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ARTICLE

Active restoration increases tree species richness and recruitment of large-seeded taxa after 16–18 years

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Abstract

Tropical forest restoration presents a potential lifeline to mitigate climate change and biodiversity crises in the Anthropocene. Yet, the extent to which human interventions, such as tree planting, accelerate the recovery of mature functioning ecosystems or redirect successional trajectories toward novel states remains uncertain due to a lack of long-term experiments. In 2004–2006, we established three 0.25-ha plots at 10 sites in southern Costa Rica to test three forest restoration approaches: natural regeneration (no planting), applied nucleation (planting in patches), and plantation (full planting). In a comprehensive survey after 16–18 years of recovery, we censused >80,000 seedlings, saplings, and trees from at least 255 species across 26 restoration plots (nine natural regeneration, nine applied nucleation, eight plantation) and six adjacent reference forests to evaluate treatment effects on recruitment patterns and community composition. Both applied nucleation and plantation treatments resulted in significantly elevated seedling and sapling establishment and more predictable community composition compared with natural regeneration. Similarity of vegetation composition to reference forest tended to scale positively with treatment planting intensity. Later-successional species with seeds ≥5 mm had significantly greater seedling and sapling abundance in the two planted treatments, and plantation showed similar recruitment densities of large-seeded (≥10 mm) species to reference forest. Plantation tended toward a lower abundance of early-successional recruits than applied nucleation. Trees (≥5 cm dbh) in all restoration treatments continued to be dominated by a few early-successional species and originally transplanted individuals. Seedling recruits of planted taxa were more abundant in applied nucleation than the other treatments though few transitioned into the sapling layer. Overall, our findings show that active tree planting accelerates the establishment of later-successional trees compared with natural regeneration after nearly two decades. While the apparent advantages of higher density tree planting on dispersal and understory establishment of larger seeded, later-successional species recruitment is notable, more time is needed to assess whether these differences will persist and transition to the more rapid development of a mature later-successional canopy. Our results underscore the need for

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ecological restoration planning and monitoring that targets biodiversity recovery over multiple decades.

KEYWORDS
applied nucleation, community composition, forest dynamics, late-successional, seed size, succession, tree islands, tropical forest

INTRODUCTION

In recent years, recognition of the regenerative potential of forests in human-modified tropical landscapes (Chazdon & Guariguata, 2016; Williams et al., 2024) has contributed to expanding investment in forest restoration as a tool to sequester carbon, preserve biodiversity, and improve human well-being (Aguirre-Gutiérrez et al., 2023; Edwards et al., 2021; Fuss et al., 2021; Koch & Kaplan, 2022; Tonetti et al., 2022). In addition to the ongoing UN Decade on Ecosystem Restoration, numerous global initiatives have emerged to plant vast numbers of trees and restore hundreds of millions of hectares of land (e.g., Trillion Trees Campaign, Bonn Challenge), largely targeting tropical regions (Brancalion & Holl, 2020; Martin et al., 2021). Although the goals of restoration vary, efforts targeting recovery of the high species diversity and complex ecological interactions characteristic of tropical forests require management strategies that promote the assembly of rich communities of native species whose composition, structure, and function closely resemble that of reference forests (Carrick & Forsythe, 2020; Gann et al., 2019). Despite a large body of research that details how tropical forests recover, well-replicated field experiments directly comparing restoration interventions that are monitored for multi-decadal timeframes relevant to successional processes remain scarce (Brancalion et al., 2019; Chazdon et al., 2017).

A suite of well-studied abiotic and biotic barriers limit the recovery of woody plant communities in tropical ecosystems; these frequently include degraded soils, extreme microclimates, competition with invasive vegetation (e.g., grasses), and seed limitation (Blackham et al., 2014; Holl et al., 2000; Zimmerman et al., 2000). Given that most tropical trees are adapted for dispersal by frugivorous animals (Howe & Smallwood, 1982), seed dispersal is a dynamic process linked to the abundance and diversity of the disperser assemblage and seed sources (Carlo & Morales, 2016; Zahawi et al., 2021). Previous studies from Neotropical forests largely show that wind, bats, and small birds consistently facilitate the dispersal of subsets of early-successional trees and shrubs that are adapted to grow quickly in high-light environments (González-Castro et al., 2019; Ingle, 2003; Palma et al., 2021).

As secondary forests age, canopy height, contiguity, and habitat complexity are linked to increased animal seed dispersal, greater incidences of large birds and mammals that are responsible for the dispersal of larger seeded, often later-successional trees (Bradfer-Lawrence et al., 2018; De La Peña-Domene et al., 2016), and understory microclimates that increasingly favor shade-tolerant species adapted to establish and grow under dense mature forest canopies (Dent et al., 2013; Rüger et al., 2023). Research on chronosequence studies consistently shows that naturally regenerating secondary tropical forests take a half century or more to recover similar species composition to primary forests (Finegan, 1996; Rozendaal et al., 2019). Recovery of maturing forests at these stages is driven by the transition of mid- and late-successional tree species into the canopy and continued colonization of rare and dispersal-limited trees that are most characteristic of old growth forests (Martínez-Garza & Howe, 2003; Muscarella et al., 2017; Rüger et al., 2023). Therefore, a rapid recovery of biomass and initial canopy structure is not necessarily predictive of later-successional processes.

Active restoration through tree planting has long been heralded as a key approach to accelerate tropical forest succession (Brancalion & Holl, 2020; Chazdon, 2008; Holl et al., 2000). Numerous field experiments have shown that tree planting interventions often produce greater tree cover and woody recruitment than in paired natural regeneration sites during the first two decades of recovery (Li et al., 2018; Osuri et al., 2019; Trujillo-Miranda et al., 2018; Wilson & Rhemtulla, 2016), although some studies show minimal difference in diversity or compositional measures (Gilman et al., 2016; Meli et al., 2017; Ssekuubwa et al., 2019). Tree planting typically increases the rate of recovery of early-successional (i.e., pioneer) species by enhancing seed dispersal and overcoming barriers to establishment (de la Peña-Domene et al., 2013; Osuri et al., 2019; Parrotta et al., 1997). Nevertheless, conventional tree plantations with fixed spacing in grids (hereafter "plantations") can create homogeneous habitat conditions, and strong legacy effects from initially planted species can direct succession toward a community composition considerably different from what is found in reference forests

(César et al., 2018; Cusack & Montagnini, 2004; Wills et al., 2017).

Spatially patterned planting methods (sensu Shaw et al., 2020), such as applied nucleation (planting trees in patches), are hypothesized to have similar effects as plantations in overcoming barriers to recovery by enhancing seed dispersal and seedling establishment (Benayas et al., 2008; Zahawi & Augspurger, 2006), without redirecting natural successional trajectories to the same extent as plantations. According to nucleation theory, initial patches of recovering vegetation facilitate recruitment of other species via enhanced seed dispersal and improved establishment conditions (e.g., grass suppression, minimizing temperature, and moisture extremes), regenerating outward and gradually coalescing with other nuclei (Yarranton & Morrison, 1974). Applied nucleation presents an attractive option for restoration managers to accelerate recovery of spatially heterogenous ecosystems, while also reducing project costs (Benayas et al., 2008; Corbin & Holl, 2012; Holl et al., 2011; Robinson & Handel, 2000). Prior studies of applied nucleation support its effectiveness in facilitating tropical forest recovery during the early years of restoration through increased bird activity, seed rain, and seedling establishment (Holl et al., 2020; Piiroinen et al., 2015; Ramírez-Soto et al., 2018; Zahawi & Augspurger, 2006). However, the tradeoffs between applied nucleation and traditional planting methods have rarely been directly compared (Corbin et al., 2016; Holl et al., 2020), and few field studies have been sustained long enough to observe the effects of differing management interventions on successional processes over multi-decadal timeframes in tropical forests.

Here, we report on a comprehensive census of all tree recruits ≥20 cm in height from a spatially replicated restoration experiment after almost two decades of recovery, comparing three restoration interventions (natural regeneration, applied nucleation, and plantation-style tree plantings) and nearby reference forests. We examine how species richness, community composition, and relative abundance of tree recruits of different successional stages and seed sizes differ among treatments. Results from the first decade of this experiment previously showed positive effects of both planted treatments compared with natural regeneration on abundance and richness of tree seedlings (Holl et al., 2017; Werden et al., 2022). However, plantations have significantly greater overall canopy cover (Holl et al., 2020) and more frequent incidence of large frugivores (Reid et al., 2021), which could facilitate greater colonization by later-successional larger seeded trees over time. In contrast, applied nucleation treatments have many fewer planted trees with lower and more heterogenous canopy cover (Holl et al., 2020; Zahawi, Dandois, et al., 2015) that have previously fostered greater seedling survival and sapling growth rates (Kulikowski et al., 2023). Through an exhaustive census of tree recruits, we sought to evaluate how the differential effects of restoration treatments influence community assembly after nearly two decades.

METHODS

Study region

We conducted this study at 10 sites spread across a ~100-km^2 area between the Las Cruces Biological Station (LCBS; 8°47′7″ N, 82°57′32″ W) and Agua Buena (8°44′42″ N, 82°56′53″ W) in southern Costa Rica. The sites are at the boundary between Tropical Premontane Wet and Rain Forest life zones (Holdridge et al., 1971), range in elevation from 1100 to 1430 m, receive mean annual rainfall of 3500 to 4000 mm with a dry season from December to March, and have a mean annual temperature of ~21°C. All sites are separated by a minimum of 700 m, and the surrounding landscape is a mosaic of agricultural fields and pasture interspersed with remnant forest patches (Zahawi, Duran, et al., 2015). All sites were farmed or grazed by cattle for ≥18 year and most were dominated by non-native forage grasses prior to the start of the study. Most sites are steeply sloped (15–35°). Soils are volcanic in origin, mildly acidic (pH $= 5.3 \pm 0.04$; mean ± SE), low in P (Mehlich III: 3.9 ± 0.4 mg/kg), and high in organic matter (16.7 ± 0.8%) (Holl & Zahawi, 2014).

Experimental design

At each site, we established three 0.25-ha plots separated by a ≥5-m buffer. In 2004–2006, each plot received one of the three randomized treatments: natural regeneration, applied nucleation, or plantation. By the time of this census, three sites were missing one or two treatments due to major human disturbances over the nearly two decades of the study: natural regeneration ($n = 9$) plots, applied nucleation ($n = 9$), and plantation ($n = 8$). Plantations were uniformly planted with tree seedlings, while the applied nucleation treatment was planted with six tree islands of three sizes: two each from 4×4, 8×8, and 12×12 m. Planted seedling spacing was kept constant (~2.8 m) in plantation and applied nucleation treatments; 313 trees were planted in plantation, 86 in applied nucleation, and none in natural regeneration plots (Holl et al., 2011). All plots (including natural regeneration) were cleared to ground level by machete at ~3-month intervals for the first 2.5 years to allow planted tree seedlings to grow above existing vegetation. We planted seedlings (20–30 cm tall) of four tree species: these included two native late-successional species, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), and two naturalized early-successional species, *Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. (both Fabaceae), that are used widely in intercropping systems in Central America. By the time of the surveys presented here, a majority of the planted softwoods had died (mean survival and SD: *E. poeppigiana* 34.5 ± 28.5%; *I. edulis* 22.9 ± 18.5%). The survival of the other two species remained high (*V. guatemalensis* 82.8 ± 18.4%; *T. amazonia* 82.1 ± 17.8%). At six sites, we also sampled adjacent remnant forests to serve as references. These reference forests ranged in size from 2 to 320 ha and showed no evidence of clearing in the last 75 years since aerial photographs have been available (Zahawi, Duran, et al., 2015). All have been impacted to some extent by human disturbance, as "pristine" forests are not present in our study area (Clement & Horn, 2001).

Data collection

During June and July 2022, 16–18 years after establishing plots, we censused all naturally recruiting trees ≥20 cm height (hereafter "recruits") throughout each restoration treatment plot. We mapped individual recruits to a grid of 3 × 3 m quadrats and counted the number of seedlings ≥20 cm but <1 cm dbh of each species within each quadrat. We measured dbh for all recruits ≥1 cm and categorized each into sapling (1–<5 cm dbh) or tree (≥5 cm dbh) size classes. If an individual had multiple stems, we based our size classification on the largest stem. Individual restoration plots were mostly 48 × 48 m (256 3 × 3 m quadrats), but in some cases, plots were 42 × 54 m (252 quadrats) due to constraints in the landscape at initial plot setup. In a few cases, a smaller plot area was sampled primarily due to extensive anthropogenic damage to a section of the plot (Appendix S1: Table S1). The layout of the reference forest plots was slightly different and consisted of four 21 × 21 m plots (196 quadrats) at five sites and three 21 × 21 m plots (147 quadrats) at one site. Tree recruits were identified to the lowest operational taxonomic unit (hereafter referred to as "species") following the nomenclature of Tropicos (https://www.tropicos.org).

Data analysis

We categorized recruits of all species that were not planted as part of restoration treatments as either early-, mid-, or late-successional (Appendix S1: Table S2), based on the extensive observations and botanical expertise of two of the authors (RAZ and FOB) who have sampled vegetation composition in many sites in the region for over two decades. We considered early-successional taxa (37 spp.) as pioneer trees which are commonly found in disturbed environments and young secondary forests but typically are not found in mature forests; nearly all early-successional recruits have animal-dispersed seeds <5 mm in width or wind-dispersed seeds. Mid-successional taxa (referred to as "both" in Werden et al., 2021) include tree species that colonize at any stage of forest succession but are well represented in old growth forests. We considered late-successional species as taxa typically observed in mature forests only. Both mid- and late-successional taxa had a range of seed sizes, so we further categorized the latter two successional groups based on seed width: <5 mm, 5–<10 mm, and ≥10 mm, referred to as small, medium, and large, respectively. Successional groups and seed size are not independent, with most (64%) mid-successional species having small seeds, whereas 71% of late-successional species had seeds ≥5 mm (i.e., medium and large). We use the term "later-successional" when referring to these two groups collectively. A few distinct taxa (i.e., *Citrus* spp. and *Heliocarpus* spp.) were not consistently identified to species level and, therefore, grouped together in analyses of diversity and species composition. A small number of individuals (0.04%) in the census were not identified and were excluded from analyses.

For analyses of taxonomic richness among experimental treatments, we separated recruit data by size class: seedling (<1 cm dbh), sapling (1–<5 cm dbh), or tree (≥5 cm dbh). All statistical analyses were performed in R 4.3.3 (R Core Team, 2024). We summarized species richness of experimental treatments using species accumulation models from the "iNEXT" package (Hsieh et al., 2016), in which rarefied, observed, and extrapolated richness were calculated from incidence data across sampling quadrats. Estimated sampling completeness was high across all size classes and successional groups (85%–99%). We made statistical inferences from sample-sized-based calculations of bootstrapped ($n = 1000$) 95% CIs for accumulated richness at 1.01 ha, which was the minimum area sampled for all four treatments.

To compare the composition of communities, we used nonmetric multidimensional scaling (NMDS) of the species abundance matrices of each experimental plot with distances calculated from the Chao dissimilarity index and 95% CIs calculated from within-treatment variability in the "vegan" package (Chao et al., 2005; Oksanen et al., 2022). We compared groups using pairwise permutational analysis of variance (PERMANOVA) between centroids and adjusted p-values using the Bonferroni method for multiple tests.

We drew further inferences on community composition differences through variation in densities of successional groups and recruit size classes among treatments. For each grouping (e.g., early-successional saplings), we used generalized linear mixed models with a negative binomial distribution to analyze the effect of restoration treatment using the “glmmTMB” package (Brooks et al., 2017). Site was included as a random factor, and an offset term was used to account for differing sampling areas. We interpreted pairwise comparisons of estimated marginal means of treatment groups with a Bonferroni correction to resulting *p*-values using the “emmeans” package (Lenth, 2021).

RESULTS

Species richness

We censused a total of 66,446 seedling, 14,038 sapling, and 3842 tree recruits representing 255 operational taxonomic units from 65 families, as well as 1941 survivors of the originally planted trees. Of the naturally recruited taxa (hereafter, species), we identified 94.2% of individuals to species, 4.6% to genus, and 1.1% to family levels. Overall observed species richness among the treatments increased across the planting gradient with natural regeneration lowest (156); and applied nucleation (185) and plantation (196) intermediate; species richness of reference forest (205) highest; despite the fact that total reference forest sampling area was approximately half that of the three restoration treatments. All but 10.5% of tree species recorded in reference forest were found to have colonized at least one restoration plot.

Early-successional seedling and sapling richness were consistently higher across restoration treatments than in reference forest (Figure 1A,D; Appendix S1: Table S3), and while seedling richness was similar among the restoration treatments, sapling richness was notably higher in applied nucleation than plantation. Species richness of early-successional trees (≥5 cm dbh) was greater in natural regeneration and applied nucleation than in plantations and was intermediate in reference forest (Figure 1G; Appendix S1: Table S3). We observed higher richness of mid-successional seedlings in plantation than in the other restoration treatments (Figure 1B; Appendix S1: Table S3). Mid-successional saplings and late-successional seedlings and saplings showed a similar trend of the highest richness in reference forest, intermediate richness in both planted treatments, and the lowest in natural regeneration (Figure 1C,E,F; Appendix S1: Table S3). This pattern was strongest for late-successional saplings with both planted treatments having >50% more species than natural regeneration, but only approximately half the number of late-successional species that were censused in reference forest (Figure 1F). Later-successional tree communities showed similarly low richness across all restoration treatments (Figure 1H,I), with only approximately 50% of mid- and 15% of late-successional species recorded in the tree size class of any restoration treatment compared with that in reference forest.

Community composition

Seedling and sapling community composition tended to increase similar to reference forest with the extent of the planting treatment (Figure 2A,B), although for seedlings the differences among restoration treatments were not significant but all restoration treatments differed from reference forest. For saplings, all treatments differed significantly except applied nucleation and plantation (Appendix S1: Table S4). The compositional differences among restoration treatments in the sapling layer were partly driven by the relative abundance of early-successional species (e.g., *Koanophyllon pittieri*, *Myrsine coriacea*, *Conostegia xalapensis*, *Psidium guajava*, and *Viburnum costaricanum*); early-successional taxa made up 54.0% and 43.3% of saplings in natural regeneration and applied nucleation, but only 18.6% in plantations. Species commonly found in reference forest that were rarely recorded as saplings in restored sites included *Drypetes brownii*, *Guarea montana*, *Inga punctata*, *Garcinia intermedia, Desmopsis oerstedii*, and *Posoqueria costaricensis*. Both seedling and sapling communities showed greater variability in species composition under natural regeneration than in either planting intervention.

The community composition of recruited trees in restoration treatments had no overlap with reference forest (Figure 2C), and differences among restoration treatments resulted primarily from higher densities of the originally planted trees (Figure 3C), as the difference disappeared when planted trees were removed from the analysis (Appendix S1: Figure S1). Naturally recruited trees in restored plots were largely comprised of a handful of early-successional taxa—*Cecropia obtusifolia*, *Hampea appendiculata*, *Koanophyllon pittieri*, *Myrsine coriacea, Viburnum costaricanum*, *Heliocarpus* spp., and several Melastomataceae that accounted for >75% censused individuals.

Abundance of naturally recruiting trees

Seedlings from planted tree species formed a small percentage of the total number of recruiting seedlings across

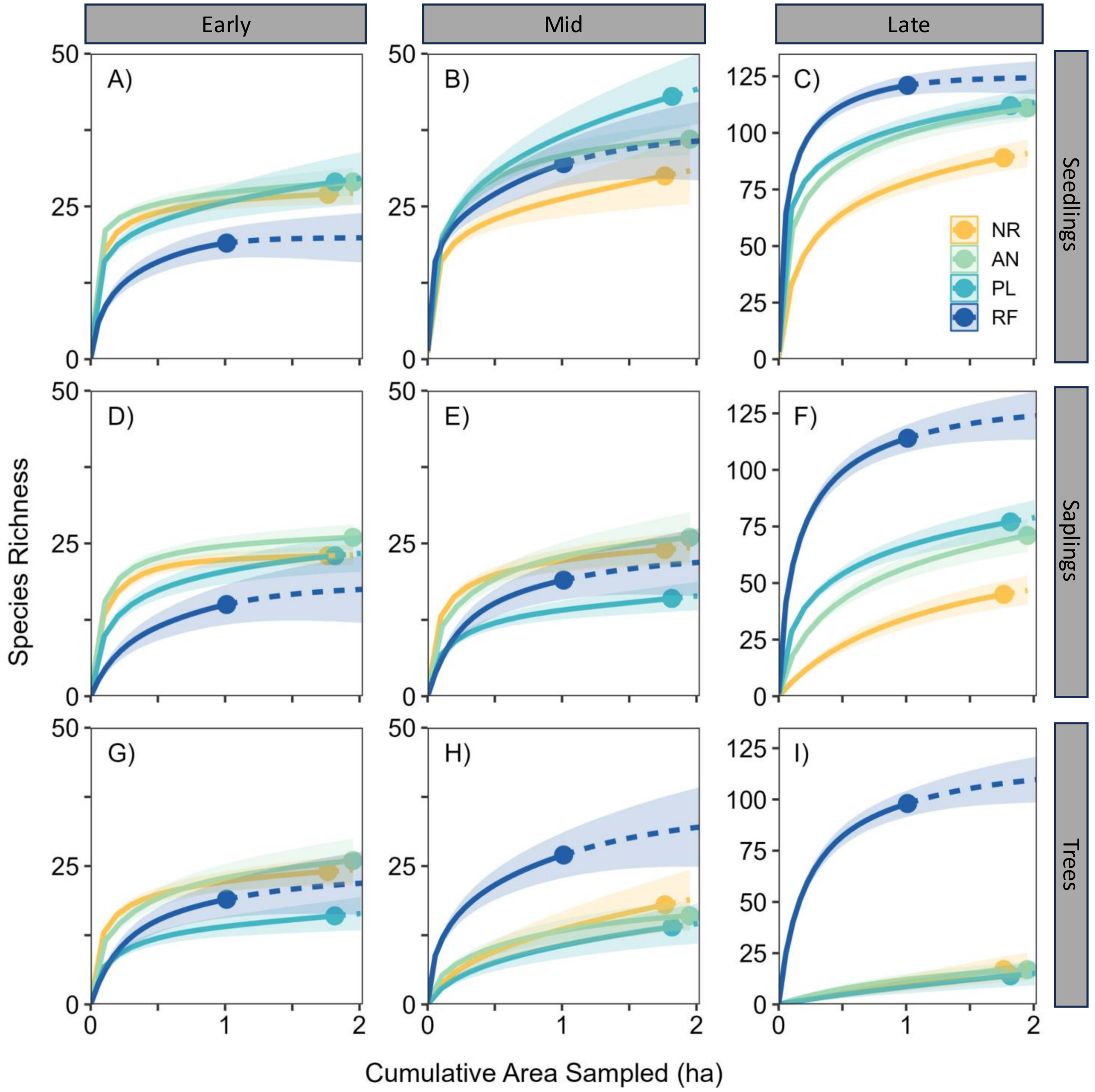

FIGURE 1 Species accumulation curves for seedling, sapling, and tree recruits for early- ($n = 38$ spp.), mid- ($n = 52$ spp.), and late-successional species ($n = 163$ spp.) in natural regeneration (NR), applied nucleation (AN), plantation (PL), and reference forest (RF). Rarefaction was performed across randomized samples of 3 × 3 m quadrats with 95% CIs, displayed as shaded area. Dotted sections of curves indicate extrapolated calculations. See Appendix S1: Table S3 for statistical comparisons of species richness estimates.

all treatments, but their abundance, particularly of *I. edulis* and *V. guatemalensis*, was significantly greater in applied nucleation (13.0%) than plantation (4.7%), despite the difference in original planting intensity (Figure 3A). There were relatively few saplings of planted species in any treatment (1.8% of all saplings), and 60% of these stems in the two planted treatments were originally planted individuals that never grew into the tree size class. All trees (≥5 cm dbh) of these species in applied nucleation and plantation were planted as part of the initial restoration (Figure 3C). The few saplings and trees of planted species in natural regeneration were largely *E. poeppigiana* that had resprouted from individuals present prior to the start of the study.

Early-successional seedling and sapling abundance did not differ significantly across restoration treatments, but there was a trend toward a larger number of individuals in applied nucleation plots (Figure 3A,B).

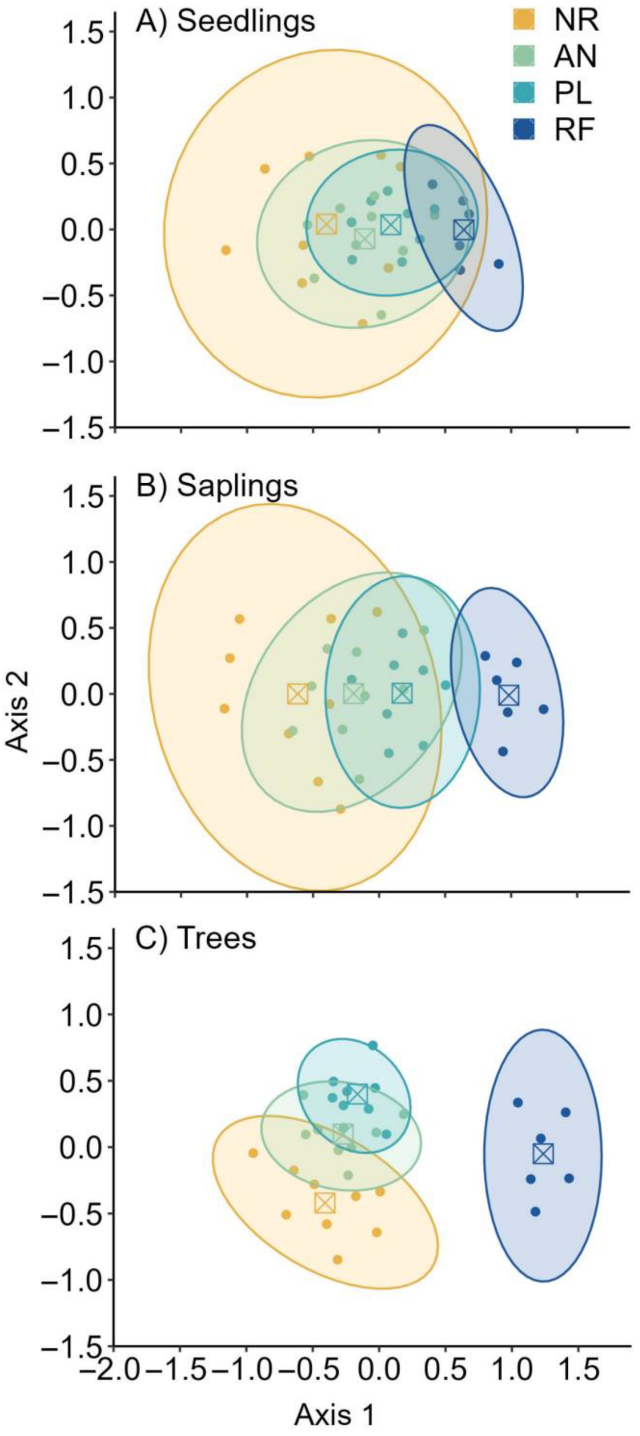

FIGURE 2 Nonmetric multidimensional scaling plot of Chao dissimilarity distances among site community matrices based on total species abundances for (A) seedling, (B) sapling, and (C) tree recruits from natural regeneration (NR), applied nucleation (AN), plantation (PL), and reference forest (RF). Shaded ellipses indicate 95% CIs of within-group variance. Plot values are shown as small circles, and treatment group centroids are large cross-filled squares. Stress = 0.17–0.18 for all three vegetation size classes. See Appendix S1: Table S4 for pairwise comparisons of treatments.

The abundance of early-successional trees was greater in both natural regeneration and applied nucleation than plantation and reference forest treatments (Figure 3C).

Density of later-successional individuals in the tree size class across all restoration treatments was a small fraction (8%) of that in reference forest, although applied nucleation showed marginally higher densities of small- and medium-seeded recruits than did the other restoration treatments (Figure 3C; Appendix S1: Figure S2). Differences in abundance of later-successional seedlings and saplings across treatments varied by seed size. Small-seeded, later-successional seedlings showed similar abundance across all treatments (Figure 3A), whereas sapling densities were lower in natural regeneration (Figure 3B). *Miconia* spp. and *Palicourea padifolia* were particularly common mid-successional taxa across all restoration treatments, though *P. padifolia* was rarely observed in reference forest (Appendix S1: Figures S3 and S4). Small-seeded, late-successional saplings were more abundant in reference forest (Appendix S1: Figure S2B) largely driven by *Trophis mexicana* and *Lacistema aggregatum* (Appendix S1: Figure S4D).

Seedlings and sapling density of later-successional species with medium and large seeds generally were lowest in natural regeneration, intermediate in applied nucleation, and highest in plantation and reference forest with the pattern being strongest for large-seeded late-successional taxa (Figure 3A,B; Appendix S1: Figure S2A,B). Medium-seeded, mid-successional saplings (e.g., *Ocotea puberula, Allophylus psilospermus*; Appendix S1: Figure S3) had the lowest densities in natural regeneration while both planted treatments had densities at least equal to those observed in reference forest (Appendix S1: Figure S2A,B).

DISCUSSION

After nearly two decades, our comprehensive census of experimental restoration plots showed that the naturally recruiting tree communities are still limited to planted and early-successional taxa, but understory communities show high potential for future forest recovery. Natural regeneration plots had more than twice the expected number of species (corrected for differences in sampling area) as recorded in surveys 7 years prior (Holl et al., 2017). In turn, both planted treatments produced similarly elevated richness of recruiting seedling and sapling communities as compared to natural regeneration, but the relative abundance of late-successional recruits,

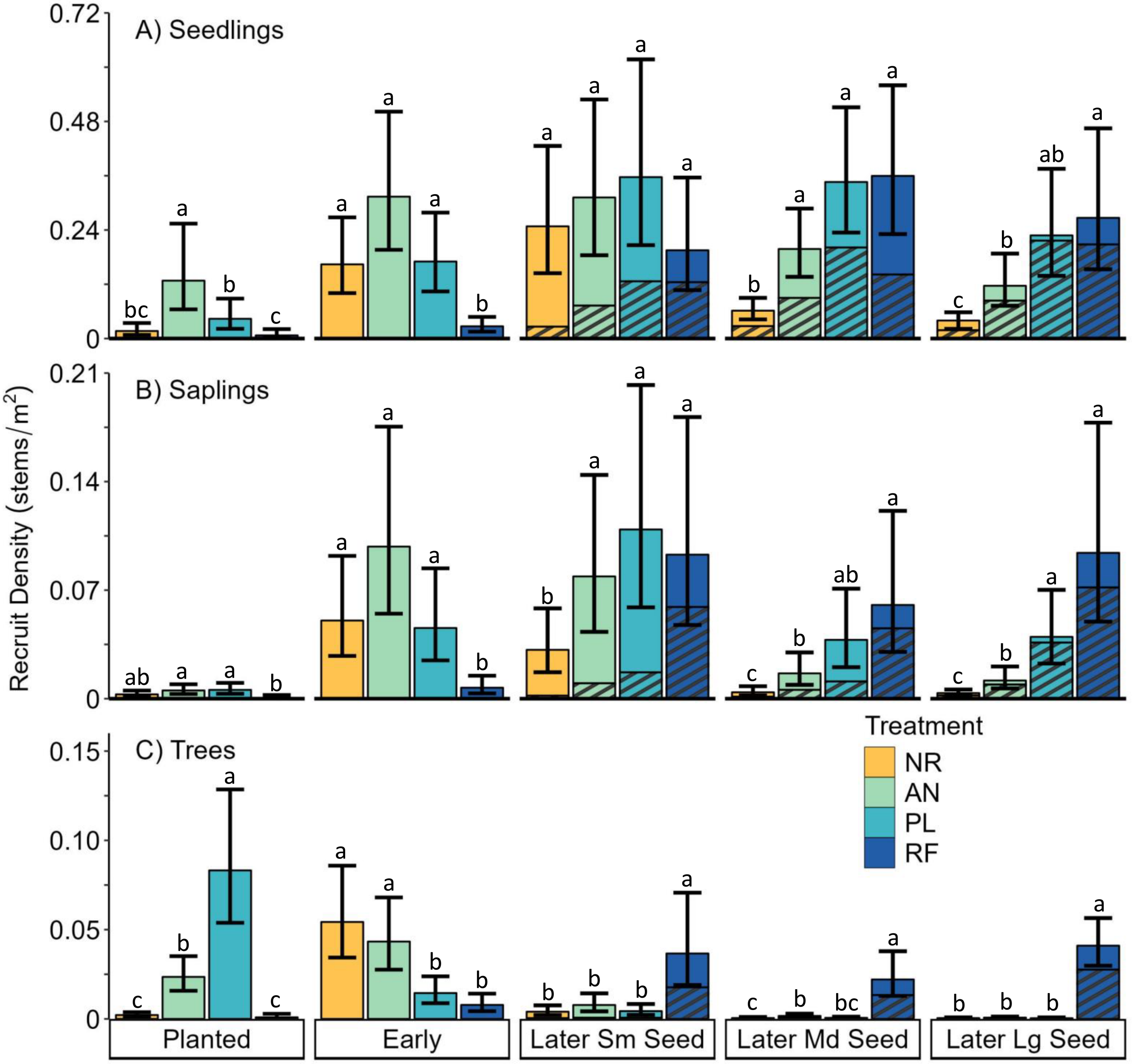

FIGURE 3 Mean stem densities of (A) seedlings, (B) saplings, and (C) trees of planted, early successional, and later-successional species with small (Sm, <5 mm), medium (Md, 5–<10 mm), and large (Lg, ≥10 mm) seeds across the four treatments: natural regeneration (NR), applied nucleation (AN), plantation (PL), and reference forest (RF). Later-successional species include mid- (no cross hatching) and late- (cross hatching) species. Error bars represent 95% CIs. Note different *y*-axis scales. Means with the same letter do not differ significantly ($p > 0.05$) using pairwise comparisons of estimated marginal means with a Bonferroni correction to resulting *p*-values. See Appendix S1: Figure S2 for statistical comparisons of mid- and late-successional species separately.

particularly those with large seeds, was greatest in plantation plots. Any positive effects of either tree planting strategy on later-successional species recruitment, however, were not yet detectable among the largest stem sizes, and the overall composition of all restoration treatments still differed substantially from reference forest. These demographic and compositional patterns signal that differing restoration approaches could have diverging effects on both the pace and trajectory of succession beyond the second decade of recovery.

Although previous observations from this study have consistently shown similar effects of the two planting methods on the recovery of seed dispersal and seedlings (e.g., Holl et al., 2017; Werden et al., 2022), our comprehensive census reveals subtle compositional differences between applied nucleation and plantation treatments after nearly two decades. First, we found evidence of recruitment limitation as a function of seed size that is curtailed through active planting. Recruit densities of late-successional seedling and sapling species with medium and large seeds were consistently greater in the planted treatments than natural regeneration, and plantation showed comparable densities to reference forest. Our findings support the importance of canopy formation to facilitate colonization of large-seeded species during tropical forest succession, a result consistent with many prior studies (De La Peña-Domene et al., 2016; Rivas-Alonso et al., 2021). Despite increasing canopy cover in applied nucleation plots, plantations continue to have a more uniform canopy cover than applied nucleation in this second decade of recovery (Holl et al., 2020; Zahawi et al., unpublished data). In turn, large birds such as toucans, which are a key disperser of large seeds in our study region, visited plantations more frequently than they did applied nucleation plots over a decade-long period (Reid et al., 2021). Whereas differential seed fates among treatments present an alternative explanation to the observed treatment effects, large-seeded trees are generally not strongly establishment-limited during tropical secondary succession (de la Pena-Domene et al., 2018; Metz et al., 2023; Pereira et al., 2013), and prior data from our experiment suggested dispersal—rather than establishment—limitation as the primary driver of variation among treatments (Werden et al., 2020). Recent seed dispersal data (San José et al. unpublished), however, indicate that differences in abundance of medium- and large-seeded, later-successional seeds dispersed to the three treatments have diminished substantially in the past few, suggesting that recruit similarity across restoration treatments may converge over time.

A second pattern we observed is that applied nucleation plots tended toward higher densities of early-successional seedlings than plantations, although the difference was not significant due to high within-treatment variation. Given the ubiquitous dispersal of these taxa in our study system (Reid et al., 2015; Werden et al., 2021), their varying recruit densities are indicative of differing ecological filtering between the two planted treatments. Varying canopy development and light environments are often important drivers of tropical forest plant size class distributions, particularly as succession proceeds (Balderrama & Chazdon, 2005; Nicotra et al., 1999; Van Breugel et al., 2019). The greater canopy cover in plantations corresponds with increased shade and litter depth, both of which inhibit the germination and emergence of early-successional tropical trees with small seeds (Celentano et al., 2011; Muscarella et al., 2013).

At the same time, the slightly more open canopy, and in turn light availability, in applied nucleation environments has the potential to enhance growth and transition of recruits to larger size classes (Caughlin et al., 2019). Indeed, there were more early-successional trees in applied nucleation and natural regeneration than in plantation plots, and saplings showed a similar trend. However, we observed an overall suppression of natural recruits reaching the canopy in plantations and a trend toward accelerated recruit growth (i.e., more tree-sized stems) in applied nucleation for some later-successional species, which has also been supported by individual sapling measurements over time (Kulikowski et al., 2023). These demographic trade-offs in restoration strategies present important questions about late-successional processes which have rarely been investigated. As seed rain becomes more similar to the restored forest stand over time (Huanca Nuñez et al., 2021), local abiotic and biotic conditions—light availability in particular—will determine which species survive and transition into the canopy layer (Caughlin et al., 2019) while the canopy cover across treatments is also slowly converging over time (Zahawi et al., unpublished data).

A major open question in the forest restoration literature is the extent to which active planting interventions have legacy effects on successional trajectories over time as compared to naturally generating forest. In recent years, we have observed high mortality of our two fast-growing planted species, *E. poeppigiana* and *I. edulis*, of which only ~30% survived after 16–18 years. Nonetheless, the tree layer in plantations remains dominated by planted species, all of which are now reproductive, so recruits of these species could influence the successional trajectory. Contrary to expectation, however, abundance of planted tree recruits did not correspond with greater initial planting densities as applied nucleation had greater seedling abundance of these species, which was likely facilitated by the more heterogenous and open canopy during the first decade. That said, the abundance of saplings of planted species was similarly low across restoration treatments which is consistent with our observations of very high seedling mortality of these species that is likely driven by shading and herbivory (Holl et al., 2022; Kulikowski et al., 2022).

Beyond the initial two decades of forest recovery, tropical forest succession is largely dependent on the mortality of pioneers and planted tree species to drive gap dynamic processes and growth of later-successional species (Finegan, 1996; Philipson et al., 2012; Swinfield et al., 2016). Until now, however, canopy openings created by *E. poeppigiana* and *I. edulis* mortality have been filled quickly by the expanding crowns of *V. guatemalensis* and early-successional trees, such as *Koanophyllon pittieri*, *Hampea appendiculata*, and *Heliocarpus* spp.

(Lanuza et al., 2018). Whether gap dynamics occur naturally or are facilitated by subsequent felling by restoration managers to enhance growth of later-successional species will depend on the specific tree species used in restoration interventions and long-term project goals.

Many past studies show that natural regeneration, while often a cost-effective restoration option, can have highly unpredictable recovery outcomes (e.g., Atkinson et al., 2022; Chazdon et al., 2020; Chazdon & Guariguata, 2016). Additionally, in the absence of active management, there is a much stronger likelihood that succession under natural regeneration will become arrested or not proceed along a timeline that is relevant to restoration goals (Benayas et al., 2009; Meli et al., 2017). Natural regeneration plots in our study consistently supported substantial abundance of early-successional trees and some seedlings and saplings of later-successional species, suggesting that succession is progressing, albeit slowly. Yet, natural regeneration had more variable composition among plots for seedling and saplings than did both planted treatments. Even under conditions with high natural regeneration potential, the stochastic recovery pattern can produce alternative successional trajectories that are dependent on local seed sources, the regional species pool, and land use history (Atkinson et al., 2022; Mesquita et al., 2015; Norden et al., 2015). These variable trajectories can include facilitating actively invading non-native species, which tend to have pioneer life history strategies (Catterall, 2016). Indeed, our natural regeneration plots assembled communities that were disproportionately dominated by early-successional species compared with active restoration and also showed a propensity to amplify legacies from prior land use conditions. Namely, several natural regeneration plots had substantial abundances of non-native (albeit naturalized) species such as *E. poeppigiana*, *Citrus* spp., and *Syzygium jambos* that are common in agricultural landscapes. *E. poeppigiana* and *Citrus* spp. primarily occurred from resprouting of cut stems established before restoration had begun, whereas *S. jambos* established from seeds dispersed by bats. Importantly, actively restored plots had fewer individuals of these non-native species growing past the seedling stage. In sum, the greater likelihood of poor outcomes such as stalled recovery or invasion make natural regeneration a potentially risky strategy for restoration practitioners aiming to achieve specific long-term restoration outcomes, although allowing recovery to proceed for a couple of years before choosing whether intervention is necessary can help to reduce this uncertainty (Holl et al., 2018), and thereby allocate limiting resources more effectively. Such preparatory monitoring periods also provide an opportunity to identify naturally regenerating trees, which can be assisted (e.g., grass clearing, preventing fires) in tandem with more targeted plantings in areas with sparse seedling growth.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Our study is one of the few with the longevity, replication, and thorough sampling to compare the effects of restoration interventions on mid-successional filtering, revealing several key management implications. First, we show in a multisite experiment that earlier patterns of active tree planting (applied nucleation and plantation strategies) accelerating recovery over natural regeneration continue through the second decade. Planting only four species of trees substantially increased the number of species and individuals of later-successional species and, importantly, reduced variability in recovery across sites. This contrasts with prior meta-analyses of active versus passive tree planting strategies that mostly compared results from sites with different land use histories and studies of single restoration interventions and suggested that natural regeneration results in similar or faster recovery rates to active tree planting (Crouzeilles et al., 2017; Meli et al., 2017). Given the highly variable recovery patterns in natural regeneration, active planting strategies should be encouraged when land use history and seed sources are either poorly documented or known to be unfavorable.

Second, whereas both applied nucleation and plantation restoration strategies accelerated recovery, nuanced ecological trade-offs emerged in the second decade. We found a new trend of greater abundance of larger seeded, late-successional species in plantation than applied nucleation plots, but longer term data are needed to determine whether these comparatively rich understory communities will transition into mature canopy trees more rapidly than in applied nucleation. In fact, data presented here and growth measurements of marked recruits over time (Kulikowski et al., 2023) suggest that recruits are likely to mature more rapidly in the slightly more open canopy of the applied nucleation treatment. Given that the plantation treatment canopy remains dominated by planted species, canopy thinning might help to further accelerate recovery processes (Swinfield et al., 2016) but needs testing.

Finally, the fact that we observed ~90% of reference forest species in our restored plots after less than two decades supports the potential for tropical forests to recover from intensive prior agricultural land use. Nonetheless, we hasten to reiterate that the overall structure and composition of all our restoration treatments are still substantially different from reference forest, and full recovery is likely to take several decades to centuries (Elsy et al., 2024). Moreover, the rapid recolonization rate of a diverse suite of species is partly a function of the extensive seed sources remaining in remnant forests, along fence lines, and in active agricultural lands in the region (Zahawi et al., 2021; Zahawi, Dandois, et al., 2015) and would likely be substantially slower in more deforested landscapes (Pardini et al., 2010). So, protecting existing tropical forests must be the first priority (Brancalion & Holl, 2020; Di Sacco et al., 2021). Taken together, our results highlight (1) the value of multi-decadal, well-replicated studies to evaluate the effect restoration on successional trajectories and (2) the importance of long-term commitments to forest restoration to achieve promised biodiversity outcomes.

AUTHOR CONTRIBUTIONS

Karen D. Holl and Rakan A. Zahawi conceived the study, designed the protocol for sampling, and contributed to the writing and revision of the final manuscript. F. Oviedo Brenes oversaw the botanical identification. All authors contributed to data collection. Spencer C. Schubert analyzed the data and led the writing and revision of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Schubert et al., 2024a) are available in Dryad at https://doi.org/10.5061/dryad.s7h44j1gc. Code (Schubert et al., 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.13338363.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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