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3 **Restoration method influences spatial patterns of tree seedling and sapling recruitment in**
4 **the second decade of tropical forest recovery**

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27 Karen D. Holl: initial design, data collection, first draft, revision of drafts. Rakan A. Zahawi:
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29 plant identification. Juan A. Rosales: data collection and plant identification. Spencer C.
30 Schubert: data analysis, first draft, revision of drafts.

31
32 **DATA AVAILABILITY STATEMENT**

33 The data and code necessary to reproduce our analyses can be found on Dryad:
34 <https://doi.org/10.5061/dryad.s7h44j1gc>.

ABSTRACT

AIMS: Fine scale floristic heterogeneity is a hallmark of mature tropical forests. Restoring such patterns in degraded habitats should produce more resilient and biodiverse systems, yet these end-goals are rarely compared across multiple restoration scenarios. We analyzed fine scale spatial tree recruitment patterns in a long-term tropical forest restoration experiment.

LOCATION: Coto Brus county in southern Costa Rica, 1100–1430 m above sea level.

METHODS: We censused seedlings and saplings in 26 experimental restoration plots (0.25 ha) after 16-18 years and six reference forests. Restoration treatments included: (1) plantation - four tree species planted in rows; (2) applied nucleation - six tree nuclei of varying sizes planted with the same four species; and (3) natural regeneration – no trees planted. In 2022, we censused all tree stems ≥ 20 cm and mapped each to 3×3-m grid cells.

RESULTS: Mean local species density of seedlings (per 6×6-m quadrat) was significantly greater in plantation (10.9; 95CI = 10.0–11.9) and applied nucleation (8.4; 95CI = 7.7–9.3) than in natural regeneration subplots (5.0; 95CI = 4.5–5.5), as the latter commonly had quadrats with no recruits. Within-plot Bray-Curtis dissimilarity was highest in natural regeneration, intermediate in applied nucleation, and lowest in plantations. Differences arose primarily from variation in seedling abundance, rather than species turnover but did not differ in sapling communities. Recruits of large-seeded, later-successional species were significantly less clustered and established more frequently in plot interiors of planted treatments compared to natural regeneration.

CONCLUSIONS: After nearly two decades, the extent of initial planted trees did not substantially influence the fine scale heterogeneity of recruit community composition beyond spatial variation in seedling density. However, both applied nucleation and plantation restoration approaches resulted in a more even spatial distribution large-seeded recruits, highlighting the importance of tree planting for facilitating the recovery of dispersal-limited species.

66 **Keywords:** applied nucleation, fine scale diversity, floristic heterogeneity, restoration, spatial
67 patterning, tropical forests

1. INTRODUCTION

As global demand for restoration initiatives to address climate and biodiversity crises reaches all-time highs, tropical forests remain a major opportunity with an estimated 215 million hectares across more than 30 countries supporting the necessary biophysical conditions for tropical forests to recover (Williams et al. 2024). A large body of research demonstrates that approaches ranging from natural regeneration to tree planting can result in recovery of species richness, biomass, and ecosystem functions, though the extent of recovery varies greatly depending on past land use history and availability of propagules in the surrounding landscape (Rozendaal et al. 2019; Romanelli et al. 2022). Yet, the conservation value of tropical forest restoration is handicapped by the time needed to recover complex communities resembling mature forests. Even under favorable conditions succession can take over a century to recover the diversity observed in mature systems (Elsy et al. 2024), and the biotic composition of many such forests is largely distinct from the pre-Anthropocene state (Lugo et al. 2020). Long-term monitoring data are essential to understanding the tradeoffs of different restoration interventions on later stages of forest community assembly, which are necessary to guide the growing demand on decision makers to apply these measures at scale (Werden et al. 2024).

Fine scale heterogeneity is one of the hallmarks of biotic diversity in mature tropical forests, where subtle, local variation in seed rain, light availability, moisture, and soil nutrients have a strong bearing on regeneration dynamics (Nicotra et al. 1999; Uriarte et al. 2018). Feedbacks between local floristic and microenvironmental variation further maintain species diversity, both by presenting a broader array of niches for species establishment (Yasuhiro et al. 2004) and through reduced likelihood of competitive exclusion (Chesson 2000). Despite the fundamental importance of heterogeneity in promoting the assembly of complex communities, many restoration actions inadvertently impede its development to the point of inhibiting biodiversity recovery (Larkin et al. 2016; Holl et al. 2022). For example, planting trees in systematically spaced grids in managed rotation cycles can rapidly recover biomass and canopy structure, but such plantations often result in uniform abiotic conditions that limit species richness of new recruits in the understory (Brockhoff et al. 2008; de Oliveira et al. 2019). Furthermore, in tropical regions, forests are often restored in land where prior agricultural uses have homogenized small scale topographic and soil nutrient differences (Silver et al. 2000), making it is nearly impossible to restore fine scale abiotic variability.

Seed dispersal strongly limits community assembly during tropical forest succession (Finegan 1996), as up to 90% of tree species are dispersed by frugivorous vertebrates in neotropical forests (Jordano 2000). Seed disperser movement in human-modified landscapes is highly dependent on tree canopy cover (Reid et al. 2021). The most abundant seed dispersers transiting through agricultural landscapes with fragmented forests primarily transport tree species with relatively small seeds and pioneer life history traits (de la Peña-Domene et al. 2014; Emer et al. 2018). By contrast, large-seeded trees typical of mature forests can take decades or more to be detected in secondary forests, and seed dispersal is often concentrated close to remnant seed sources at the edge of recovering areas (Vespa et al. 2014; Zahawi et al. 2021).

Likewise, a host of factors can inhibit seedling establishment and growth in former agricultural lands (Holl 2017). Early seedling establishment is often limited by competition with aggressive pasture grasses or ferns, which compete for light, nutrients, and moisture and emit allelopathic chemicals (Dos Santos Rabelo et al. 2023; Maidana-Tuco et al. 2025). As the tree canopy develops, ongoing competition for resources, particularly light in moist tropical forests, affect seedling growth rates and, in turn, transition from the seedling to sapling stages (Dupuy and Chazdon 2006; Rüger et al. 2012).

Active restoration through tree planting facilitates regeneration by creating vegetation structure that both attracts seed dispersers and modifies microenvironments (e.g., shade, understory cover). However, numerous studies have demonstrated how tropical tree plantations often harbor relatively depauperate frugivore communities and seedling banks (Barlow et al. 2007; Simões et al. 2024). Moreover, planting and maintaining large numbers of trees for the first couple of years until they have overtopped grasses can be expensive (Busch et al. 2024), and as the scale forest restoration increases seed and seedling sources increasingly constrain planting efforts (Bosshard et al. 2021). As a result, spatially patterned planting designs (i.e., planting in clusters or strips), are becoming an increasingly attractive approach to restoration (Shaw et al. 2023; Holl et al. 2024). Tropical forest succession typically occurs in patches or nuclei with disproportionate seed dispersal and growth occurring around isolated trees (Schlawin and Zahawi 2008; Derroire et al. 2016). This progressive regeneration around nuclei has the potential to produce spatially heterogeneous community assembly by diversifying recruitment niches both temporally and spatially. Applied nucleation (i.e., planting tree nuclei) has been suggested as an approach to produce greater fine scale habitat heterogeneity and promote a more diverse

assembly of recruits dispersing to and establishing in restoration sites (Corbin and Holl 2012). However, comparing spatial patterns across restoration strategies requires replication of paired treatments and comprehensive survey data, which are rarely available.

We used complete census data from restored tropical forests in the second decade of recovery to assess spatial patterns of tree recruitment under three restoration approaches: natural regeneration (no planting), applied nucleation (planting tree clusters/nuclei), and plantation (planting entire areas in rows). We previously reported that both applied nucleation and plantation restoration methods result in greater seedling and sapling richness compared to natural regeneration with plantations having greater relative abundances of taxa with large, animal-dispersed seeds characteristic of later successional environments (Schubert et al. 2025). Yet, distribution of species across finer spatial scales is key to the development of forest structure and composition in the later stages of succession.

Here, we characterize the fine scale spatial recruitment patterns of tree seedlings and saplings resulting from the three restoration interventions and their consequences for community assembly patterns after 18 years. We compared measures of heterogeneity in community compositional dissimilarity, including turnover (i.e., species replacement) and nestedness (i.e., abundance gradient) components. We hypothesized that implementing more spatially varied planting arrays (applied nucleation) would create greater habitat variability and thus, greater floristic heterogeneity than plantations. We also quantified spatial aggregation and distribution relatively to plot edges for large-seeded, later successional recruiting species. We predicted that the greater spatial extent of planting (plantation) would reduce clustering of recruit populations by facilitating establishment of species more evenly throughout restored areas and reducing dispersal limitation.

2. METHODS

2.1 STUDY REGION & EXPERIMENTAL DESIGN

We censused experimental forest restoration plots in Coto Brus county in southern Costa Rica. Sites are located 1100–1430 m above sea level in Tropical Premontane Wet and Rain Forest life zones with mean annual rainfall of 3500–4000 mm and mean annual temperature of 21°C (Holdridge et al. 1971). This area is a mix of pasture and small subsistence farming, secondary regrowth, and sparse remnant forest patches (Zahawi et al. 2015). Forest cover in a 500-m buffer of experimental sites at the initiation of the experiment ranged from 11–88%; this includes remnant and regrowth forest fragments, and native and non-native trees growing in fence rows, pastures and tree plantations (Mendenhall et al. 2011).

Experimental forest plots were established in 2004–2006, replicating three treatments across sites spaced a minimum of 700 m apart. All sites had been cleared of forest for at least 18 years prior to experimental interventions, and at the start of the study were dominated by non-native forage grass cover sometimes mixed with ruderal forbs. Each experimental plot was ~0.25 ha and separated by a ≥ 5 -m buffer from other treatment plots at the same site. In plantation plots 313 seedlings were planted uniformly along a grid with constant spacing (~2.8 m). In applied nucleation plots, 86 seedlings were planted in six nuclei, two each of three sizes – 4×4, 8×8, and 12×12 m. No seedlings were planted in natural regeneration treatments. The planted seedlings included four species; *Erythrina poeppigiana* (Walp.) Skeels (Fabaceae), *Inga edulis* Mart (Fabaceae), *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae), and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae). All plots were managed by clearing regenerating vegetation to ground level with machetes every three months for the first 2.5 years. More details on experimental design and early conditions of the experiment can be found in Zahawi et al. (2013).

2.2 DATA COLLECTION

During June and July 2022, we identified and mapped all ≥ 20 -cm tall stems of tree taxa in 32 plots across 10 sites. Our study included 8 plantation, 9 applied nucleation, and 9 natural regeneration plots. Although all three treatments were originally replicated at each site, a few had been subjected to extensive anthropogenic disturbance after two decades and were not included in the census. We also censused reference plots at six sites with nearby mature forest. Reference

forests ranged from 2-320 ha and showed no evidence of clearing in the last 75 years since aerial photographs have been available (Zahawi et al. 2015), though selective logging may have occurred in some sites.

We sampled a 48×48-m square area centered within the 50×50-m plot boundaries in most restoration plots. A few plots had slight alterations to shape (e.g., 42×54-m) due to variations in original site dimensions to accommodate site boundaries or a subset of quadrats missing to account for partial disturbance to a plot over the course of the experiment (detailed in Schubert et al. 2025). The sample layout for reference forests differed in that each “plot” was a set of four smaller, noncontiguous 21×21-m subplots to accommodate the nuanced topographic complexities of remnant forests and census more of the forest that abutted the restoration areas. In both restoration plots and reference forests, we recorded the location of all recruits according to a Cartesian grid with the 3×3 m sub-quadrats as the smallest scale of spatial resolution (Appendix S1).

2.3 DATA ANALYSIS

The final data set included 66,446 seedlings (<1 cm DBH) and 14,038 saplings (1-<5 cm DBH) from 249 taxa. We did not analyze the 3,842 larger tree recruits (≥ 5 cm DBH) here as they were overwhelmingly dominated by a small subset of early-successional taxa, of which 6 families represented more than 75% of recorded stems and had similar relative abundance and composition across all restoration treatments (Schubert et al. 2025). Moreover, the small sample size and many quadrats with no large recruits limited our ability to quantify fine scale compositional turnover. Consequently, we focus on the more diverse and variable understory of seedling and sapling communities.

We considered three spatial scales in our analyses corresponding to our grid sampling design (Appendix S1). First, we considered 24×24-m plot quarters (hereafter “subplots”) as replicates to compare restoration subplots to 21×21-m reference forest subplots. Second, we examined occupancy and diversity measures for seedling and sapling communities at the resolution of 6×6-m quadrats. This scale allowed for sufficient quantities of stems for comparisons among treatments; this size also approximates the adult crown cover for many tropical trees (Ribbens et al. 1994; Kobe and Vriesendorp 2009). Finally, for analyses comparing relative distances of recruit distribution as a continuous variable (i.e., clustering and distance),

we considered the positions of all stems based on their spatial coordinates derived from their placement in a 3×3-m sub-quadrat grid. All analyses were completed in R 4.4.3 (R Core Team 2025). We used the ‘glmmTMB’ package for modelling (Brooks et al. 2017) and created plots of model results based on estimated marginal means of treatment groups using the ‘emmeans’ package and Tukey tests for pairwise comparisons using an alpha value of 0.05 (Lenth 2021).

Spatial Extent of Recruitment

To assess the relative completeness of regeneration across restored areas, we first measured the percentage of censused 6×6-m quadrats where any naturally recruiting trees were detected. We visualized occupancy, based on presence/absence of any seedlings and saplings across censused areas, using violin plots.

Fine scale Community Heterogeneity

We first analyzed fine scale community patterns through species density (α -diversity – i.e., number of species recorded in each 6×6-m quadrat) using the *vegan* package (Oksanen et al. 2022). For an abundance-weighted measure of dissimilarity, we calculated the mean Bray-Curtis dissimilarity value from pairwise differences between community matrices of all quadrats within each subplot. Furthermore, we used the *beta.pair.abund* function from the *betapart* package (Baselga and Orme 2012) to partition the components of this calculation: (1) balanced variation in abundance between quadrats – i.e., a quantitative measure of species turnover accounting for when individuals of some species are replaced in equal part by other species (i.e., turnover); and (2) unidirectional abundance gradients that accounts for changing number of individuals (i.e., nestedness).

We modeled the treatment effects on these resulting measurements using mixed-effect models and included site and subplot as random effects. Model families ‘genpois’, ‘tweedie’, and ‘gaussian’ (i.e., general linear model) were used for species density, turnover, and dissimilarity, respectively. Subplot sample size for this analysis was 32 for natural regeneration, 34 for applied nucleation, 33 for plantation, and 23 subplots for reference forest.

Spatial Patterning of Recruits

Previous findings from this experiment have consistently shown that early-successional species are not dispersal limited after the first few years of forest recovery (Reid et al. 2015; Werden et al. 2021). Additionally, many early-successional recruits are already reproducing within restoration plots (J. A. Rosales unpubl. data), so we focused analyses of species-level spatial patterns of later-successional species. Zoochorous species represented the vast majority of this group, with only 0.6% of censused later-successional recruits having abiotic dispersal. For our analysis, we further distinguish between “small-seeded” species that are <5 mm in diameter and “large-seeded” species ≥ 5 mm.

We quantified the spatial dispersion of later-successional recruits at the species-level using applied spatial analysis by distance indices (SADIE). The Perry Index of Aggregation (I_A) measures spatial patterning by considering the number and distance of moves required to reach a regular/uniform distribution across sampling units in a grid (Perry et al. 1999). These calculations are derived from the minimum distance of moves from the Transportation algorithm (Kennington and Helgason 1980), which we calculated from the observed dataset and the mean from 50 randomized permutations of the counts across sampling units ($I_A = D_{\text{obs}} / D_{\text{null}}$). As such, $I_A = 1$ indicates perfectly random spatial distribution, $I_A > 1$ signifies clustering, and $I_A < 1$ signifies greater uniformity. We calculated I_A for recruits separately for seedling and sapling size classes for species-subplot combinations with at least three individuals. We modeled I_A as a function of restoration treatment with random effect of species and subplot as a nested random effect within site. Finally, we examined occupancy patterns of large-seeded recruits as a function of their distance from the edge of restoration plots, defined as the perimeter of the sampling grid which was inset by 1 m from the restoration plot edges. We modelled the data using logistic regression to predict the relative likelihood of presence in 3×3 sub-quadrats distributed from plot edge to interior, considering species, site, and abundance as random effects.

3. RESULTS

3.1 SPATIAL EXTENT OF RECRUITMENT

Seedlings recruited in nearly all quadrats in applied nucleation, plantation, and reference forest subplots, whereas the percentage of quadrats with recruits was highly variable in natural regeneration (Fig. 1A); 8 subplots had $<50\%$ occupancy and 10 subplots had 100% occupancy

(median = 84%). Sapling recruitment patterns were similar with the lowest median (72%) and greatest range (13-100%) in natural regeneration (Fig. 1B); applied nucleation and plantation subplots had at least 94% and 100% occupancy, respectively with a greater range in applied nucleation.

3.2 FINE SCALE COMMUNITY HETEREGENEITY

Plantation plots had the greatest seedling species density in 6×6-m quadrats, applied nucleation and reference forest were intermediate, and natural regeneration had the lowest species density (Fig. 2A). Both applied nucleation and plantation treatments had similar sapling species densities to reference forests, whereas natural regeneration had significantly lower values (Fig. 2B).

Fine scale floristic heterogeneity of seedling communities (Bray-Curtis dissimilarity) did not differ among the seedling communities of the two planted treatments or reference forests, although plantations had significantly lower dissimilarity than natural regeneration (Fig. 2C). The turnover component of dissimilarity was similar among all treatments (Fig. 2E), whereas nestedness (i.e., variability in abundance across neighboring quadrats) was greatest in natural regeneration, intermediate in applied nucleation and lowest in plantation (Fig. 2G). Nestedness of seedling communities in applied nucleation and plantations did not differ significantly from reference forests.

Sapling communities showed similar levels of fine scale heterogeneity across all three experimental treatments, although those from plantation were significantly lower than reference forests (Fig. 2D). Both turnover and nestedness components of dissimilarity were similar for the three experimental treatments. Reference forest sapling communities had significantly higher turnover but lower nestedness than restoration treatments (Fig. 2F&H).

3.3 SPATIAL PATTERNING OF LATER-SUCCESSIONAL RECRUITS

Seedlings and saplings of later-successional species were more aggregated than expected from random across all treatments. Later successional seedlings, regardless of seed size, showed a similar pattern across treatment, where species were most aggregated in natural regeneration, intermediate in applied nucleation and least aggregated in plantation and reference forests (Figs.

3A, 3C). Sapling recruits showed the same general pattern (Fig. 3D), although treatment differences were negligible for small-seeded species (Fig. 3B).

Small-seeded recruits showed no significant pattern in their distribution from plot edges, regardless of treatment (Fig. 4A-B). The distribution of large-seeded seedlings in natural regeneration depended significantly on distance from plot edge, being 67% more likely to occur at the plot edge than center (Fig. 4C). We observed the same effect of plot edges for large-seeded saplings in natural regeneration and to a lesser degree in applied nucleation plots (Fig. 4D).

4. DISCUSSION

Using fine scale recruitment data, we show how the initial canopy development from restoration impacts not only abundance and richness, but also the spatial structure of recruit populations. Both applied nucleation and plantation restoration methods significantly enriched forest recovery through greater spatial extent of recruitment and quadrat-level species density within plots compared with natural regeneration. Fine scale turnover in recruiting seedling and sapling communities was similar in the different restoration treatments, whereas nestedness was highest in natural regeneration compared to the planted treatments and reference forest. At the species level, this pattern was demonstrated by more aggregated distributions and a lower likelihood of establishment of large-seeded recruits away from plot edges in natural regeneration than planted treatments.

We hypothesized that uniformly applied, plantation-style restoration would result in lower fine scale floristic heterogeneity in recruit communities than the other restoration approaches. Yet, we did not find strong differences among treatments in this regard. Abundance-weighted dissimilarity of seedling communities was highest in natural regeneration, intermediate in applied nucleation and reference forests, and lowest in plantations, a pattern that was accounted for by variability in abundance of seedlings in neighboring quadrats rather than species turnover. The nestedness result is consistent with our observation of more even dispersion of recruits and suggests that the more expansive tree canopy provides structure to attract fauna and overcome dispersal limitation (de la Peña-Domene and Martínez-Garza 2018; Palma et al. 2020), which is supported by the greater seedling species density in plantation quadrats and by results of other tropical forest restoration studies (Li et al. 2018, Mendes et al. 2021). Furthermore, it is notable that the greater spatial heterogeneity in seedling abundance in

natural regeneration was not observed in the sapling communities, reflecting that these patterns may not persist at later stages of growth.

After nearly two decades of recovery, naturally regenerated areas consistently showed more clustered and patchy tree recruitment and less colonization in plot interiors, indicating that barriers to recruitment persist, yet we find evidence that these challenges have been abated in both nucleation and plantation treatments. The more limited distribution of large-seeded recruits in the interiors of natural regeneration certainly arises from a combination of dispersal patterns and response to the varying microsite conditions (e.g., high grass cover versus understory of established early-successional recruits), and demonstrates the advantages of tree planting for facilitating recruitment of these relatively uncommon species beyond simply increasing plot-scale abundance (Schubert et al. 2025). Landscape forest composition and distance to potential seed-bearing individuals are well known to affect the dispersal of large-seeded trees that are heavily reliant on large-bodied, forest-dependent birds and mammals (de la Peña-Domene et al. 2016). A survey of plantation plots five years prior to ours that included explicit mapping of potential source-trees for several dozen large-seeded species revealed a similar distance-dependent establishment pattern with quadrat-level abundance significantly linked to distance from mother trees (Zahawi et al. 2021). Now, with time for additional recruitment and exhaustive sampling of all three restoration treatments, we find that distance-dependence of recruitment is significantly stronger in natural regeneration than the two planted treatments.

The fact that natural regeneration subplots still had substantial areas with no tree regeneration is likely in part due to competition of young seedlings with aggressive pasture grasses, in particular *Axonopus scoparius* (Flüggé) Kuhlman and *Pennisetum purpureum* Schumacher at our sites (Hooper et al. 2005; Kulikowski et al. 2023). Curiously, the spatial extent of tree recruitment in natural regeneration subplots shows a largely bimodal pattern in which about half the subplots have >75% quadrat occupancy whereas the remainder have a substantial number of quadrats with no recruitment. This result indicates that a benefit of tree planting may be to reduce variability in recovery rates across quadrats, and supports the recommendation to monitor the rate of natural regeneration for the first couple of years prior to deciding whether it is a judicious use of resources to plant trees to facilitate recovery at a particular site (Holl et al. 2018).

Differences in fine scale spatial distribution of saplings were much weaker or non-existent as compared to seedlings, suggesting the role of microsite conditions, likely light limitation (Hubbell et al. 1999; Montgomery and Chazdon 2002) in affecting seedling survival and growth, and in turn, the seedling-to-sapling transition (Chang-Yang et al. 2021). Indeed, work at our and other sites suggests that seedling survival (Bertacchi et al. 2016; Kulikowski et al. 2022; Joyce et al. 2025) and growth (Wright et al. 2010; Caughlin et al. 2019) is lower in sites with a dense tree canopy, which comprises a filter that counteracts the greater number of species and individuals establishing in plantation plots.

Over time, however, the canopy cover in applied nucleation and plantation plots has become more similar due to expanding canopy cover in applied nucleation treatments and mortality of two relatively short-lived planted tree species (Holl et al. 2020). By the time of our study, only about 25% of planted *Inga edulis* and *Erythrina poeppigiana* survived; this mortality increased canopy heterogeneity and opened temporary gaps for recruitment of other species, particularly in plantations, though those gaps quickly closed largely due to rapid growth of planted *Vochysia guatemalensis* (Holl et al. 2020). Such forest dynamics have likely played an important role in reducing the initially homogenous nature of the plantation treatment, and we expect non-random mortality and microsite variation affecting seedling-to-sapling transitions to increase as succession proceeds (Dupuy and Chazdon 2006; Green et al. 2014; Zhu et al. 2018).

It is less clear whether fine scale patterns of saplings portend future forest species composition, given that few recruits from slower growing shade tolerant species have transitioned to the tree layer, particularly in the plantation treatment (Schubert et al. 2025). Both our research (Kulikowski et al. 2023) and that of Caughlin et al. (2019) show that tree recruits grow faster and hence transition more frequently into large size classes in natural regeneration and applied nucleation treatments than in plantations, though thus far that pattern is dominated by early successional species that are typically light-demanding (Schubert et al. 2025) and more time is needed to determine whether that trend will hold for shade-tolerant later successional species. As many of the early advantages of initial tree planting begin to equalize across restoration designs over time, the causal links between initial interventions and forest development are likely to become increasingly weaker compared to stochastic and landscape-level environmental conditions. Understanding how emerging spatial and compositional patterns

feedback on key demographic processes and the extent to which these maintain or diverge from natural systems will be key to informing future restoration efforts.

Overall, we find that planting trees of a few species accelerated recruitment of myriad additional species after nearly two decades. Whereas varying the spatial extent of planting in restoration areas might be expected to produce divergent patterns of community assembly, our long-term experiment finds little to no difference in the fine scale spatial patterning of recruiting tree seedling and sapling communities between applied nucleation and plantation treatments. Our findings shed light on the medium-term effects of tree planting methods in tropical landscapes and point to the viability of both applied nucleation and plantation approaches to facilitating succession of native tree communities, following initial stand establishment.

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634 **SUPPORTING INFORMATION**

635 Additional supporting information can be found online in **Appendix S1**: AppendixS1.docx – A
636 diagram of a sample survey grid with spatial hierarchy.
637

638 **FIGURES**

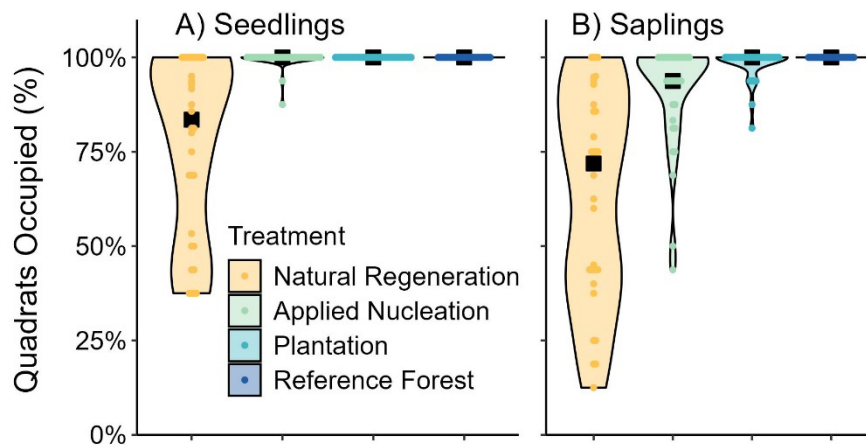


Figure 1. Violin plot distributions of the percentage of 6×6 m quadrats in each subplot that were occupied by at least one (A) seedling or (B) sapling. Large black squares indicate the median value by treatment, and colored points correspond to individual subplot values. Natural Regeneration (n = 32 subplots); Applied Nucleation (n = 34); Plantation (n = 33); Reference Forest (n = 23).

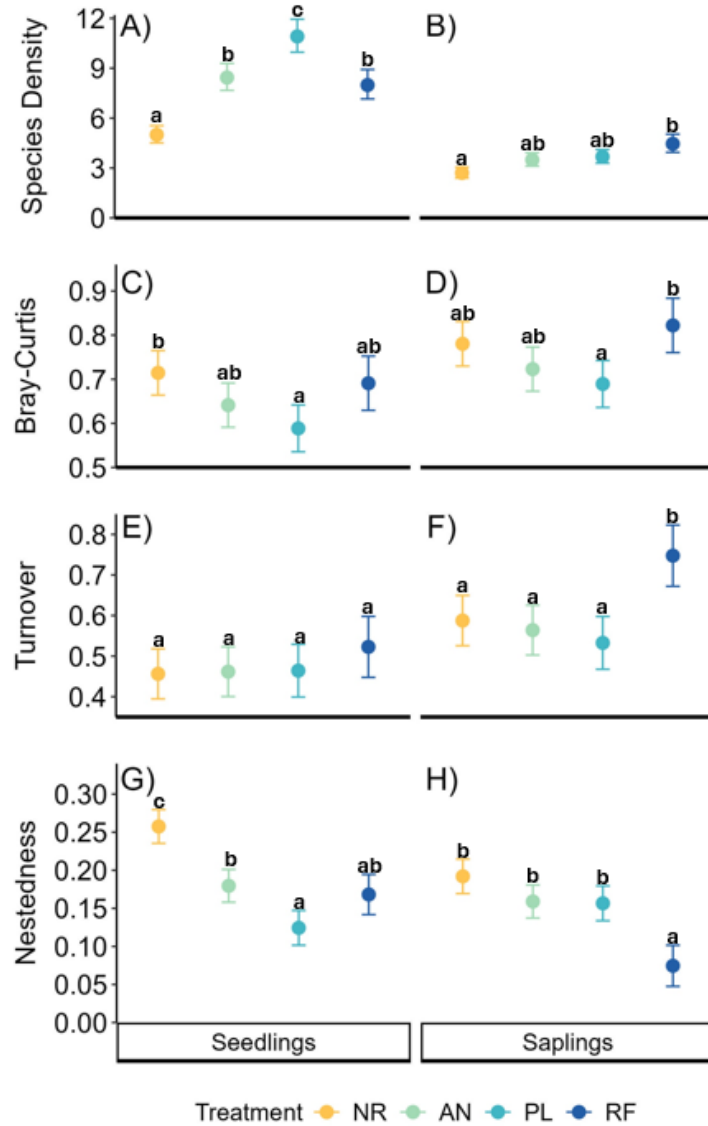


Figure 2. Estimated marginal means from GLMM with 95% CIs for (A-B) species density as mean number of species per 6×6-m quadrat, (C-D) mean Bray-Curtis dissimilarity between quadrats, and the quantitative components of Bray Curtis due to (E-F) turnover, and (G-H) nestedness. Natural Regeneration (NR, n = 32 subplots); Applied Nucleation (AN, n = 34); Plantation (PL, n = 33); Reference Forest (RF, n = 23). Error bars represent 95% confidence intervals. Letters indicate significant differences ($p < 0.05$) using a Tukey's mean comparison procedure.

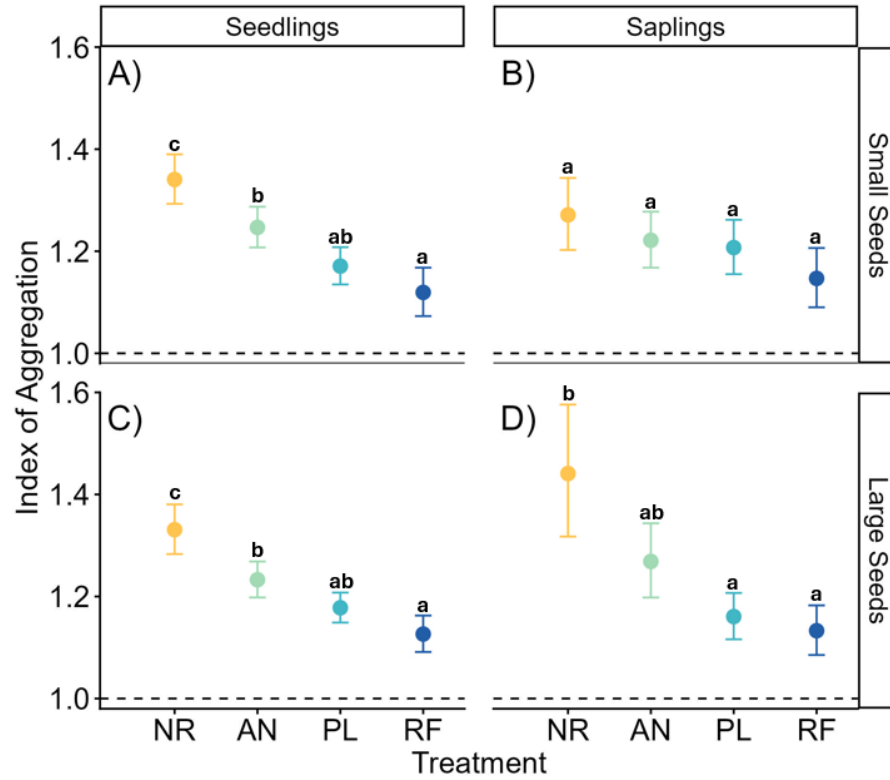


Figure 3. GLMM group estimated marginal means plot for Index of Aggregation across size classes and seed size for later-successional trees: (A) Small-seeded seedlings, (B) Small-seeded saplings, (C) Large-seeded seedlings, (D) Large-seeded Saplings. Natural Regeneration (NR); Applied Nucleation (AN); Plantation (PL); Reference Forest (RF). Error bars represent 95% confidence intervals. Dotted line (1) = random spatial dispersion. Letters indicate significant differences ($p < 0.05$) using a Tukey's mean comparison procedure.

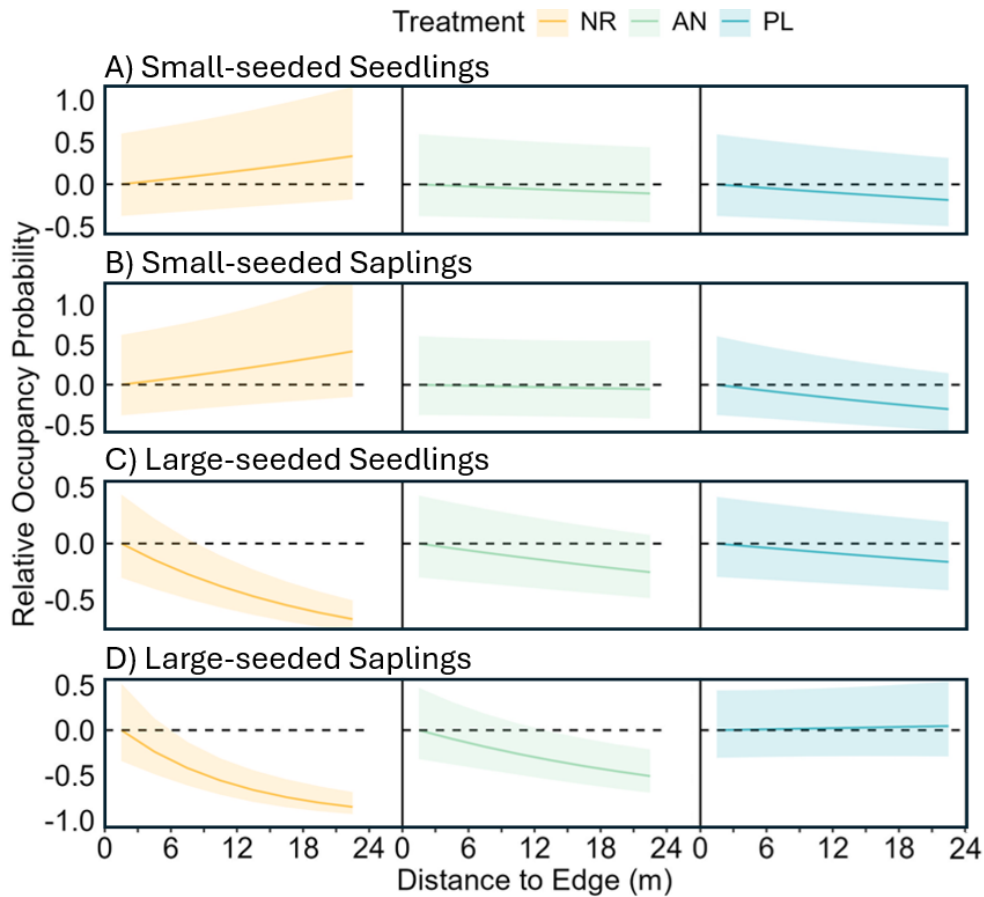


Figure 4. Predicted values of the relative probability of later-successional recruit occupancy (3×3 m subquadrats) across the three restoration treatments – Natural Regeneration (NR); Applied Nucleation (AN); Plantation (PL) – relative to plot edge for seedlings and saplings separated by seed size; based on estimated marginal means from logistic regressions. Horizontal dashed lines represent the reference parameter value from the outermost subquadrats in the data set to which model estimates are scaled as reference value. Occupancy is defined as the presence of at least one stem of any species. Only species with non-zero regeneration for a particular plot were included in the analysis – i.e., species never detected in the plot were excluded.