates the introduction of late-successional species, a key factor in restoring full ecological functionality (Schubert, 2025). Tropical forests possess a remarkable capacity for recovery, capable of regaining a significant portion of old-growth functions within two decades (Poorter et al., 2021), suggesting that targeted active measures may be most effective when aimed at harnessing and enhancing this inherent regenerative capacity (Axelsson et al., 2012). Resolving these uncertainties — specifically when active planting is necessary, which formats are most effective, and how initial site condition affects restoration outcomes — will ultimately require long-term data from operational restoration projects across a range of degradation severities (Crouzeilles, 2017).

1.3 Purpose and research objectives

Addressing this lack of long-term field evidence requires large-scale restoration projects capable of capturing the gradual successional dynamics that define tropical forest recovery (Crouzeilles, 2017). Among the active interventions applied within ANR, enrichment planting — the targeted introduction of native seedlings into degraded forest — represents a key strategy for accelerating recovery where natural regeneration is insufficient. Two enrichment planting formats are evaluated in this thesis. Line planting involves placing seedlings at regular intervals along cleared strips, providing a structured and systematic approach to stand restoration. Gap-cluster planting places seedlings within existing or created canopy gaps rather than along fixed corridors, more closely mimicking the spatial patterns of natural forest regeneration and potentially exploiting the favorable light conditions and microclimatic variation that naturally occurring gaps provide for seedling establishment and growth. Both formats have been applied within ANR frameworks across degraded dipterocarp landscapes in

Sabah, including at the INIKEA restoration project, alongside systematic competition control through weeding and climber cutting (Axelsson et al., 2024).

This thesis evaluates nearly three decades of outcomes from these interventions at the INIKEA restoration project in Sabah, Malaysian Borneo, which is one of the few tropical restoration projects of sufficient age and scale to assess treatment outcomes across a gradient of initial site degradation. The questions this study aims to answer are the following:

1. How does aboveground biomass differ between gap planting, line planting, and untreated control sites in degraded tropical rainforest?
2. To what extent do observed treatment effects reflect the survival and growth of planted material versus maintenance-facilitated natural regeneration?
3. Does initial site degradation level interact with planting treatment to influence restoration outcomes?
4. Does planting format (gap vs. line) influence planted seedling survival and establishment success?

2. Methodology

2.1 Project background, local ecology and plot selection

The site for the fieldwork that this thesis is based on is located within the INIKEA project site in northern Borneo, in the Malaysian state of Sabah, situated at (4°36'N, 117°12'E). The INIKEA project, established in 1998 as a coordinated effort between Yayasan Sabah, IKEA, and the Swedish University of Agricultural Sciences (SLU), was set up to restore 18,500 hectares of degraded forest in Sabah, Malaysian Borneo through active restoration measures (Alloysius et al., 2010; Suding, 2011).

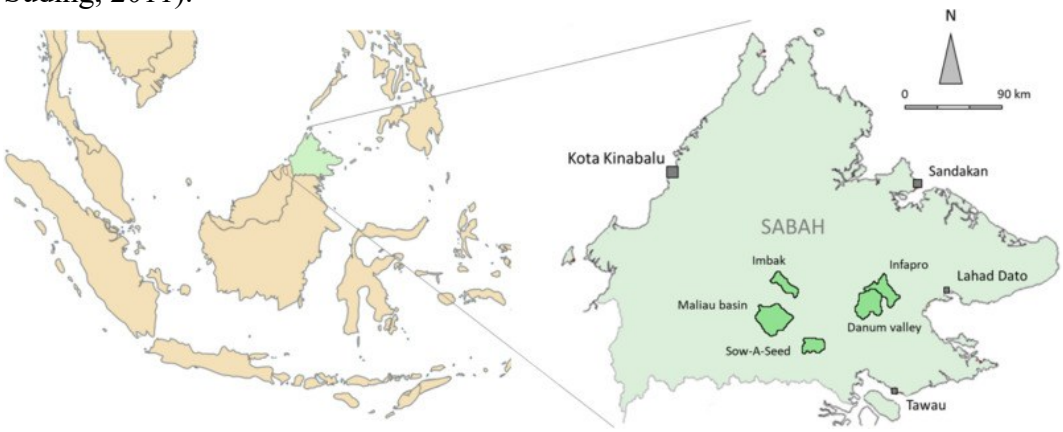

Figure 1: Map depicting the state of Sabah,Borneo, with its location in relation to the other countries in Southeast Asia. Sow-A-Seed/INIKEA research site marked (Axelsson, 2024).

The degradation of these forests originated from intensive selective logging, which damaged forest structure and rendered it susceptible to the El Niño-induced droughts and fires of 1982–83, during which an estimated 1 million hectares burned in the state of Sabah — predominantly in over-logged forests (Beaman et al., 1985; Woods, 1989; Wright et al., 1999; Siegert et al., 2001).

The late-successional species of Borneo consist predominantly of trees from the family Dipterocarpaceae, which includes 521 species globally; of these, 269 are found in Borneo, with 162 being endemic to the island (Bartholomew, Barstow & Randi, 2021). This makes Borneo the primary center of dipterocarp biodiversity, though the majority of these endemic species are currently listed as threatened (Barstow & Bartholomew, 2022). The extensive logging history of Borneo stems from the high timber quality of these dipterocarps (Collins, Sayer & Whitmore, 1991). Following disturbance, such as the 1982–83 fires, the replacement canopy typically consists of fast-growing, early-successional pioneer species such as Macaranga spp. or Mallotus spp., which lack both the ecological

complexity and commercial value of the primary dipterocarp forest (Slik et al., 2003).

Within the INIKEA project, three types of ANR were applied depending on the severity of degradation, though during the initial setup only two methods were used. The project was structured into distinct phases: Phase 1 (1998–2003), Phase 2 (2004–2008), Phase 3 (2009–2014), and Phase 4 (2015–2020). The two treatments applied in Phase 1 were line planting and gap-cluster planting, and this is the period with which this thesis is concerned. The seedlings planted during Phase 1 comprised approximately 92 native tree species, categorized into three groups: dipterocarps (70%), late-successional non-dipterocarps (25%), and wild fruit trees (5%).

Line planting consisted of clearing 2-meter-wide strips of trees and vegetation at 10-meter intervals within treatment blocks, with seedlings planted every 3 meters along each strip. The gap-cluster method divided each treatment block into 10 × 10-meter squares, within which a gap with suitable light conditions was identified and planted with three seedlings of multiple species. Where no suitable gap could be identified, one was created by girdling one or more early-successional trees to establish appropriate light conditions.

Following initial planting, all sites underwent intensive maintenance, including weeding and climber cutting, for the first three years, with periodic liberation tending continuing for up to 10 years to ensure canopy recruitment (Axelsson et al., 2024). Line planting is the more conventional and widely used of the two methods, whereas the intention of the gap-cluster planting is to more closely mimic natural regeneration by utilizing the natural structural variation of the forest to identify suitable planting locations.

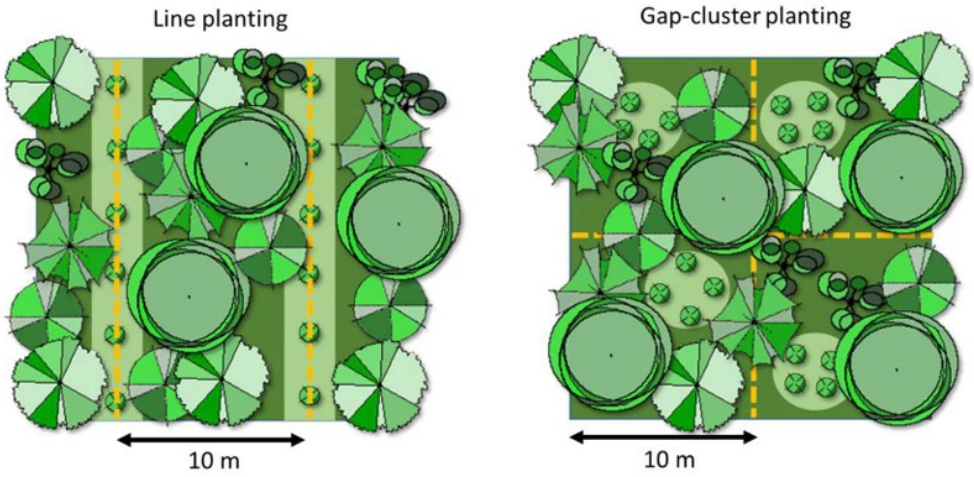

Figure 2: Illustration of the gap and line enrichment planting seen from above. Planted trees are represented by small green circles with a black cross, larger green circles illustrate mature trees. The yellow lines in the illustration to the left represent the planting lines within the 2-meter-wide strips that have been cleared. The yellow lines in the illustration to the right clarifies the four

quadrants in which each gap intended for planting has been located and created (Axelsson et al., 2024).

As this study focuses on the long-term evaluation of tropical forest restoration, Phase 1, as the oldest section of the INIKEA project, is of primary interest. Encompassing 4,000 hectares, Phase 1 was characterized by severe degradation. Each phase was divided into operational blocks of 30–60 hectares, with each block assigned an enrichment strategy based on initial degradation levels, a process carried out by on-site staff without standardized criteria or subsequent validation. Although line planting was generally intended for severely degraded sites and gap-cluster planting for intermediate sites, the lack of strict execution criteria resulted in significant overlap in site conditions across the two treatment types. In this study, this overlap was intentionally targeted during sampling to facilitate direct comparison between strategies across sites with similar degradation levels and a broad environmental gradient.

To adequately capture block-level conditions, at least two plots were sampled per block. In Phase 1, 50 plots were established, split equally between line planting (n = 25) and gap-cluster planting (n = 25). An additional 10 plots were established to serve as untreated controls, located approximately 5 kilometers from the enrichment plots. The separate location of the control plots reflects the operational design of the INIKEA project, in which the original restoration design did not include untreated control plots. As all Phase 1 plots within the operational area had received enrichment planting, control plots had to be established in an adjacent unrestored area. Although geographically distant, the control plots shared a similar history of logging and fire (1982–83) and reflected the initial site conditions of Phase 1 prior to the 1998–2003 restoration activities. Due to the control plots sharing the same disturbance history as the enrichment plots, they are referred to throughout this thesis as control plots rather than as reference sites, as they represent the passive recovery trajectory, not the restoration target. The sample size discrepancy between treatment and control groups reflects logistical constraints that limited the number of accessible control plots during fieldwork.

To minimize edge effects and avoid oversampling spatially dependent features, for instance the influence of a single mother tree, plots were established at a minimum of 120 m from roads and 150 m from neighboring plots.

Plots were located using handheld GPS devices and local maps, supplemented by the expertise of local forest rangers. In areas where difficult terrain or dense canopy compromised GPS accuracy, final plot selection and positional estimations relied on the rangers' local knowledge.

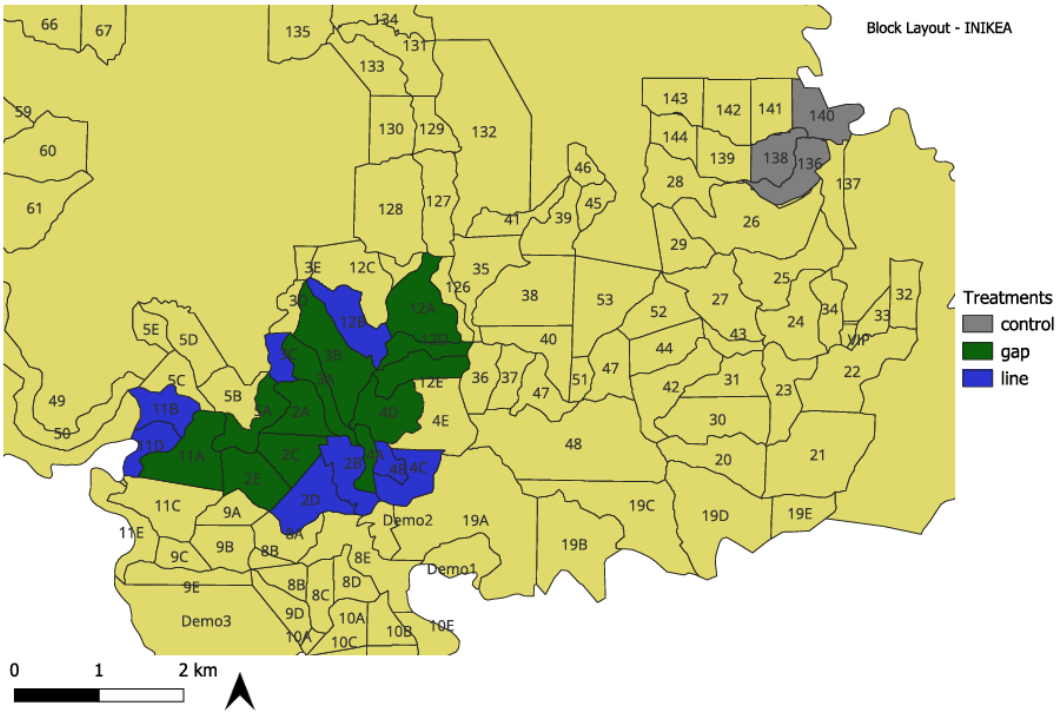

Figure 3: Block layout of the INIKEA restoration project site in Sabah, Malaysian Borneo. Colored blocks indicate those sampled in this study. Gap and line blocks are spatially clustered in the central-western portion of the project area, while control blocks are located approximately 5 km to the northeast.

2.2 Plot set up and data collection

2.2.1 Plot establishment and marking

Once a location was identified, the plot center was marked with a 1-meter PVC pipe (red or blue) to enable future relocation. Coordinates were logged using a Garmin 64S (WGS84) upon arrival and verified at the conclusion of sampling. Lines of 20 meters were extended from the center in each cardinal direction, establishing a 40 × 40 m plot (0.16 ha), further divided into four 20 × 20 m subplots (A–D) in a clockwise sequence starting from the northwest (A). Subplot

boundaries and corner points were marked with 50-cm PVC pipes, see Figure 4.

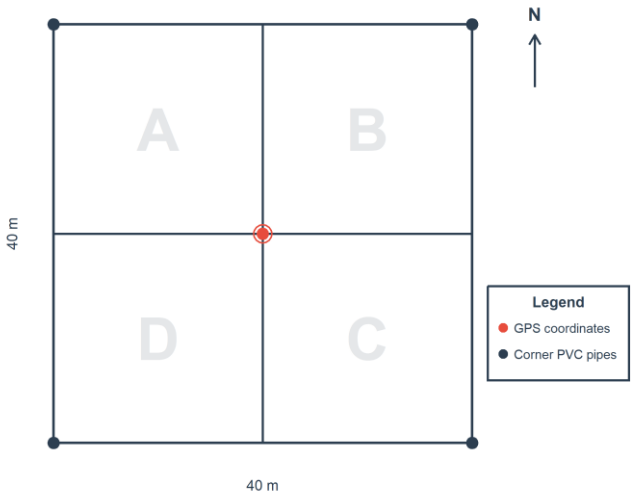

Figure 4: Sampling plot layout showing the 40 × 40 m plot divided into four 20 × 20 m subplots (A–D). In all four subplots were inventory of stems ≥ 10 cm DBH, as well as all planted stems above 1.3 m. The red marker indicates the plot center, and dark circles indicate corner PVC pipes used for plot demarcation and relocation.

2.2.2 Inventory and Measurement protocol

Within the 40 × 40 m area, all trees ≥ 10 cm in diameter at breast height (DBH) were measured. Recorded data included DBH, species identification, and whether the individual was a legacy tree or enrichment planted. For trees with buttresses exceeding 1.3 m, DBH was measured 30 cm above the buttress or estimated by expert rangers when physical measurement was deemed unsafe.

Enrichment planted trees were identified through a combination of physical markers, ranger expertise, directional cues such as planting lines, and species composition. By employing multiple identification methods rather than relying solely on physical markers, planted trees could be located even where markers had been lost because of disturbance or decomposition.

2.3 Biomass Estimation and Covariate Characterization

Aboveground biomass (AGB) was estimated using the site-appropriate multi-species allometric equation developed by Ketterings et al. (2001) for mixed secondary forests in Indonesia:

$$Biomass\ (kg) = 0.066 \times DBH^{2.59}$$

where DBH is expressed in centimeters. Plot-level total biomass (Mg/ha) was calculated as the sum of individual stem estimates, divided by the plot area (0.16 ha) and converted from kilograms to megagrams.

Site condition was characterized by the level of structural degradation, proxied by the basal area of remnant trees — defined as naturally regenerating stems with a DBH ≥ 60 cm, excluding pioneer genera Macaranga and Mallotus. The 60 cm threshold was selected to capture the pre-disturbance structural framework, while limiting the risk of including stems that established naturally post-disturbance or planted stems that were misclassified as naturally regenerated during inventory. While the largest confirmed planted stem recorded was 66 cm in DBH, only two additional planted stems exceeded 60 cm, representing negligible contamination risk. To account for pre-existing variation in site conditions and avoid confounding the treatment comparison, remnant basal area (m²/ha) was included as a continuous covariate in all models.

Prior to modeling, treatment groups were assessed for comparability in remnant basal area to verify that the covariate was not confounded with treatment assignment. A one-way ANOVA across all three treatments revealed no significant difference ($F_{2,57} = 0.257$, $p = 0.774$), and Tukey pairwise comparisons confirmed no individual treatment pair differed significantly (all $p > 0.76$). Mean remnant basal area was similar across treatments (control: 9.33 ± 6.73 m²/ha, $n = 10$; gap: 8.96 ± 6.27 m²/ha, $n = 25$; line: 10.34 ± 7.60 m²/ha, $n = 25$).

As a secondary check, pioneer genus proportion (Macaranga and Mallotus as a fraction of total natural basal area ≥10 cm DBH) was compared between gap and line plots as an independent indicator of pre-treatment disturbance history, and likewise revealed no significant difference ($t = -1.43$, $df = 33.1$, $p = 0.163$).

Collectively, these results are consistent with comparable site conditions across treatments prior to restoration intervention, supporting the use of remnant basal area as a covariate.

2.4 Statistical Analysis

All statistical analyses were performed in R version 4.5.2 (R Core Team, 2025) using the following packages: lme4 (Bates et al., 2015) for model fitting; lmerTest (Kuznetsova et al., 2017) for Kenward-Roger degrees of freedom; emmeans (Lenth, 2023) for post-hoc comparisons; car (Fox & Weisberg, 2019) for Wald tests; and performance (Lüdecke et al., 2021) for ICC calculation and model diagnostics. Unless otherwise stated, a significance threshold of $\alpha = 0.05$ was applied throughout all analyses.

2.4.1 Primary biomass analysis: Linear Mixed ANCOVA

To compare the effects of restoration treatments (gap, line, and control) on biomass, a linear mixed-effects model was applied, using the lme4 package in R (Bates et al., 2015). This model structure constitutes a mixed analysis of covariance — ANCOVA — in which treatment group means are compared after statistical adjustment for the continuous covariate remnant basal area, with block as a random intercept to account for the clustered sampling design. The model included total biomass as the response variable, treatment and remnant basal area as fixed effects, and block identity as a random intercept:

$$Total\ biomass \sim Remnant\ BA + Treatment + (1|Block)$$

where (1|Block) denotes a random intercept for each operational block. Operational blocks represent the project's administrative management units rather than experimentally assigned blocks and were included as a random effect to account for the spatial clustering of plots within management units.

To assess whether treatment effects varied across the remnant BA gradient, additive and interactive model structures were compared using likelihood ratio tests (LRT) and the Akaike Information Criterion (AIC). The additive model was retained for both total and natural biomass, following the principle of parsimony, as interactions were non-significant and AIC comparisons favored the simpler structure (total biomass: $p = 0.326$, $\Delta AIC = 1.8$; natural biomass: $p = 0.209$, $\Delta AIC = 0.9$). This indicated that the influence of restoration treatments on biomass accumulation did not vary significantly across the observed range of remnant forest density. Final model parameters were estimated using Restricted Maximum Likelihood (REML). To account for the unbalanced design and the limited replication in the control group ($n = 3$ blocks), the Kenward-Roger approximation was applied for calculating denominator degrees of freedom and p-values via the lmerTest package (Kuznetsova et al., 2017).

The Intraclass Correlation Coefficient (ICC) was calculated to assess the proportion of variance attributable to the block-level clustering structure. Pairwise treatment contrasts were performed using estimated marginal means via the emmeans package (Lenth, 2023), with Tukey adjustment for multiple comparisons.

A complementary model restricted to the 50 active treatment plots was additionally fitted using the same model structure, excluding control plots to obtain a cleaner estimate of block-level variance from the better-replicated gap and line groups. Full details and results are presented in Appendix 2.

2.4.2 Post-restoration Biomass – Isolating New Growth

To isolate the effect of restoration treatments on biomass accumulated since intervention, an additional set of linear mixed-effects models was fitted using post-restoration biomass as the response variable. Post-restoration biomass was defined as the sum of all naturally regenerating stems within the 10–60 cm DBH range and all planted stems, thereby excluding remnant stems exceeding 60 cm DBH. This definition removes the direct contribution of remnant stems from the response variable, eliminating the circularity inherent in models where remnant stems contribute to both the covariate (remnant BA) and the response (total biomass), providing a cleaner test of treatment efficacy in driving new biomass accumulation since restoration.

The same mixed ANCOVA structure as described in section 2.4.1 was applied. Additive and interactive model structures were compared using LRT and AIC, and the additive model was retained ($p = 0.573$, $\Delta AIC = 2.9$). The complementary gap versus line model followed the same structure, full results are reported in Appendix 2. Final parameters were estimated using REML, with Kenward-Roger degrees of freedom and Tukey-adjusted pairwise contrasts via emmeans (Lenth, 2023).

2.4.3 Planted biomass contribution

To address research question two — the extent to which treatment effects reflect planted stem contribution versus maintenance-facilitated natural regeneration — planted biomass contribution was calculated at the plot level as the proportion of total stand biomass attributable to planted stems. The logit-squish transformation was applied prior to modelling to map the bounded proportion scale onto an unbounded scale suitable for linear mixed-effects modelling and to handle boundary values of exactly zero. Each proportion p was first transformed as $p' = (p \times (n - 1) + 0.5) / n$, where n is the number of plots (n = 50), before applying the logit function $\log(p' / (1 - p'))$. Although beta regression represents an alternative approach for proportion data, the logit-squish linear mixed-effects model was preferred to maintain consistency with the lme4 framework and Kenward-Roger approximation applied throughout all primary analyses. Given that observed planted biomass contributions ranged from 0 to 0.46 and never approached the upper boundary of one, the potential for transformation-induced bias is considered limited (Smithson & Verkuilen, 2006).

The transformed proportion was modelled using a linear mixed-effects model with treatment as a fixed effect and block as a random intercept:

$$logit(p') \sim Treatment + (1 \mid Block)$$

where (1|Block) denotes a random intercept for each operational block.

Model parameters were estimated using Restricted Maximum Likelihood, and p-values for fixed effects were obtained via the Kenward-Roger approximation for denominator degrees of freedom, consistent with the primary mixed ANCOVA analyses (sections 2.4.1–2.4.3). Estimated marginal means were back-transformed from the logit scale to the proportion scale for interpretation using emmeans (Lenth, 2023).

The effect of remnant basal area on planted biomass contribution is examined through an extended version of this model described in section 2.6.

2.4.4 Supplementary Biomass Analyses: Size Class partitioning and Non-Remnant Dipterocarp Biomass

To further characterize the mechanisms underlying treatment differences in biomass accumulation, two supplementary analyses were conducted. First, non-remnant dipterocarp biomass, which was defined as the summed biomass of all dipterocarp stems below 60 cm DBH, including both planted and naturally regenerating individuals, was calculated at the plot level and compared between treatments using the same mixed ANCOVA structure as the primary biomass analyses (sections 2.4.1–2.4.2). Control plots were included in this analysis to provide a passive recovery reference point for the broader treatment versus control comparison.

Second, total non-remnant biomass was partitioned into four DBH size classes — 10–20, 20–30, 30–40, and 40–60 cm — to examine at what stem size range treatment differences were concentrated. For each size class, a separate linear mixed-effects model was fitted with treatment as a fixed effect, remnant basal area as a continuous covariate, and block as a random intercept, using the Kenward-Roger approximation for denominator degrees of freedom. Plots with no stems recorded in a given size class were assigned a biomass value of zero for that size class. Size class models were restricted to gap and line plots, as the three available control blocks provided insufficient replication for a reliable three-treatment mixed ANCOVA at the size class level. Both analyses are interpreted as diagnostic and exploratory rather than as primary hypothesis tests.

2.4.5 Outlier and Influential Observation Diagnostics

Model assumptions and the potential influence of outlying observations were assessed using diagnostics appropriate for linear mixed-effects models. The following criteria were evaluated for all models:

Normality and homoscedasticity were assessed through visual inspection of residuals versus fitted and normal Q-Q plots. which indicated that residuals were approximately normally distributed and that variance remained relatively constant across the range of fitted values.

Plot-level outliers were identified by examining standardized residuals at the plot level. Observations exceeding a threshold of $|z| > 2.5$ were flagged as potential outliers but were only considered for exclusion if they represented clear measurement or recording errors. No such errors were identified, and no plots were excluded on this basis.

Block-level influence was assessed via a leave-one-block-out sensitivity analysis, in which each of the 23 blocks was systematically excluded and the model refitted to evaluate whether treatment estimates were disproportionately driven by any single management unit.

2.5 Seedling Performance: Generalized Linear Mixed Models

To address research question four — whether planting format influences planted seedling survival and establishment — outcomes were analyzed using known planting densities derived from project records (gap: 48 seedlings per plot; line: 53 seedlings per plot).

Survival was calculated as the proportion of planted seedlings recorded at measurement. Establishment was defined as the proportion of originally planted seedlings that reached ≥ 10 cm DBH. Establishment among survivors — the proportion of surviving seedlings that reached ≥ 10 cm DBH — was additionally assessed to isolate growth performance from initial survival and is reported in appendix 3.

Treatment differences were tested using generalized linear mixed models (GLMMs) with a binomial error distribution, logit link function, and block as a random intercept:

$$\text{logit}(p) = \text{Treatment} + (1|\text{Block})$$

where p is the probability of success (survival or establishment). The denominators for survival and establishment models were the original planting numbers per plot (gap: $n = 48$; line: $n = 53$). For establishment among survivors, the model structure was identical, but the denominator was the number of surviving seedlings per plot rather than the original planting number.

Overdispersion was assessed using the ratio of Pearson chi-square to residual degrees of freedom, and observation-level random effects were added where overdispersion was detected (ratio > 2.0) following Zuur et al. (2009). Estimated marginal means and pairwise treatment contrasts were computed using the emmeans package (Lenth, 2023), with results back-transformed from the logit scale to the probability scale for interpretation.

2.5.1 The effect of remnant basal area on seedling performance

To address research questions three and four — whether initial site degradation level influences restoration outcomes through interaction with treatment and whether site degradation level modulates planted seedling outcomes — remnant basal area was incorporated as a continuous fixed effect in each of the three binomial GLMMs described in section 2.5 and in the logit-squish linear mixed-effects model for planted biomass contribution described in section 2.4.4. For each outcome — survival, establishment, establishment among survivors, and planted biomass contribution — an additive model including treatment and remnant basal area as fixed effects and block as a random intercept, and an interactive model additionally including the treatment × remnant basal area interaction term, were fitted and compared using AIC. The interactive model was preferred only if its AIC was more than two units lower than that of the additive model (Burnham & Anderson, 2002). Where overdispersion was detected in the additive binomial GLMM (Pearson $\chi^2/df > 2.0$; Zuur et al., 2009), an observation-level random effect was incorporated.

The additive model was retained in all four cases (survival: $\Delta AIC = 90.0$; establishment: $\Delta AIC = 32.7$; establishment among survivors: $\Delta AIC = 1.42$; planted biomass contribution: $\Delta AIC = 6.82$). Establishment among survivors is reported in Appendix 3. All models were fitted using lme4 (Bates et al., 2015), with p-values for linear mixed-effects model fixed effects obtained via the Kenward-Roger approximation, consistent with the primary mixed ANCOVA analyses (sections 2.4.1–2.4.3), and estimated marginal means extracted using emmeans (Lenth, 2023).

3. Results

3.1.1 Primary Biomass Analysis: Linear Mixed ANCOVA

Restoration treatments significantly influenced total aboveground biomass ($F(2, 17.56) = 4.71$, $p = 0.023$). The gap treatment exhibited the highest mean biomass, significantly exceeding the control by 53.9 ± 18.4 Mg/ha ($p = 0.019$). While the line treatment also showed higher mean biomass than the control (+30.4 ± 19.1 Mg/ha), this difference did not reach statistical significance after Tukey adjustment ($p = 0.267$). The ICC for total biomass was 0.339, indicating that 33.9% of the observed variance was attributable to block-level differences.

When the analysis was restricted to natural biomass, the treatment effect did not reach statistical significance ($F(2, 17.81) = 2.93$, $p = 0.080$), with an ICC of 0.390. The contrast between gap and control decreased to +43.3 ± 19.1 Mg/ha ($p = 0.079$). Across all models, remnant basal area was a dominant predictor of biomass, with each 1 m²/ha increase associated with an estimated 11.51 ± 0.63 Mg/ha increase in total biomass ($p < 0.001$).

A complementary model restricted to the 50 active treatment plots confirmed this result, with the gap treatment producing an estimated 23.0 ± 12.8 Mg/ha more biomass than line ($t[16.2] = 1.80$, $p = 0.091$; Appendix 2). The lower ICC in this model (0.29 compared to 0.339 in the primary mixed ANCOVA) is consistent with the geographically separated control blocks contributing disproportionately to block-level variance in the primary analysis.

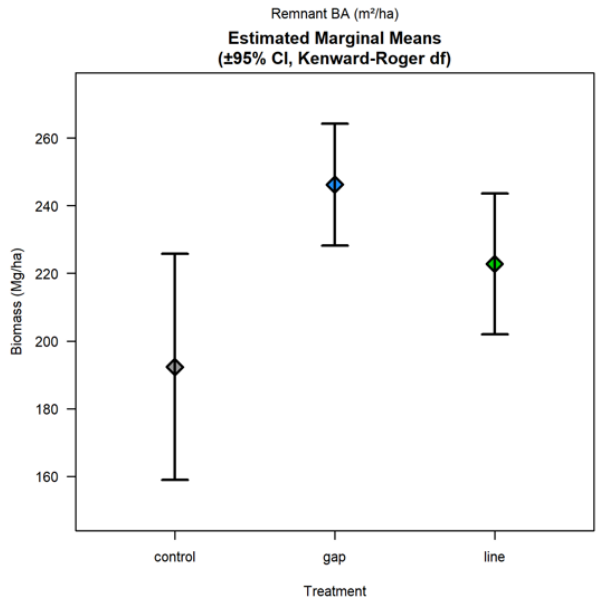

Figure 5: Estimated marginal means of total aboveground biomass (Mg/ha) across restoration treatments, adjusted for remnant basal area. Error bars denote 95% confidence intervals (Kenward-Roger approximation).

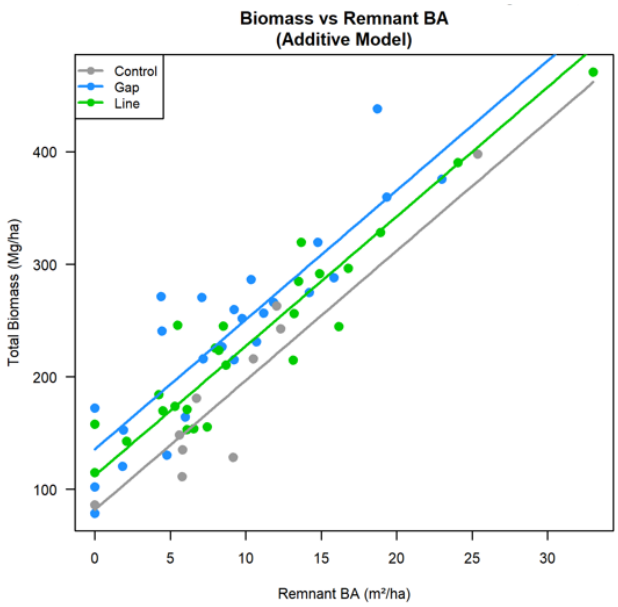

Figure 6: Relationship between remnant basal area (natural stems > 60 cm DBH) and total aboveground biomass across three restoration treatments. Parallel slopes reflect the additive model structure; remnant basal area contributed an estimated 11.51 ± 0.63 Mg/ha per m²/ha increase ($p < 0.001$).

3.1.2 Post-restoration Biomass – Isolating New Growth

When post-restoration biomass — defined as naturally regenerating stems (10–60 cm DBH) plus all planted stems, excluding remnant stems > 60 cm DBH — was used as the response variable, treatment effects were consistent with the primary biomass analysis.

Restoration treatment was a significant predictor of post-restoration biomass ($F(2, 17.7) = 4.41$, $p = 0.028$). The gap treatment produced an estimated 54.6 ± 18.8 Mg/ha more post-restoration biomass than the control ($p = 0.025$), while the line treatment showed a non-significant positive trend relative to the control (+33.8 ± 19.5 Mg/ha, $p = 0.223$). The gap versus line contrast was not statistically significant (20.8 ± 13.7 Mg/ha, $p = 0.307$). Estimated marginal means were 136.9 ± 9.0 Mg/ha for gap, 116.1 ± 10.3 Mg/ha for line, and 82.3 ± 16.6 Mg/ha for control. The ICC was 0.443, indicating that 44.3% of variance in post-restoration biomass was attributable to block-level differences.

Notably, the remnant BA coefficient was effectively zero in the post-restoration model ($\beta = 0.08 \pm 0.64$ Mg/ha per m²/ha, $p = 0.898$), in marked contrast to the strong positive association observed in the total and natural biomass models ($\beta \approx 11.5$–12.0 Mg/ha per m²/ha, $p < 0.001$), confirming that new biomass accumulation was independent of initial site condition when remnant stems are excluded (figure 7).

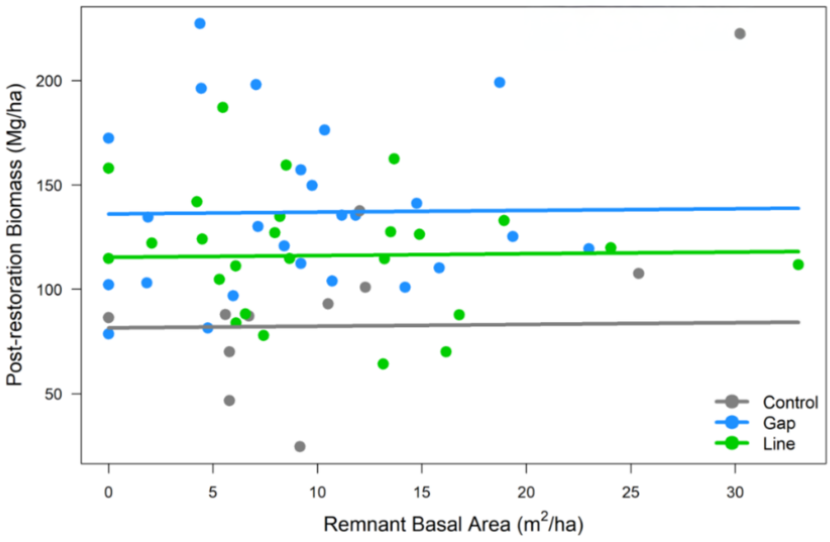

Figure 7: Post-restoration biomass plotted against remnant basal area for gap, line, and control plots. Lines represent population-level model predictions from the primary three-treatment mixed ANCOVA with parallel slopes retained following likelihood ratio test and AIC comparison (p = 0.573, ΔAIC = 2.9). Points represent observed plot-level values.

3.1.3 Non-remnant Dipterocarp biomass and total biomass by size class

The following supplementary analyses address research question two by examining where in the species composition and stem size distribution the treatment differences are concentrated.

Non-remnant dipterocarp biomass was higher in gap plots (51.3 ± 36.0 Mg/ha) than in line plots (39.4 ± 22.5 Mg/ha) and control plots (24.2 ± 18.7 Mg/ha), though no pairwise contrast reached statistical significance (all $p > 0.11$). The high within-treatment variance, particularly in gap plots, likely contributes to the absence of significant pairwise contrasts in this supplementary analysis. Remnant basal area was not a significant predictor of non-remnant dipterocarp biomass $F(1, 46.5) = 0.84$, in contrast to its strong positive effect in the primary mixed ANCOVA analyses.

Size class partitioning revealed that treatment differences in biomass were absent in the 10–20 cm class but increased progressively in larger size classes, with the largest separation observed in the 40–60 cm class (gap: 59.7 ± 26.3 Mg/ha; line: 53.5 ± 25.2 Mg/ha; control: 35.9 ± 16.7 Mg/ha). No individual size class linear mixed-effects model returned a significant treatment effect (all $p > 0.30$), but the directional pattern was consistent across all size classes above 10–20 cm (Figure 8).

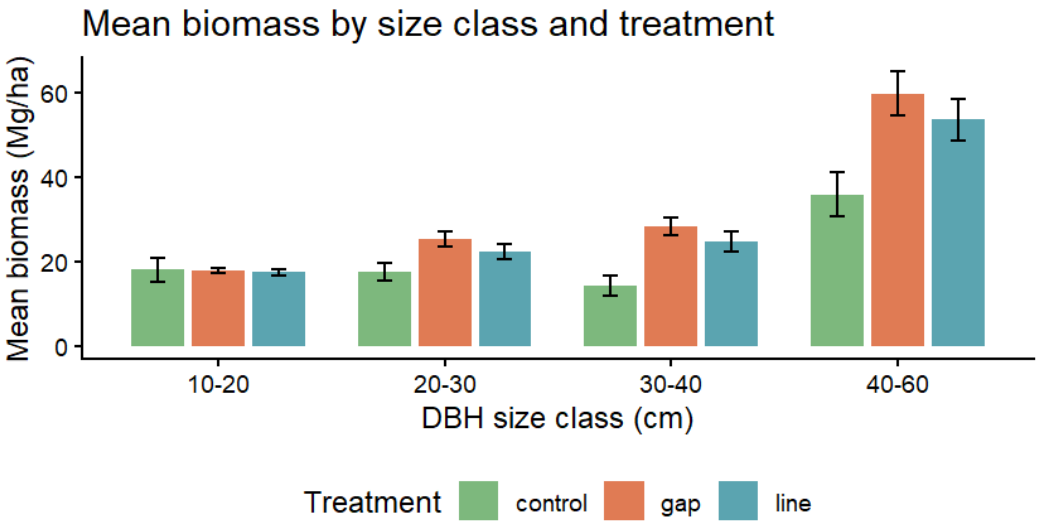

Figure 8: Mean non-remnant aboveground biomass (Mg/ha) by DBH size class and restoration treatment. Bars represent plot-level means and error bars denote ±1 standard error. Non-remnant stems are defined as all naturally regenerating and planted stems below 60 cm DBH. Control plots are included for descriptive reference only and were excluded from formal linear mixed-effects model comparisons due to insufficient block replication (n = 3 blocks).

3.1.4 Outlier and Influential Observation Diagnostics

Diagnostic plots for all models indicated that assumptions of normality and homoscedasticity were sufficiently met. No plots exceeded the standardized residual threshold of $|z| > 2.5$ and no observations were excluded. Full diagnostic output is presented in Appendix 1.

3.2 Seedling Performance: Generalized Linear Mixed Models

The following analyses address research question four — whether planting format influences planted seedling survival and establishment.

Planted seedling survival did not differ significantly between treatments 25 years post-planting (table 1). Gap plots averaged 15.4% survival (95% CI: 9.6–21.9%) compared to 16.3% for line plots (95% CI: 10.4–24.7%; odds ratio = 0.89, $z = -0.34$, $p = 0.734$). Establishment rates (proportion of originally planted seedlings reaching ≥ 10 cm DBH) were similarly low with no significant treatment effect (gap: 7.5%, 95% CI: 4.5–12.2%; line: 9.7%, 95% CI: 5.7–15.9%; odds ratio = 0.76, $z = -0.70$, $p = 0.485$).

Establishment among survivors (the proportion of surviving seedlings reaching ≥10 cm DBH) did not differ significantly between treatments and was unaffected by remnant basal area (p = 0.905 and p = 0.363 respectively), indicating that post-survival growth was not a limiting factor for establishment. Full results are reported in Appendix 3.

Collectively, these results indicate that planting format influenced neither mean survival nor the subsequent growth performance of survivors, suggesting that where establishment occurred, post-survival growth was not the limiting factor.

Table 1: Estimated marginal means (95% confidence intervals) for planted seedling survival and establishment by treatment, from binomial generalized linear mixed-effects models with block as a random intercept. Odds ratios less than 1 indicate lower probability in gap relative to line. Pairwise treatment contrasts are reported in section 3.2.1.

Metric	Gap	Line	Odds Ratio	z	p
Survival (%)	15.4 (9.6-21.9)	16.3 (10.4-24.7)	0.89	-0.34	0.734
Establishment (%)	7.5 (4.5-12.2)	9.7 (5.7-15.9)	0.76	-0.70	0.485

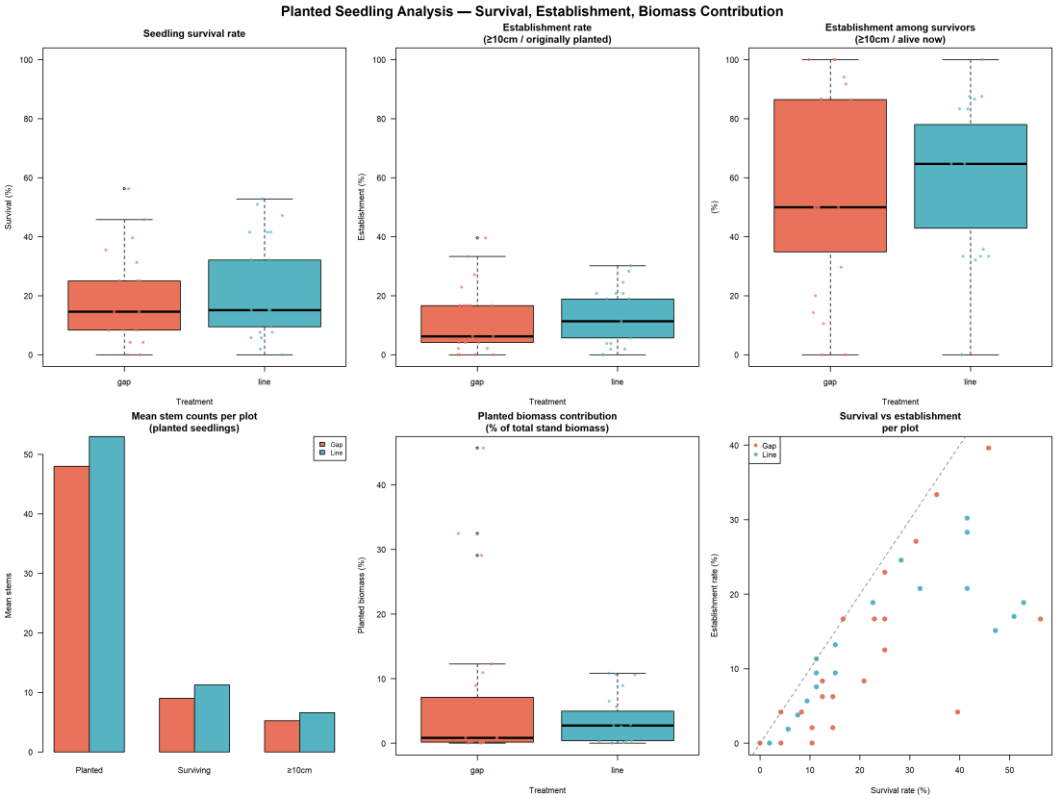

Figure 9: Summary of planted seedling outcomes by treatment. Top row: survival rate, establishment rate, and establishment among survivors. Bottom row: mean stem counts per plot across planting stages, planted biomass contribution, and the relationship between plot-level survival and establishment rates. The dashed line in the bottom right panel represents the 1:1 reference line.

3.2.1 The effect of remnant basal area on seedling performance

The following analyses address research questions three and four — whether initial site degradation level interacts with planting treatment to influence seedling outcomes, and whether site condition modulates individual planted seedling fate independently of planting format.

Remnant basal area was a significant negative predictor of planted seedling survival. The additive model, retained on the basis of substantially lower AIC relative to the interactive model (ΔAIC = 90.0), indicated that survival probability declined with increasing remnant basal area ($\beta = -0.046$, SE = 0.022, $z = -2.07$, p = 0.038; Figure 10). Both gap and line treatments showed this negative relationship, and the treatment contrast remained non-significant after accounting for remnant basal area (odds ratio = 0.83, $z = -0.51$, $p = 0.610$), consistent with the treatment-only model. Survival was overdispersed (Pearson $\chi^2/df = 3.65$) and an OLRE was incorporated in the additive model; because this altered the random effect structure, the additive and interactive models were compared by AIC only.

A comparable pattern was observed for establishment. Remnant basal area negatively predicted the probability of planted stems reaching ≥10 cm DBH ($\beta = -0.032$, SE = 0.013, $z = -2.43$, $p = 0.015$), and the treatment contrast remained non-significant (odds ratio = 0.76, $z = -0.70$, $p = 0.459$). The establishment model was similarly overdispersed (Pearson $\chi^2/df = 2.12$), and the OLRE-corrected additive model was retained by AIC (ΔAIC = 32.7 relative to the interactive model without OLRE). Coefficients from the OLRE-corrected model should be interpreted directionally rather than as precise effect size estimates, given the known sensitivity of OLRE standard errors to the degree of overdispersion; the values reported here are therefore taken from the pre-correction additive model.

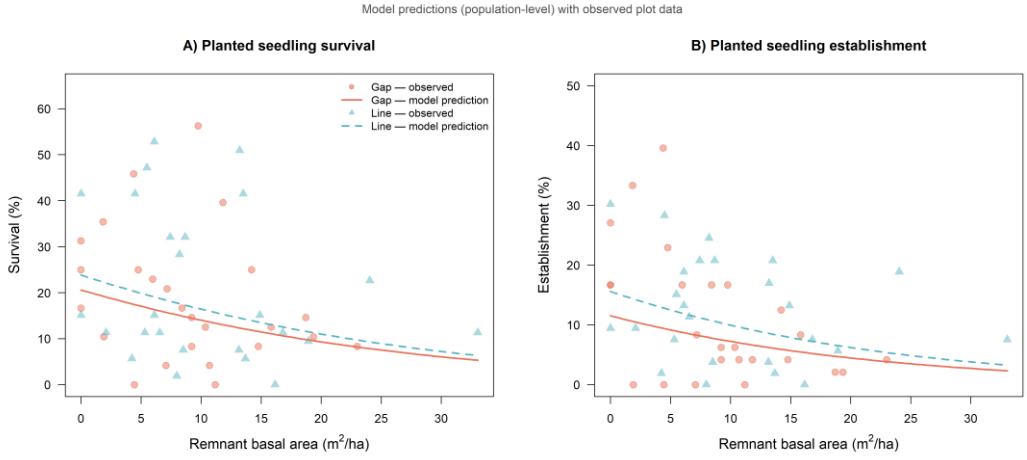

Figure 10: Figure 10. Planted seedling survival (A) and establishment (B) as a function of remnant basal area for gap (circles) and line (triangles) treatment plots. Curves represent population-level predictions back-transformed from the logit scale, with parallel slopes retained following AIC

comparison. Pairwise treatment contrasts and remnant basal area effects are reported in section 3.2.1.

The treatment-only model indicated no significant difference in planted biomass contribution between gap and line plots ($\beta = 0.14$, SE = 0.43, $t(16.0) = 0.32$, $p = 0.749$), consistent with the absence of treatment effects observed across all three seedling outcomes. Across both treatments, planted stems contributed a mean of 5.1% of total stand biomass (gap: 6.5% ± 12.1 SD; line: 3.7% ± 3.5 SD), with the highest contributions observed in plots with low remnant basal area and near-zero contributions at the upper end of the gradient. The contribution of planted stems to total stand biomass declined significantly with increasing remnant basal area ($F(1, 37.22) = 16.48$, $p < 0.001$; figure 11), with a regression coefficient of $\beta = -0.070$ (SE = 0.017) on the logit scale. The additive model was strongly preferred over the interactive model ($\Delta AIC = 6.82$), indicating that both gap and line treatments showed the same rate of decline in planted biomass contribution along the remnant basal area gradient. This result provides stand-level confirmation of the seedling-level pattern: at sites with low remnant basal area, planted stems contributed a greater proportion of total stand biomass, while at sites with high remnant basal area their contribution was negligible.

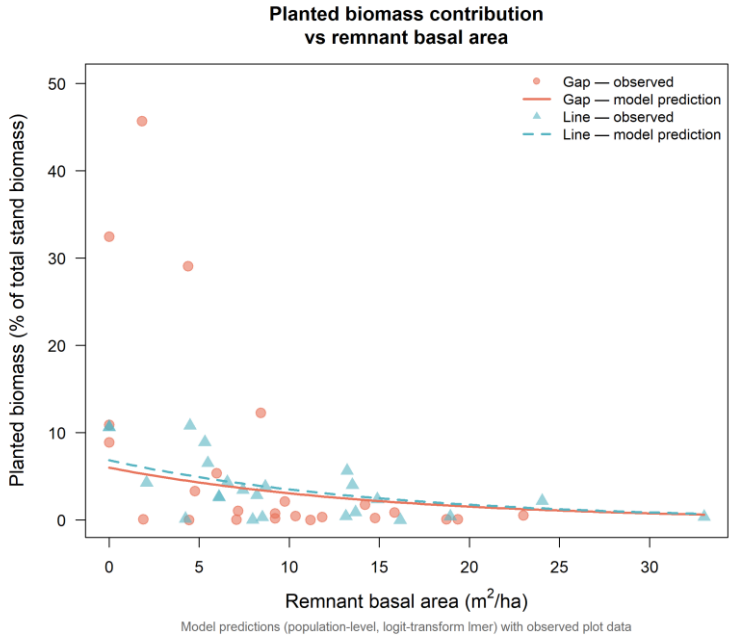

Figure 11: Planted biomass contribution (% of total stand biomass) as a function of remnant basal area for gap (circles) and line (triangles) treatment plots. Curves represent population-level predictions back-transformed from the logit scale, with parallel slopes retained following AIC comparison ($\Delta AIC = 6.82$). Statistical results are reported in section 3.2.1.

Taken together, these results describe a coherent gradient in planted seedling performance across the remnant basal area axis. Survival and establishment declined significantly with increasing remnant basal area, establishment among survivors was unaffected (Appendix 3), and the stand-level contribution of planted material declined strongly along the same gradient, as measured by its

proportional contribution to total biomass. The treatment format did not affect any of these relationships, indicating that the degradation gradient operated independently of the planting method applied.

4. Discussion

4.1 Biomass accumulation and treatment effects

The gap planting treatment produced significantly higher total aboveground biomass than unplanted control plots 25 years after restoration, while the line treatment showed a consistent positive trend that did not reach statistical significance. This pattern held across all three biomass response variables — total biomass, natural biomass, and post-restoration biomass — confirming that gap planting produces a genuine effect on biomass accumulation. The key implication is that active enrichment planting, specifically gap planting, can meaningfully accelerate biomass accumulation in heavily degraded secondary dipterocarp forest relative to natural recovery alone, and enables bypassing the slower early successional stages that characterize passive regeneration in landscapes where natural recruitment has been suppressed by repeated logging and fire (Romell et al., 2008; Axelsson et al., 2024). That this difference remained detectable despite the conservative Kenward-Roger approximation and the limited control replication (n = 3), strengthens rather than weakens confidence in the biological reality of the effect.

The gap versus line difference, while consistent in direction across all models (~20–23 Mg/ha), did not reach statistical significance in any comparison ($p = 0.091$). This should be interpreted cautiously. The high ICC values across models (total biomass: 0.339; natural biomass: 0.390; post-restoration biomass: 0.443) indicate that between a third and nearly half of all variance in stand biomass was attributable to block-level differences rather than treatment, reflecting the considerable site-to-site variation inherent to a landscape-scale restoration project that spans across management units that differ in soil condition, disturbance history, and microclimate. Historical logging often produces patchy soil compaction and nutrient depletion across a landscape (Poorter et al., 2021), meaning that restoration plots in one block may operate under fundamentally different conditions than plots in another, even when initial site condition as measured by remnant basal area is comparable. In this statistical environment — where the treatment signal must be detected through considerable site-level noise — a p-value of 0.091 for a consistent ~23 Mg/ha gap advantage may more plausibly reflect insufficient power than a genuine absence of effect. The Kenward-Roger approximation, while appropriate for this unbalanced design, is deliberately conservative in allocating denominator degrees of freedom, and with only 23 blocks available to estimate block-level variance the effective degrees of freedom for treatment contrasts are inherently limited. A Type II error cannot be excluded, and the contrast between the gap and line treatments warrants continued monitoring as the stands mature.

Several mechanisms may explain the trend toward a gap planting advantage. Concentrated planting within defined canopy gaps may create more favorable irradiance and microclimate conditions for dipterocarp seedling growth compared to the more dispersed corridor structure of line planting, potentially accelerating the growth of individual planted stems in gap plots relative to those in line plots. Gap creation and pioneer suppression through maintenance activities have additionally been shown to improve dipterocarp seedling survival and growth in comparable secondary forests in Sabah (Romell et al., 2008; Axelsson et al., 2012) and may have contributed to the observed increase in stand-level biomass. Although no significant difference in planted biomass contribution was detected between treatments, the combination of equivalent seedling survival and establishment rates alongside a consistently higher mean planted biomass contribution in gap plots (6.5% vs 3.7%) is tentatively consistent with a growth rather than survival advantage for planted material in gap plots, implying that the microsite conditions created or targeted by gap planting may have favored individual stem development rather than seedling survival per se.

The divergence between total and natural biomass results in the primary mixed ANCOVA calls for careful interpretation. The gap treatment effect was significant for total biomass ($F(2, 17.56) = 4.71$, $p = 0.023$) but not for natural biomass alone ($F(2, 17.81) = 2.93$, $p = 0.080$), with the gap vs. control contrast declining from 53.9 ± 18.4 Mg/ha to 43.3 ± 19.1 Mg/ha when planted stems were excluded. This decrease suggests that a meaningful portion of the gap treatment advantage is carried directly by the planted stems themselves rather than solely by enhanced natural regeneration, consistent with the seedling-level findings in section 3.2.1, where planted stem contribution to total biomass declined significantly along the remnant basal area gradient.

Size class partitioning of non-remnant stand biomass provides additional diagnostic insight into the possible mechanisms underlying the gap treatment's superior biomass accumulation, though the results should be interpreted cautiously given that no individual size class LMM returned a statistically significant treatment effect (all $p > 0.30$).

The descriptive pattern of treatment equivalence in the 10–20 cm size class and a progressive gap advantage in larger classes, most pronounced in the 40–60 cm range, is consistent with the interpretation that the gap advantage is concentrated in stems that were planted roughly 25 years ago. Planted dipterocarps established in 1998–2003 would plausibly occupy the 30–60 cm size range by the time of measurement, making the concentration of the gap advantage in this size range consistent with a planted stem contribution mechanism. This interpretation is further supported by a separate analysis of non-remnant dipterocarp biomass, comprising only dipterocarp stems below 60 cm DBH rather than all non-remnant species. In this analysis gap plots showed the highest dipterocarp biomass (51.3

Mg/ha) relative to line (39.4 Mg/ha) and control plots (24.2 Mg/ha), and remnant basal area was not a significant predictor ($F(1, 46.5) = 0.84$, $p = 0.364$), contrasting with its dominant role in the primary biomass models and suggesting that the dipterocarp biomass signal at the stand level is driven by stem size and density rather than by site condition.

The non-significance of the size class LMMs means these patterns cannot be formally confirmed within the current dataset. The high within-treatment variance, particularly in gap plots, limits the power available to detect size-class-specific effects, and this non-significance is consistent with the borderline overall gap versus line result ($p = 0.091$) and the conservative Kenward-Roger approximation that constrained power throughout the primary analyses. The apparent gap and line advantage over control plots in the larger size classes similarly cannot be formally confirmed given the limited control replication ($n = 3$), which rendered control group estimates too imprecise for reliable pairwise comparisons at the size class level. Nevertheless, the directional consistency of the pattern across all size classes above 10–20 cm gives it some credibility as a genuine biological signal rather than random noise, even if formal confirmation requires a larger and more balanced dataset.

A further interpretive caution concerns the gap-cluster planting method, which places stems in locations that mimic natural gap regeneration, making planted individuals spatially less distinguishable from naturally recruiting stems as the stand matures. It is plausible that some larger dipterocarp stems in gap plots classified as naturally regenerating during inventory were in fact planted individuals whose markers had been lost after 25 years of growth. If so, the gap advantage in larger-stem dipterocarp biomass may partly reflect a misclassification artefact rather than a genuine difference in natural regeneration between treatments. This is a possibility that cannot be resolved retrospectively but that underscores the importance of systematic stem tagging in long-term restoration projects. Importantly, if misclassification occurred, it would imply that true planted stem survival and biomass contribution in gap plots are higher than the formal seedling-level analyses indicate, further supporting the planted stem contribution hypothesis, rather than contradicting it.

The gap versus control difference of 43.3 Mg/ha in natural biomass alone, while falling short of statistical significance after Tukey adjustment ($p = 0.079$), represents a biologically meaningful magnitude relative to the 25-year recovery trajectory and may reflect genuine treatment-driven enhancement of natural regeneration that the study was underpowered to detect formally. Recovery of biomass to old-growth levels in secondary tropical forests has been estimated to require more than 12 decades globally (Poorter et al., 2021), and while recovery rates in Sabah may be faster, even moderate treatment-driven acceleration of this trajectory would carry significant implications for long-term carbon sequestration

and biodiversity recovery in the INIKEA landscape. This mirrors findings from a comparable degraded dipterocarp landscape in Sabah, where active restoration through enrichment planting accelerated aboveground carbon recovery by approximately 50% relative to natural regeneration alone, from 2.9 to 4.4 Mg C/ha/year (Philipson et al., 2020).

The dominance of remnant basal area as a predictor of total and natural biomass, which contributed an estimated 11.5 Mg/ha per m²/ha increase ($p < 0.001$), confirms that pre-existing site condition was a far stronger determinant of stand-level biomass than treatment format. This finding is consistent with the broader literature emphasizing the primacy of structural and floristic legacies in driving long-term biomass trajectories in secondary tropical forests (Chazdon, 2014; Poorter et al., 2021), and mirrors findings from a comparable Sabah landscape where the structural legacy of pre-logging conditions was shown to shape tree community composition and biomass recovery over three decades of post-disturbance succession (Hayward et al., 2021). Restoration outcomes in this landscape are therefore as much a function of where planting occurs as of how it is carried out.

The effective disappearance of the remnant basal area effect in the post-restoration models ($\beta = 0.08$ Mg/ha per m²/ha, $p = 0.89$) confirms that the strong remnant basal area association in the total and natural biomass models operates through the standing biomass of remnant stems themselves rather than through any legacy facilitation of new growth. When the direct contribution of remnant stems is removed from the response variable, site degradation level shows no significant association with new biomass accumulation. Rather than indicating an absence of facilitation, this null result supports a compensatory dynamic in which facilitation of natural regeneration at high remnant basal area sites is offset by competitive suppression of planted stems — producing a near-zero net effect on total new biomass accumulation across the degradation gradient that will be developed further in the following section.

4.2 Seedling performance and the remnant basal area gradient

The survival and establishment of planted seedlings were low across both treatments after 25 years, with mean survival rates of approximately 15–17% and establishment rates of 8–10% of originally planted stems. While these figures may appear modest, they are broadly consistent with long-term planted seedling attrition reported in other tropical restoration studies, where post-planting mortality commonly exceeds 50% within the first several years even under favorable conditions (Shono et al., 2007; Holl & Aide, 2011), and with survival trajectories documented across the full operational timeline of the Sow-A-Seed project itself (Axelsson et al., 2024). The proportion of planted stems reaching

canopy-relevant size thresholds over decadal timescales is similarly low across comparable restoration contexts (Axelsson et al., 2024; Schubert et al., 2025). In the context of heavily degraded dipterocarp forest, where abiotic stress, herbivory, and competition from pioneer vegetation impose persistent constraints on seedling recruitment, survival rates in this range may reflect the inherent difficulty of establishing planted material rather than a failure of the restoration approach.

No significant difference in survival, establishment, or establishment among survivors was detected between gap-cluster and line planting formats. This null result is consistent across all three metrics and indicates that the spatial arrangement of planted stems did not confer any measurable advantage to individual seedling fate over the 25-year study period. The result is perhaps unsurprising given that both formats introduced the same species mix into broadly comparable site conditions, and that the distinctions between gap-cluster and line planting are primarily structural, relating to spatial configuration and density, rather than to the identity or quality of planted material. Any initial microsite differences created by the two planting formats, such as differences in local light availability or soil disturbance, may have become negligible as the surrounding vegetation developed over the course of 25 years. The absence of a treatment-effect on individual seedling fate stands in apparent contrast to the stand-level finding that gap planting produced significantly greater total biomass than untreated control plots. This contrast points to an important distinction between the performance of planted individuals and the broader ecological effect of the planting intervention. If planted seedlings in gap and line plots survived and established at equivalent rates, then the biomass advantage observed in gap plots cannot be attributed primarily to the planted material itself, directing attention toward processes beyond individual seedling fate as the more likely drivers of stand-level differences between treatments.

The negative relationship between remnant basal area and planted seedling survival and establishment is consistent with a competitive inhibition mechanism operating at the individual stem level. Planted seedlings introduced into plots with dense legacy canopy faced greater competition for light and potentially below-ground resources from established remnant stems, reducing both their probability of surviving and, among those that survived, their probability of reaching the ≥10 cm DBH threshold within the 25-year study window. This interpretation aligns with findings from enrichment planting studies in comparable secondary dipterocarp forests in Sabah, where dense pioneer canopy has been shown to reduce light availability and suppress the survival and growth of planted dipterocarp seedlings (Romell et al., 2008), and with the broader literature documenting competitive suppression of introduced propagules by residual canopy in enrichment planting contexts (Shono et al., 2007).

Importantly, this competitive inhibition at the seedling level does not translate into reduced stand-level biomass accumulation at high remnant basal area sites. The post-restoration biomass models demonstrated that total new biomass, comprising natural regeneration and planted stems, was independent of initial remnant basal area, suggesting a compensatory dynamic across the degradation gradient. One plausible explanation is that at sites with high remnant canopy density, the structural legacy of the pre-disturbance forest facilitates natural regeneration — potentially through seed dispersal, modified microclimatic conditions, or other facilitation pathways — offsetting the reduced contribution of planted material. At low remnant basal area sites, planted seedlings survived and established at higher rates (section 3.2), contributed a greater proportion of total stand biomass (section 3.2.1), and natural dipterocarp regeneration may have been more limited, consistent with reduced seed source availability at the most heavily degraded sites.

The two pathways of stand development thus appear to partially offset each other, but the mechanisms underlying this compensation and the degree to which it produces consistent outcomes across the gradient cannot be established without direct measurement of natural regeneration dynamics.

These patterns cautiously suggest that remnant basal area may serve as a useful screening criterion for prioritizing active planting interventions. At sites with low remnant basal area, below roughly 5–7 m^2/ha, where the present data indicate both higher planted seedling survival and steeper biomass contributions from planted material, active planting appears to supplement natural regeneration in a way that contributes meaningfully to stand development. At sites with higher remnant basal area, particularly above 15–20 m^2/ha, planted seedling survival was consistently low, planted biomass contributions were minimal, and total new biomass accumulation was comparable to that of untreated control plots after accounting for remnant structure. This raises the possibility that management resources at such sites could be more effectively directed toward protecting and facilitating natural regeneration, for example through invasive species control, wildlife exclusion, or enrichment with propagules of target species known to establish in partial shade, rather than toward large-scale planting programs. However, this inference rests on observational data from a single restoration system and should be regarded as exploratory. Formal threshold identification would require an experiment stratifying planting treatments across a controlled degradation gradient, with unplanted controls at each level of initial canopy cover.

The high variance in planted biomass contribution observed in the gap treatment (SD = 12.1% relative to a mean of 6.5%) warrants some interpretive caution. This variance was driven primarily by a small number of gap plots at near-zero remnant basal area that showed exceptionally high planted biomass proportions — up to 46% of total stand biomass — likely reflecting the combined

effect of low competition from remnant stems and relatively high planted seedling survival at the least degraded end of the gradient. The line treatment showed considerably lower variance (SD = 3.5%), reflecting a more consistent and modest planted biomass contribution across the full remnant basal area range. This asymmetry may partly reflect the clustered spatial arrangement of gap planting, in which seedlings within each cluster share the same microsite and are subject to correlated fate — a single unfavorable gap producing wholesale cluster failure, a favorable one producing disproportionately high local survival. The modest difference in planting density between treatments (53 vs. 48 seedlings per plot) may contribute additionally, though this effect is likely secondary. Taken together, these structural features of gap planting suggest it may be an inherently higher-variance strategy. Whether this translates into a systematic advantage at low remnant basal area sites remains uncertain given the limited number of such plots and the absence of a significant treatment × remnant basal area interaction, but it suggests that the choice between planting formats may carry higher practical stakes at the least degraded end of the gradient than the mean-level analysis alone implies.

Several methodological constraints limit the strength of inferences drawn from the seedling analyses. The identification of planted individuals during field inventory presents a potential source of differential detection error between gap-cluster and line planting formats. Line-planted stems follow a predictable spatial arrangement that may facilitate systematic identification, whereas gap-cluster planting was designed to emulate natural regeneration, potentially making the spatial arrangement of planted stems less distinct from naturally regenerating individuals as the stand matured. If planted stems in gap plots were more frequently misclassified as natural regeneration during inventory, the survival and establishment count for gap plots would be systematically underestimated relative to line plots. The survival gradient across the remnant basal area axis is less susceptible to this bias, as it appears consistently across both treatments and relies on the count of living stems rather than on their correct classification. Nonetheless, the absolute survival and establishment figures reported here should be interpreted with this caveat in mind.

4.3 Limitations and future directions

A number of broader limitations of this study warrant consideration.

The study design was developed in response to logistical constraints that precluded the originally planned experimental comparison, and the observational nature of the resulting design reflects the practical realities of conducting research within an operational restoration project. The most consequential of the resulting limitations is the limited replication of the control group (n = 3 plots across 3 blocks), which substantially constrained the statistical power of treatment

comparisons involving the control and increased the risk of Type II error in borderline contrasts such as the line vs. control comparison ($p = 0.267$) and the natural biomass treatment effect ($p = 0.080$). While the Kenward-Roger approximation appropriately accounts for this imbalance, it cannot compensate for the fundamental information deficit that three control plots represent in a landscape as heterogeneous as the INIKEA project area.

The high block-level ICC values (0.29–0.44) further underscore this limitation: with nearly a third to nearly half of all biomass variance attributable to site-level differences among administrative blocks, the effective sample size for treatment comparisons is considerably smaller than the plot count suggests. A structural limitation of the study design is the geographic separation of control blocks from active treatment blocks, located approximately 5 km northeast of the gap and line plots. While remnant basal area did not differ significantly between treatment groups and site conditions are broadly comparable across the project area, this separation introduces the possibility of undetected environmental differences not captured by the covariate, and should be noted when interpreting treatment vs. control contrasts. Future studies in comparable landscapes would benefit from a more balanced allocation of control plots across the full range of site conditions represented by the block structure, ideally distributed across the same geographic area as the active treatment plots.

All biomass estimates derive from a single measurement campaign conducted approximately 25 years post-intervention, meaning that the trajectory of biomass accumulation over time cannot be assessed. It is plausible that the gap advantage strengthens as planted crowns expand and gap-level canopy closure becomes increasingly complete, or alternatively that the two active treatments converge as natural regeneration catches up under closed-canopy conditions. Long-term monitoring of the Sow-A-Seed project indicates that annual planted seedling mortality was highest in the first three years before declining substantially in subsequent decades (Axelsson et al., 2024), suggesting that planted stem losses had largely stabilized by the time this study was conducted. This mortality pattern does not resolve whether stand-level biomass accumulation between gap and line formats will converge or diverge as stands continue to mature. Long-term, site-specific biomass monitoring is required to distinguish between these scenarios.

A related constraint is that the breakdown of treatment effects into contributions from planted material versus facilitated natural regeneration rests on indirect inference from model comparisons across response variables rather than on direct measurement of natural regeneration dynamics. Without plot-level data on natural recruitment rates, seed rain, or understory light conditions, the compensatory role attributed to natural regeneration at high remnant basal area sites cannot be confirmed, and the relative contributions of the two pathways to the observed gap advantage remain uncertain. Longitudinal plot-level monitoring

of natural regeneration alongside planted stem tracking would be required to resolve this question directly. Separately, a direct analysis of planted stem size distribution across the remnant basal area gradient was beyond the scope of this study but would provide more rigorous confirmation of the planted stem contribution mechanism proposed here.

The use of remnant basal area as a proxy for site degradation captures only one dimension of what is likely a multifaceted site condition gradient. The species composition, structural complexity, and health of remnant trees vary considerably across plots but are not captured by basal area alone, and this unmodelled variation likely contributes to the residual block-level variance reflected in the ICC.

Uncertainty in the allometric equation represents an additional source of error. The Ketterings et al. (2001) equation was developed for mixed secondary forests in Sumatra and may not perfectly capture the allometric relationships of dipterocarp-dominated stands in Sabah. Systematic bias would affect all plots equally and therefore would not distort treatment comparisons, but it does introduce uncertainty into the absolute biomass estimates and limits direct comparison with studies using alternative allometric approaches. It is worth noting that the non-linear structure of the allometric equation means that any deviation from the true allometric relationship is amplified at larger DBH values. Given that planted dipterocarps after 25 years of growth are expected to occupy the 30 to 60 cm size range, biomass estimates for this size class may be disproportionately affected by any discrepancies in the allometric relationship, and the true planted stem contribution may be somewhat larger than reported here. Species-specific allometric equations incorporating wood density variation would improve absolute biomass precision but are unlikely to alter treatment comparison conclusions given the broadly comparable species composition across treatments.

The identification of planted stems in the field introduced measurement uncertainty that is difficult to quantify. After 25 years of growth some planted individuals may have been misidentified as naturally regenerating stems, and vice versa. This misclassification risk is asymmetric and would tend to underestimate the true survival and establishment rates, as well as the planted biomass contribution. As discussed in section 4.1, if misclassification was more prevalent in gap plots due to the spatial design of gap-cluster planting, the true planted stem contribution in gap plots may be systematically higher than reported, with implications for the interpretation of both the seedling-level null result and the stand-level biomass advantage.

5. Conclusions

This study evaluated 25-year outcomes of gap-cluster and line enrichment planting at the INIKEA restoration project in Sabah, Malaysian Borneo, against untreated control plots across a gradient of initial site degradation. Four research questions were addressed.

Gap planting produced significantly greater total aboveground biomass than untreated control plots ($p = 0.019$), and this advantage was robust across all three biomass response variables — total biomass, natural biomass, and post-restoration biomass. Line planting showed a consistent positive trend relative to controls that did not reach statistical significance. The gap versus line difference of approximately 23 Mg/ha was similarly non-significant ($p = 0.091$), though the high block-level variance, limited control replication, and conservative Kenward-Roger approximation suggest that a Type II error cannot be excluded.

The gap treatment advantage is consistent with a combination of direct planted stem contribution and compensatory natural regeneration dynamics across the degradation gradient. Size class partitioning and non-remnant dipterocarp biomass analyses indicate that the gap advantage is concentrated in the 30–60 cm size range consistent with 25-year-old planted stems, while treatment differences are absent in the smallest size class where recent natural recruits dominate. At low remnant basal area sites, planted stems contributed more directly to stand development; at high remnant basal area sites, natural regeneration compensated for reduced planted stem establishment, producing relatively consistent total biomass accumulation across the gradient.

The effectiveness of planting treatments relative to untreated controls did not vary significantly with initial site degradation, though this possibly reflects the limits of statistical power as much as a genuine absence of effect modification.

Planting format did not influence individual planted seedling survival or establishment indicating that the spatial arrangement of planting conferred no measurable advantage to individual stem fate over the 25-year study period.

Remnant basal area was the strongest predictor of total and natural biomass, underscoring that restoration outcomes in this landscape are as much a function of where planting occurs as of how it is carried out. The contrasting effects of remnant basal area on individual planted stems versus stand-level biomass accumulation — suppression at one scale, compensation at the other — highlight how structural legacies of past disturbance shape restoration trajectories as powerfully as the active interventions applied to overcome them. The data tentatively suggests that remnant basal area may serve as a practical screening criterion for prioritizing active planting interventions, with the marginal value of planting greatest at severely degraded sites where natural regeneration capacity is most constrained.

The finding that gap planting produced a significant and sustained biomass advantage over passive recovery after 25 years in degraded dipterocarp forest landscapes in Sabah adds to a growing body of site-specific evidence that active enrichment planting can deliver measurable ecological returns in landscapes where natural successional processes have been severely disrupted. As global commitments to forest restoration scale up, the need for long-term, site-specific, treatment-level evidence from operational restoration projects become increasingly acute. The INIKEA project, and studies like this one, represent the kind of field evidence required to move restoration planning from general principles toward site-informed, ecologically grounded intervention design.

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Restoring Borneo’s Rainforests: The Right Strategy in the Right Place

Tropical forests cover only a small fraction of Earth's surface yet harbor more than half of all species on the planet. They support the livelihoods of hundreds of millions of people, regulate rainfall, and store large quantities of carbon. Despite this they are disappearing at an alarming rate globally, being cleared in favor of agriculture, degraded by logging, and ravaged by fire. To counter this, governments and organizations across the world have committed to restore millions of hectares of degraded forests over the coming decades.

However, committing to restore is not equivalent to successful restoration. In degraded tropical forests where natural regeneration has been severely constrained by logging and fire, active planting of native trees is often needed to enable and accelerate recovery. Yet the long-term effectiveness of different planting strategies remains poorly understood.

The INIKEA restoration project, established in 1998 in Sabah, Malaysian Borneo, offers a rare opportunity to address this. As one of the longest-running tropical restoration projects in the world it has planted approximately five million native tree seedlings across 18,500 hectares of severely degraded forest using two strategies — line planting, where seedlings are planted at regular intervals along cleared strips, and gap-cluster planting, where seedlings are introduced into existing or created canopy gaps to mimic natural forest regeneration.

This thesis evaluated the outcomes of these strategies 25 years after planting, measuring forest biomass accumulation and planted seedling performance. Two major findings emerged.

First, gap-cluster planting produced significantly more biomass than plots left to recover without intervention, approximately 54 additional tonnes per hectare after 25 years.

Second, the condition of the forest at the time of planting matters as much as the choice of strategy. At severely degraded sites planted seedlings established well and contributed directly to recovery. At less degraded sites natural regeneration compensated for reduced planting success, producing comparable recovery through a different pathway.

In short, gap-cluster planting is the more effective restoration format, but its value depends on where it is applied. At severely degraded sites active planting delivers clear and measurable returns. At structurally intact sites natural regeneration may suffice. As global restoration commitments scale up, knowing both where and how to plant is essential.

Acknowledgements

Thank you to my supervisor Ulrik Ilstedt for giving me the opportunity to perform this research, and for your invaluable guidance along the way.

Thank you to my assistant supervisors, Petter Axelsson and Arvid Lindh, for your support and constructive feedback and for playing a vital role in the set up of the field work on site back in February 2025.

Thank you, all field staff in INIKEA, without your expertise and tenacity, the field work would not have been possible.

Thank you, Adrien Lamodière, without you the field work would not have been half as fun, nor half as memorable. Good times.

In addition, I would like to thank the SLU statistic support for their key input concerning statistical matters.

Parts of the statistical analysis and R code development were aided by the use of Claude, an AI assistant developed by Anthropic. All analytical decisions, interpretations and conclusions remain entirely my own.

Appendix 1 – Diagnostic plots and outlier analysis

Visual inspection of the diagnostic plots indicated that the final models met the fundamental assumptions of linear mixed-effects modeling.

The residuals vs. fitted plot for the three-way model showed a random distribution of residuals around zero with no systematic patterns or evidence of heteroscedasticity, though a slight downward trend in the scale-location plot at higher fitted values suggests mild variance reduction at the upper end of the biomass range. This is noted as a minor deviation but is not considered to materially affect the validity of the model inferences.

The normal Q-Q plot demonstrated that residuals closely followed the theoretical line through the central range, with only minor deviation at the tails, indicating that the assumption of normally distributed error terms was reasonably satisfied.

The residuals-by-treatment panel indicated that variance was relatively consistent across control, gap, and line groups, with no systematic differences in residual spread between treatments. One observation with a residual of approximately +65 Mg/ha was visible across several diagnostic panels and was evaluated against the standardized residual threshold of $|z| > 2.5$. This observation did not exceed the threshold and was retained in the final analysis.

Diagnostic plots for the gap vs. line model indicated broadly similar patterns. The scale-location plot showed more stable variance across the fitted range compared to the three-way model, and no observations exceeded the standardized residual threshold of $|z| > 2.5$. The residuals-by-treatment panel indicated greater spread in the line group relative to gap, driven by two observations in the upper tail, though neither exceeded the exclusion threshold and both were retained in the final analysis.

Collectively, these diagnostics indicated that model assumptions were sufficiently met to proceed with inference.

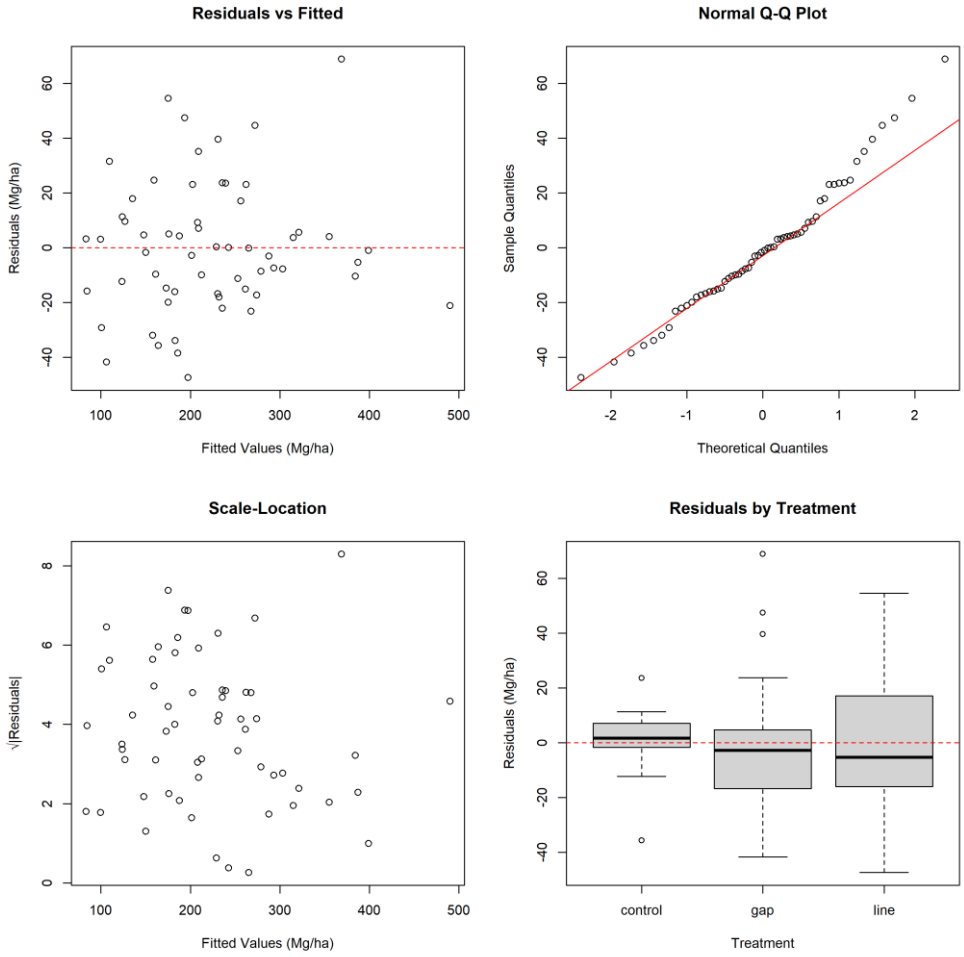

Figure 12: Diagnostic plots for the three-way linear mixed-effects model (total aboveground biomass). Top left: residuals vs. fitted values. Top right: normal Q-Q plot. Bottom left: scale location plot. Bottom right: residuals by treatment group.

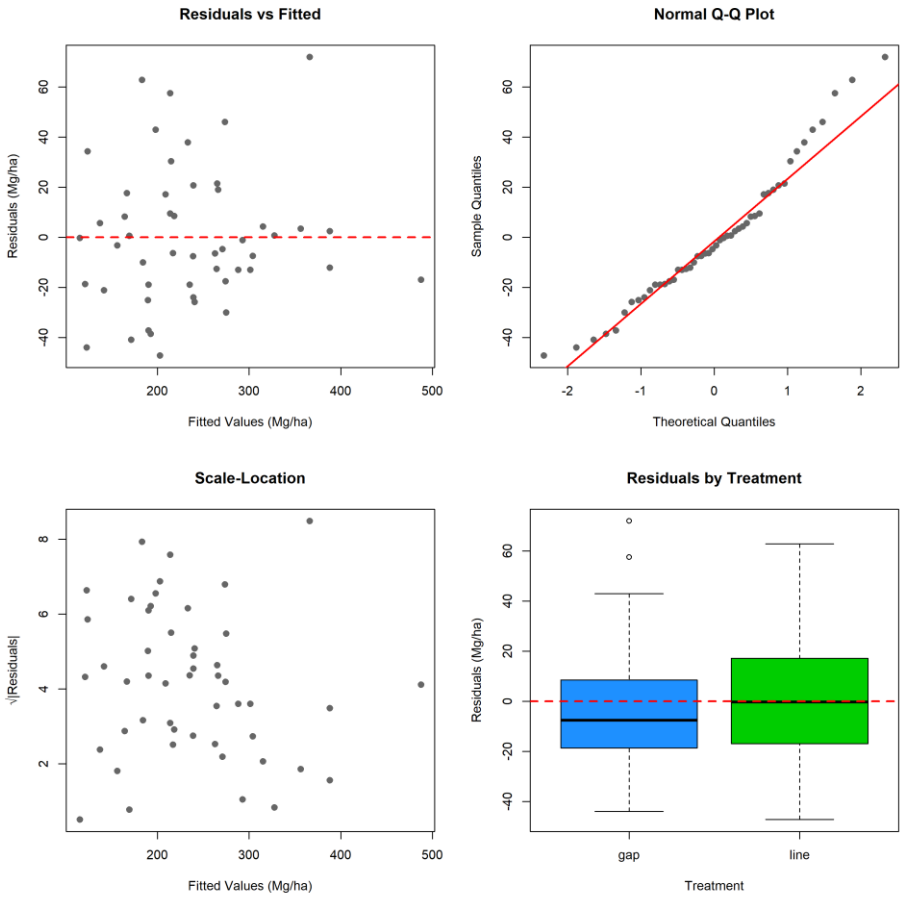

Figure 13: Diagnostic plots for the gap vs. line linear mixed-effects model (total aboveground biomass). Top left: residuals vs. fitted values. Top right: normal Q-Q plot. Bottom left: scale-location plot. Bottom right: residuals by treatment group.

Appendix 2 – Gap vs. line two-treatment mixed ANCOVA

After accounting for remnant BA and block-level clustering, the gap treatment produced an estimated 23.0 ± 12.8 Mg/ha more total biomass than the line treatment, though this difference was not statistically significant at the conventional threshold (t[16.2] = 1.80, $p = 0.091$).

Remnant BA remained a highly significant predictor of total biomass, contributing an estimated 11.35 ± 0.75 Mg/ha per unit increase in basal area ($p < 0.001$). The ICC was 0.29, indicating that 29% of the variance in stand biomass was attributable to block-level differences.

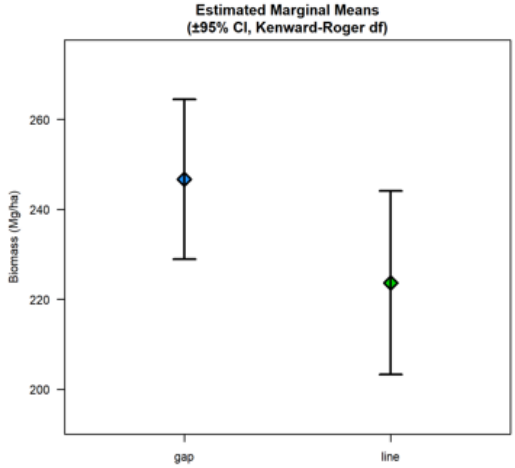

Figure 14: Estimated marginal means of total aboveground biomass (Mg/ha) for gap and line treatments, adjusted for remnant basal area. Error bars denote 95% confidence intervals (Kenward-Roger approximation). The gap treatment (246.2 ± 8.86 Mg/ha) produced higher mean biomass than the line treatment (223.2 ± 10.12 Mg/ha), though the difference did not reach statistical significance (p = 0.091).

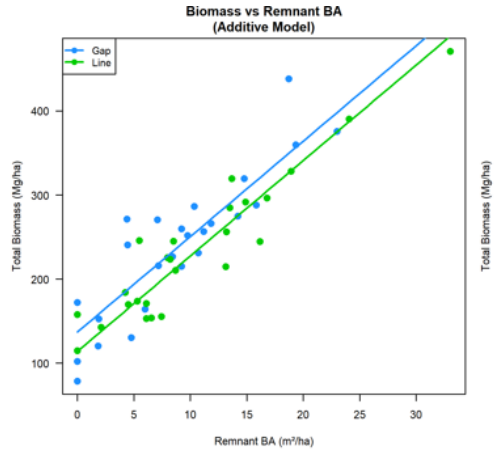

Figure 15: Relationship between remnant basal area (natural stems > 60 cm DBH) and total aboveground biomass for gap and line treatments. Parallel slopes reflect the additive model

structure; remnant basal area contributed an estimated 11.35 ± 0.75 Mg/ha per m²/ha increase ($p < 0.001$).

Appendix 3 – Establishment among survivors

Among plots in which at least one seedling was recorded as surviving (23 gap plots, 24 line plots), approximately 62% of surviving seedlings had reached ≥ 10 cm DBH, with no significant difference between treatments (gap: 61.5%, 95% CI: 43.1–77.1%; line: 63.7%, 95% CI: 43.4–80.1%; odds ratio = 0.91, $z = -0.17$, $p = 0.868$).

For establishment among survivors, no overdispersion was detected (Pearson $\chi^2/df = 0.96$) and the additive and interactive models were directly comparable by likelihood ratio test. Neither the LRT ($p = 0.064$) nor AIC (ΔAIC = 1.42) provided support for a treatment × remnant basal area interaction, and the additive model was retained. Under the additive model, remnant basal area was not a significant predictor of establishment among survivors ($\beta = 0.021$, SE = 0.023, $z = 0.91$, $p = 0.363$), and the treatment contrast remained non-significant ($p = 0.905$). This indicates that once a planted seedling survived, its probability of reaching ≥10 cm DBH was unrelated to the surrounding remnant canopy density.

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