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Tree recruitment dynamics over two decades of tropical forest restoration

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Abstract

Ambitious global targets to restore tropical forests would benefit from long-term, multi-site field evaluations that compare restoration strategies. We monitored 10,310 individuals across 11 sites in southern Costa Rica to compare tree recruit dynamics in three restoration interventions and reference forests through the second decade of recovery. Early-successional recruits had greater seedling-to-sapling transitions and sapling growth in natural regeneration and applied nucleation compared to plantation treatments during early recovery. Seedling and sapling demographic rates largely converged for all successional groups across restoration treatments after nearly two decades. Whereas species composition in restored plots is following a successional trajectory toward reference forest, all treatments still differ substantially from reference forest, further supporting that tropical forest recovery takes decades to centuries even with active restoration. The persistent divergence in community composition, paired with the scarcity of late-successional recruits, particularly in natural regeneration, underscores that long-term recovery is primarily driven by dispersal limitation.

Introduction

Despite the urgent need and numerous commitments to restore tropical forests across thousands of hectares[1], most restoration studies take place at one or a few sites in experimental plots spanning only tens to hundreds of meters[2]. Further, field projects rarely compare restoration strategies directly and typically monitor for fewer than three years[3,4] — a serious limitation, given that meaningful biodiversity and carbon benefits typically take decades or centuries to accrue[5–7]. Most studies and active projects also focus on the survival and growth of planted trees[2,8], yet long-term recovery in diverse tropical forests hinges on the recruitment and long-term survival and growth of naturally recruiting seedlings and saplings, which ultimately shape forest composition and successional trajectories. Quantifying these demographic processes is essential to assess the extent and rate of recovery under different restoration interventions. Yet monitoring at the spatial and temporal scales needed to capture long-term outcomes has rarely been done[2,9,10], given cost and time limitations.

Forest restoration strategies span a continuum from low- to high-intensity interventions[11]. Three widely implemented strategies along this continuum are natural regeneration, applied nucleation, and plantation-style planting[12], which differ substantially in cost, design, and potential outcomes. Natural regeneration, in which degraded land recovers without active planting, is widespread across the tropics and offers the greatest potential for restoring large areas at low cost[13,14]. It can yield greater floristic diversity and spatial heterogeneity than extensive planting, but perceived risk and widely variable outcomes have largely excluded it from the growing carbon market[15,16]. Plantation-style restoration, the most common active strategy[2], plants trees at high density in uniform patterns. Although practitioners increasingly use diverse species assemblages, plantations yield a relatively homogeneous stand structure[17] and are favored for faster establishment and more predictable results[2,18], despite carrying high nursery, planting, and maintenance costs. Applied nucleation, an intermediate approach, uses

clustered or spatially patterned plantings that require fewer resources than plantations and may accelerate broader recovery and promote structural heterogeneity[19]. Yet few field studies have compared demographic rates and composition of recovering trees across these strategies over the multi-decadal timeframe necessary to assess forest recovery trajectories.

In wet tropical forest recovery, the early stages of succession are dominated by fast-growing, short-lived, light-demanding taxa that slowly give way to slower-growing, shade-tolerant species and assemblages more closely resembling reference forests[20]. On deforested lands, the pace of this turnover—seedling recruitment, survival, growth, transition to saplings, and ultimately community composition—depends on many interacting filters, including seed dispersal, surrounding vegetation, soil degradation, and other biotic and abiotic conditions [21,22]. Different restoration strategies have varied effects on these filters, which shape successional trajectories and, in turn, restoration outcomes. Caughlin, et al. [23] for example, found greater recruitment and earlier peak growth in actively planted than naturally regenerating treatments over seven years in Mexico, although planted stands took longer to reach reproductive maturity. Conversely, the greater canopy openness of naturally regenerating forests may favor seedling-to-sapling transitions, which are otherwise slowed under heavy shade[24,25]. Chronosequence studies suggest that naturally regenerating forests still differ in vegetation composition from old-growth forests after a century or more[26,27].

Our nearly two decades of continuous monitoring of demographic processes and community assembly across natural regeneration, applied nucleation, plantations, and adjacent reference forests at multiple sites in southern Costa Rica[28] offer a rare opportunity to compare these three strategies as succession unfolds. In the first decade, both planted treatments, applied nucleation and plantation, supported greater species richness and density of naturally recruiting woody seedlings than natural regeneration[29] likely due to greater seed dispersal, particularly of larger-seeded species[30], and reduced cover of competitive pasture grasses[28]. Early-successional seedling survival was greater in applied nucleation than natural regeneration, and later-successional sapling growth was slightly faster in applied nucleation than plantation, likely because the more heterogeneous canopy in the applied nucleation treatment created more favorable light levels[31]. In the second decade, establishment of mid- and late-successional recruits increased, and both planted treatments still exceeded natural regeneration in richness, recruit density, and spatial coverage, with recruitment in natural regeneration plots remaining patchy[8,32]. Despite these gains, large-seeded later-successional species remained underrepresented across all treatments, indicating an ongoing seed dispersal bottleneck[33,34]. It remains unclear whether and when these converging demographic rates will translate into a community composition more akin to reference forest, and the relative importance of demographic bottlenecks in driving these trajectories.

Here, we used 18 years of tree recruit demographic data from this multi-site experiment to compare survival, seedling-to-sapling transition, and growth of early-, mid-, and late-successional species across three restoration treatments and reference forests, and to assess whether seedling and sapling community composition in restoration treatments is converging toward reference forests or following

novel successional trajectories. We focused on seedlings and saplings, rather than adult trees, because they comprise the vast majority of stems during this study period, are not dominated by a small number of early-successional taxa as is the tree recruit category[32,35], and represent the template of the future adult tree community. By linking demographic processes (growth, survival, and size-class transitions) to community assembly outcomes, we aim to assess the mechanisms driving compositional trajectories across restoration treatments. Moreover, we aim to add to the paucity of information on the seedling-to-sapling transition filter on forest recovery[24].

Methods

Study region

We conducted this study in southern Costa Rica at 11 sites located within a ~ 100 km² area extending from the Las Cruces Biological Station (LCBS; 8°47'07" N, 82°57'32" W) to the town of Agua Buena (8°44'04" N, 82°56'05" W). The region lies at the transition between Tropical Premontane Wet and Rain Forest life zones[36]. Elevations across sites range from 1100 to 1290 m, with a mean annual temperature of about 21°C and rainfall between 3500 and 4000 mm, concentrated outside of a December–March dry season. Plots are separated by ≥ 700 m and mostly located on steep slopes of 15–35°. Soils are volcanic in origin, slightly acidic and low in phosphorus, but high in organic matter [37]. The regional landscape is a mosaic dominated by cattle pasture and low-intensity coffee production, intermixed with secondary and old-growth forest fragments that cover ~ 30% of the study area [38]. All plots had been farmed or grazed for at least 18 years before restoration [28]. At the beginning of the experiment, sites were primarily dominated by non-native pasture grasses, along with patches of forbs and the fern *Pteridium arachnoideum* (Kaulf.) Maxon.

Experimental design

Between 2004 and 2006, we established restoration experiments at each site, which included three 50 × 50 m plots separated by ≥ 5 m. Over the nearly two-decade timespan, four sites lost at least one treatment due to major human disturbance, so we include data from natural regeneration n = 9–10 plots, applied nucleation n = 9–10, plantation n = 8–11. We monitored five reference forest plots starting in 2014.

Plantations were uniformly planted with tree seedlings, whereas the applied nucleation treatment consisted of six planted tree nuclei of three different sizes (two each of 4 × 4 m, 8 × 8 m, and 12 × 12 m), with sizes arranged randomly and separated by ≥ 8 m. Planting density was identical across both planting treatments at ~ 2.8 m spacing, resulting in 313 individuals per plantation plot and 86 individuals per applied nucleation plot, whereas no seedlings were planted in natural regeneration. Seedlings (20–30 cm tall) from four species were planted: two native, later-successional hardwoods (*Terminalia amazonia* (J.F. Gmel.) Exell and *Vochysia guatemalensis* Donn. Sm.) and two naturalized, early-successional

softwoods (*Erythrina poeppigiana* (Walp.) O.F. Cook and *Inga edulis* Mart.), both commonly used in Central American agroforestry. All plots, including natural regeneration, were cleared of all unplanted vegetation every three months for the first 2.5 years to reduce competition with pasture grasses and allow planted trees to establish.

By 2024, survival of the planted species varied considerably: the-early successional species *E. poeppigiana* and *I. edulis* suffered high mortality in the second decade, with < 20% surviving at the end of this study, whereas *V. guatemalensis* and *T. amazonia* persisted at much higher rates (75–80%)[35]. Canopy cover had increased substantially over time in all treatments, exceeding 50% in natural regeneration plots and surpassing 90% in both applied nucleation and plantation treatments by the end of the study (Werden and Zahawi, unpublished data).

The five surveyed remnant forests ranged from 2 to 200 ha and based on aerial photographs, had not been cleared since at least the 1940s. While all experienced some level of human impact, primarily hunting and selective logging, they served as the most intact nearby reference ecosystems for evaluating restoration outcomes.

Data collection

We surveyed tree seedlings (≥ 20 cm tall and < 1 cm diameter-at-breast height (DBH)) and saplings (≥ 1 cm and < 5 cm DBH) in all restoration plots annually during late June-early July from 2009–2019 and in 2021, 2023, and 2025. We did not record recruits < 20 cm in height because it was impossible to reliably detect them amongst the dense understory cover of grasses and forbs in many plots. Tree seedlings were measured in 1×2-m quadrats, and saplings were measured in 2×4-m quadrats. Quadrats were grouped into four belt transects, one in each of the four quarters of the plot in natural regeneration and plantations, and six associated with each of the tree nuclei in applied nucleation (Fig. S2). The applied nucleation treatment was sampled more intensively to quantify potential differences in recruitment between planted and unplanted areas, so abundances were adjusted prior to community analyses (see Fig. S2 for details).

Each recruit was permanently tagged, and survival was recorded in subsequent sampling years. We recorded the height of seedlings ≥ 20 cm to < 50 cm tall to the nearest cm and the height of seedlings from 50-200-cm tall and < 1-cm DBH to the nearest 5 cm. For the few seedlings with height > 200 cm and DBH < 1 cm, we recorded the height as > 200 cm, given that it was difficult to measure the height accurately on steep terrain and the stems were often inclined. For saplings (DBH ≥ 1 and < 5 cm), we measured the DBH of the largest stem to the nearest mm.

Data analysis

Given our emphasis on forest succession, we omitted recruits from planted species and individuals that resprouted following previous agricultural activities (primarily *Citrus* spp. and *E. poeppigiana*). A small

number of individuals (0.75%) were not identified and were excluded from analyses. The two *Heliocarpus* species in our system (*americanus* and *appendiculatus*) were not consistently identified to species and therefore grouped by genus in composition analyses. We categorized recruit species as early-, mid-, or late-successional, based on the 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, as those commonly found in disturbed environments and young secondary forests but typically not found in mature forests. Mid-successional taxa include tree species that colonize at any stage of forest succession but are well represented in old-growth forests, whereas late-successional species are typically observed in old-growth forests only. We categorized the dispersal mode of each recruiting tree species based on local knowledge and literature reviews. We obtained all IUCN assessments available for recruit species as of July 2025 using the *rredlist* R package[39].

For temporal analyses, “years since restoration” represents the number of years since vegetation clearing ceased, 2.5 years after planting. Since reference forests do not have an initial “restoration year”, we did not include reference forests in our statistical models of demographic rates. We present the values in the text and figure for comparative purposes and refer to “sampling year” in figures, which corresponds to the middle of the initial restoration years (2005), since we set up plots over three years. All data analyses were conducted in R version 4.5.2 or later.

Modeling framework for demographic analyses

We used generalized linear mixed models (GLMMs, R packages *lme4* and *glmmTMB*) to examine how seedling and sapling demographic rates (survival, seedling-to-sapling transition, and growth) were affected by the interaction between year-since-restoration (hereafter “year”) and restoration treatment. We did not analyse seedling growth (height), as we transitioned from height to DBH growth measures at greater than 1-cm DBH; so, a seedling height analysis would be biased towards recruits with slow growth. We fit separate models for early, mid, and late-successional life-history strategies. For survival analyses, we further separated models by seedling and sapling age classes. We omitted treatment × year-since-restoration combinations with $n < 5$ plants to avoid spurious estimates, particularly in survival and seedling-to-sapling transition models. These omissions mostly occurred early in succession when recruitment was sparse. For some subsets of mid- and late-successional plants, the natural regeneration treatment had low sample sizes for most of the sampling period. In those cases, we excluded the natural regeneration treatment from analyses. We modeled annual survival and seedling-to-sapling transition using a binomial distribution with a complementary log-log link (i.e., discrete-time proportional hazards models). Binomial models included a log-interval offset to standardize observations from 2-year sampling periods to an annual hazard rate. Our response variable for survival = probability that a plant was alive in $year_t$ conditional on its presence in $year_{t-1}$. Our response variable for seedling-sapling transition is the probability that a plant transitioned to a sapling in $year_t$ conditional on its presence as a seedling in $year_{t-1}$. We modeled sapling growth as relative DBH growth rate where

$$RGR = (\ln(DBH_t) - \ln(DBH_{t-1})) / (year_t - year_{t-1}))$$

using a Tweedie distribution to account for continuous, non-negative data with many 0s. All models also included a covariate for plant size in the prior year: height (cm) for seedling survival and seedling-to-sapling transition and DBH (cm) for sapling survival and growth. All models initially included random intercepts for site and plant species. Growth models included an additional random intercept for individual plant identity to account for repeated measures.

We assessed interclass correlation coefficients (ICCs) using the R package *performance* for all random effects and dropped random effects where ICC < 0.07 to improve model fit. Occasionally, random effects in full models caused issues with singularity and lack of convergence. In these instances, we dropped individual random effects until models ran without issues and then assessed ICC as above. We tested hypotheses for the effect of covariates and their interactions on response variables using likelihood ratio tests (χ^2 test of distributions*)*. When interactions were not significant, we ran models without the interaction term and assessed only main effects of year, restoration treatment, and previous size. We estimated the marginal means of response variables using the R package *emmeans*. When interaction terms were not significant, but the main treatment effect was, we used Bonferroni-corrected multiple comparisons of estimates to assess significant differences between restoration treatments. We present conditional and marginal psuedo-R^2 values for GLMMs based on Nakagawa et al.[40]; see Tables S1-S3 for the final model structures of survival, seedling-to-sapling transition, and sapling growth, respectively.

We assessed model fit by examining plots of simulated residuals vs. a uniform distribution (Q-Q plots) and fitted vs. simulated residuals (homogeneity of variance) using the R package *DHARMa*. This approach simulates new response data from the fit model, creates a new distribution from the simulated data, and then compares observations to that new distribution, allowing the visualization and testing of non-Gaussian distributed data. Binomial models were also tested for overdispersion. When model deviation was present, we tested different distributions and/or link functions that reasonably matched the data support and structure. The distribution/link function combination that provided the best fit was selected for the final model.

Recruit community change over time

We analyzed the recovery of community composition over time at the plot level, excluding plot×year combinations for assemblages with < 5 total individuals (15.7% of seedling assemblages and 30.5% of sapling assemblages). These exclusions likely result in underestimating dissimilarities among recruit assemblages, but removing empty assemblages is unavoidable for community analyses and removing very sparse assemblages (1–4 individuals) reduces noise. To assess recovery of community composition over time for seedling and sapling assemblages, we first adjusted species abundances based on sampled area (see Fig. S2), then created a community dissimilarity matrix for each size class using the R package *vegan*. We used the Morisita-Horn dissimilarity index because it is robust to undersampling[41]. We visualized the trajectories of species composition using nonmetric

multidimensional scaling, plotting the average (centroid) NMDS scores for each treatment in each year. We used PERMANOVA to test for significant differences among restoration treatments in the final survey year (2025) using the function *adonis2* and conducted post-hoc pairwise comparisons using package *pairwiseAdonis*[42]. To examine the interactive effects of time (years-since-restoration or sampling year) and treatment on the proportion of animal-dispersed recruits over time, we also modeled the proportion of recruits that belong to animal-dispersed species using binomial GLMMs with a random intercept for plot nested within site.

Results

Overview of seedling and sapling recruitment

The final data set included 10,310 recruits belonging to 174 species and 52 families. These included 8,984 individuals of 168 species recorded as seedlings and 3,232 individuals of 134 species recorded as saplings; some seedlings that transitioned to saplings were recorded in both size classes. The vast majority (99.5%) of recruits were of native species. IUCN assessments were available for 122 species (72.6%), with 107 (63.7%) in the Least Concern category, and 15 (8.9%) in categories of conservation concern (Table S4). Of the species of concern, five were found only in restoration treatments, five only in reference forests, and five in both (Table S4). The vast majority of seedlings (> 90% in all treatments) were of animal-dispersed species. The mean percentage of animal-dispersed saplings was lower initially in all restoration treatments (65–80%) than in reference forest (99%) but increased over time (Fig. S3).

Size of recruits affected all demographic rates. Taller seedlings showed significantly greater survival for all successional stages ($p < 0.001$ in all cases, Table S1). Larger-DBH, early-successional saplings had lower survival over time ($p < 0.001$), but DBH did not affect mid- and late-successional sapling survival (Table S1). Taller seedling height in previous years was significantly positively related to the probability that a recruiting seedling transitioned to a sapling for all successional stages (Table S2). RGR was negatively correlated with DBH in the previous year for all successional stages (Table S3).

Seedling and sapling survival

Seedlings and saplings had very high annual survival in the first ~ 5 years of recovery across all treatments and successional stages (Figs. 1&2). Most differences in annual survival among treatments occurred in the second decade of our study, resulting in significant interactions (Table S1). Not surprisingly, early-successional seedling and particularly sapling survival declined dramatically during the second decade (Figs. 1a&2a). At the end of the first decade, early-successional seedling and sapling survival was 70–80% across restoration treatments, but by the end of the sampling period, it had declined to 50–60% for seedlings and 30–40% for saplings. Early-successional seedling decline was greatest in natural regeneration (50.7%), followed by plantation (45.1%) and applied nucleation (39.5%) treatments. Early-successional sapling survival declined sooner in plantation than applied nucleation and natural regeneration, driving a significant interaction ($p = 0.044$), but had converged across all treatments by the end of the sampling period (Fig. 2a).

Mid- and late-successional seedling and sapling survival also decreased in restoration treatments and reference forests in the second decade (Figs. 1b-c&2b-c, Table S1), but not as strongly as for early-successional seedlings. Through the first decade, mid- and late-successional annual seedling survival was > 90% in applied nucleation and plantation treatments, as well as reference forests, but had dropped to 60–80% by the final sampling year. Mid-successional seedling survival decreased more in applied nucleation (43.8%) compared to natural regeneration (31.5%) and plantation (35.3%)(treatment × year interaction $p < 0.0001$). The number of recruits of mid-successional saplings and late-successional seedlings and saplings in natural regeneration plots were insufficient to compare trends over time.

Late-successional seedling survival was slightly lower in the applied nucleation (88.1%) than plantation (94.2%) treatment, although the difference in mean annual survival was small. Significant treatment × year interactions in mid- and late-successional saplings were driven by a downturn in survival during the later years of the study with a greater decrease in applied nucleation than in plantation treatments (1b-c&2b-c, Table S1). This decline, which coincided with an extreme weather year (2023 had the lowest annual rainfall of the 2005–2025 study period), was particularly strong for mid-successional saplings in these two restoration treatments. Reference forest seedlings, but not saplings, showed a similar decline (Figs. 1d-e &2d-e).

Seedling-to-sapling transition

Early-successional recruits showed an ~ 86% decrease in seedling-to-sapling transition probabilities in all treatments over the study period with no significant treatment × year interaction (Fig. 3a, Table S2). Early-successional seedling-to-sapling transition rates were significantly greater in natural regeneration compared to plantation and applied nucleation (Fig. 3a, Table S2). A significant treatment × year interaction in mid-successional recruit seedling-to sapling transition probability ($p < 0.001$) was driven by greater values in early years in natural regeneration (transition probability in the first year of adequate sample size: NR = 41.5%, AN = 25.2%, PL = 12.2%), which declined substantially in both natural regeneration and applied nucleation; all treatments had low seedling-to-sapling transition rates by the end of the study that were similar to values in reference forests (NR = 1.9%, AN = 3.6%, PL = 7.1%, RF = 3.1%, Fig. 3b&3d). Percent transition of late-successional recruits was low, declined significantly over time, and was greater in applied nucleation than plantation (Fig. 3c; Table S2; first-year transition AN = 6.8%, PL = 4.1%; final-year transition AN = 1.1%, PL = 0.85%, NR omitted). The mean transition probability of late-successional seedlings in reference forests was 3.7% (Fig. 3e).

Sapling growth

Early-successional sapling RGR was greater in applied nucleation and natural regeneration than plantation treatments early in recovery (Fig. 4a; Table S3; RGR in the first year with adequate sample size: NR = 0.28, AN = 0.22, PL = 0.12). RGR in all treatments decreased over time and converged by the final year of the study (final-year RGR: NR = 0.03, AN = 0.05, PL = 0.04). Mid-successional sapling growth remained consistently greater in applied nucleation compared to plantations until late in the study when growth converged (Fig. 4b&d; Table S3; first-year RGR: AN = 0.26, PL = 0.16; final-year RGR: AN and PL =

0.08, RF = 0.043, NR omitted). Late-successional growth declined significantly over time (decrease in RGR over study period: AN = 69%, PL = 61%) and was similar in applied nucleation and plantation treatments by the end of the study period (Fig. 4c; Table S3; final-year RGR: AN = 0.09, PL = 0.08, NR omitted, Fig. 4c); this was greater than for reference forest in the same year (Fig. 4e, RGR RF = 0.047).

Community trajectories

NMDS plots showed similar compositional trajectories for seedling and sapling assemblages in restoration plots, with restoration assemblages in all treatments becoming more similar to reference forest over time yet remained distinct from reference forest assemblages, which showed no directional change over time (Fig. 5). Recruit communities in the natural regeneration plots started with distinct composition but became more similar to applied nucleation and plantation over time. By the final sampling year, seedling communities did not differ significantly among restoration treatments (R^2 = 0.10, pseudo-F = 1.34, p = 0.11, Fig. S4), and sapling communities differed significantly only between natural regeneration and plantation treatments (p-adjusted = 0.048 for NR vs. PL comparison, Fig. S4, Table S5).

Discussion

By the end of the second decade of recovery, most demographic variables had converged across restoration treatments, although low recruitment of late-successional species in natural regeneration plots limited our ability to assess late-successional demographic variables in this treatment. Recruit community composition in all treatments appears to be on a trajectory toward reference forest but remains distinct from it. This convergence is fastest in plantation, intermediate in applied nucleation, and slowest in natural regeneration, although differences among treatments are narrowing. Together with prior results[32,34,43], our current findings suggest that recovery of community composition is most strongly limited by prior and ongoing seed dispersal limitation, particularly for large-seeded, late-successional species.

Annual rates of early-successional seedling and sapling survival declined substantially over the study period, which is not surprising given their life history [44–46], and the increasing canopy cover in all treatments over time, particularly for natural regeneration and applied nucleation[28]. Annual survival of mid- and late-successional seedlings and saplings exceeded 90% for the first decade but declined thereafter, with a notable dip coinciding with the strong 2023–2024 El Niño (peak ONI ≈ 2.0°C; NOAA Climate Prediction Center 2024) and associated drier-than-average conditions at our study site. The 2023–2024 El Niño had widespread impacts globally and contributed to record temperatures and forest biomass declines in Amazonia[47,48]. A similar association between previous El Niño events and elevated tree mortality has been reported elsewhere in Central America[49,50], suggesting that drought stress is a plausible driver of the 2023–2024 declines we observed, a cause for concern given that the frequency and intensity of droughts in the tropics have increased in the past 30 years[51].

Restoration treatment effects on seedling and sapling survival were much weaker than temporal effects and varied by successional stage. Mid- and late-successional seedling (≥ 20 cm height) survival was slightly lower in applied nucleation than in plantation, particularly toward the end of the study, despite similar canopy (> 90% in all treatments) and understory (Final year: AN = 43 ± 4%, PL = 39 ± 4%) cover across treatments. In contrast, first-year survival of ≤ 20-cm seedlings of eight mid- to late-successional species directly seeded into our plots was greater in applied nucleation than plantation treatments[43]. It is difficult to explain these contrasting survival trends, particularly given that the understory and overstory cover in the two treatments were similar by the end of the study. Condit, et al. [25] show that survival from seed to 1-cm sapling can range by 1000-fold across species and varies by species across a seedling size continuum, so these overall survival differences may reflect small differences in species composition, given the relatively small number of individuals, particularly of late-successional species.

Mid-successional sapling survival appeared to be lower in both applied nucleation (final year estimate [95% confidence limits]: AN = 62% [47–77], plantation = 71% [56–85]) than in reference forest (92% [81–97]. We do not know the age of most saplings in reference forest, as they were present at the beginning of sampling, but the mean DBH of both mid- and late- successional saplings was greater in reference than restored plots (mid-successional: AN = 1.85 ± 0.017 mm, PL = 1.68 ± 0.021, RF = 2.22 ± 0.043; late-successional: AN = 1.86 ± 0.039 mm, PL = 1.72 ± 0.038, RF = 2.30 ± 0.0312). So, it may be that these individuals were older and hence had already passed through critical mortality filters[24,25,52].

Seedling-to-sapling transition probabilities and sapling growth rates were greater for early-successional species in natural regeneration and applied nucleation plots than plantations at the start of the study period, which is consistent with other studies[23,31] and light limitation typical of shaded tropical forests e.g.,[53,54]. As expected, seedling-to-sapling transitions and sapling growth rates have slowed and converged across restoration treatments over time, as canopy cover has increased in natural regeneration and applied nucleation treatments. Studies in mature, closed-canopy forests show that seedling-to-sapling transition probabilities are extremely low[24,25,55]. For example, Clark and Clark [52] reported that it may take 4–12 years for a 50-cm seedling in a neotropical forest to reach 1-cm DBH. It is important to note that the planted, early-successional tree species *Inga edulis*, which comprised ~ 70% of canopy cover in the first few years after restoration[56], has suffered high mortality in the past decade with only 12% surviving in plantations as of 2025[35], which has created short-term lights gaps in the canopy in planted treatments and in turn likely enhanced the seedling-to-sapling transition[57].

Despite convergence in most demographic rates across treatments, sapling community composition still differed between natural regeneration and plantation treatments after nearly 20 years, suggesting that initial restoration interventions can have long-term legacy effects on recovery trajectories. This pattern is consistent with long-term studies of tropical forest natural regeneration showing that initial floristic composition can have a lasting influence on successional trajectories[58,59]. However, findings from the few other studies that directly compare restoration treatments over more than a few years suggest greater convergence in community composition after two decades. Beltrán et al.[60] reported that recruit

density and species density were greater in planted than naturally regenerating plots after 17 years in Mexico, but species composition overlapped across treatments. Dai et al.[61] found that after 20 years, species richness of recruits was greater in applied nucleation than natural regeneration plots in a study system in China, but composition was similar between the two treatments, and both treatments were much less similar to reference forest than in our study, likely reflecting limited late-successional seed sources in the surrounding landscape (L. Song, pers. comm.).

Together, these comparisons suggest that active planting interventions can shape not only the pace of recovery but also the persistence of compositional differences among restoration approaches. Our results are consistent with extensive prior research in the tropics showing that active tree planting often accelerates recovery in heavily used former agricultural land with minimal tree cover e.g.,[60,62]. Most of the data from our study sites to date have shown that applied nucleation facilitates similar overall tree recruitment to fully planting a site[10,28], though an exhaustive tree seedling census in 2022 indicated similar species richness but greater abundance of late-successional seedlings and saplings in plantation than applied nucleation treatments[32]. This suggests that recruitment quantity and quality, in terms of successional stage, may diverge between these treatments even when total richness does not.

Many past studies evaluating seed dispersal[34,63], direct seeding[43,64], detailed spatial recruitment patterns[21,65], along with recent syntheses[66,67], consistently show that limited seed source and dispersal, particularly of large-seeded, animal-dispersed species, is a major constraint on tropical forest recovery. Because recruit survival and growth rates are now similar across treatments, compositional differences among treatments after nearly two decades are likely more attributable to differences in propagule arrival than to differences in post-establishment demographic performance, consistent with the persistent role of dispersal limitation. This highlights the importance of maintaining large seed dispersers in a landscape that retains tree cover[30,66,68]. In our study system, remnant pasture trees, living fences, and forest remnants provide over 30% tree cover[38], yet compositional divergence between treatments persisted after two decades, implying that dispersal limitation for late-successional, animal-dispersed species remains a barrier to recovery. Hence, enrichment planting of some later-successional species may help enhance forest recovery[69,70].

Taken together, our results indicate that recruit composition in all restoration treatments is following a successional trajectory toward reference forest over time. Nonetheless, the composition of seedlings and saplings in all restoration treatments still differs substantially from neighboring mature forest after nearly two decades, and both the decreasing relative growth rates of saplings and the shortening segment lengths in the NMDS of community composition (Fig. 5) suggest that the rate of compositional change is slowing. We did not compare the composition of recruiting trees ≥ 5 cm DBH because species overlap between restoration and reference plots was minimal[32]. This is unsurprising as transitions from small sapling to canopy tree can take more than 150 years in primary forest[52], and forest recovery is broadly understood to unfold over decades to centuries[5,7,26]. We close by highlighting the oft-repeated

point that whereas natural regeneration and active restoration interventions can provide biodiversity and ecosystem service benefits, they are not a substitute for conserving relatively intact ecosystems.

Declarations

Conflict of interest declaration

We declare we have no competing interests.

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Author Contribution

KDH and RAZ initially designed the experiment; all authors collected the data; FHJ and AJK analyzed the data, RJC, KDH, FHJ, and AJK co-wrote the first draft of the manuscript, and RAZ provided editorial feedback on multiple drafts of the manuscript. RJC, KDH, FHJ, AJK, and RAZ gave final approval for publication and agreed to be held accountable for the work performed therein.

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Data Availability

Data availability. Data will be archived on the Dryad Digital Repository upon acceptance. Code availability. Code will be archived in Zenodo upon acceptance.

Code availability.

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Figures

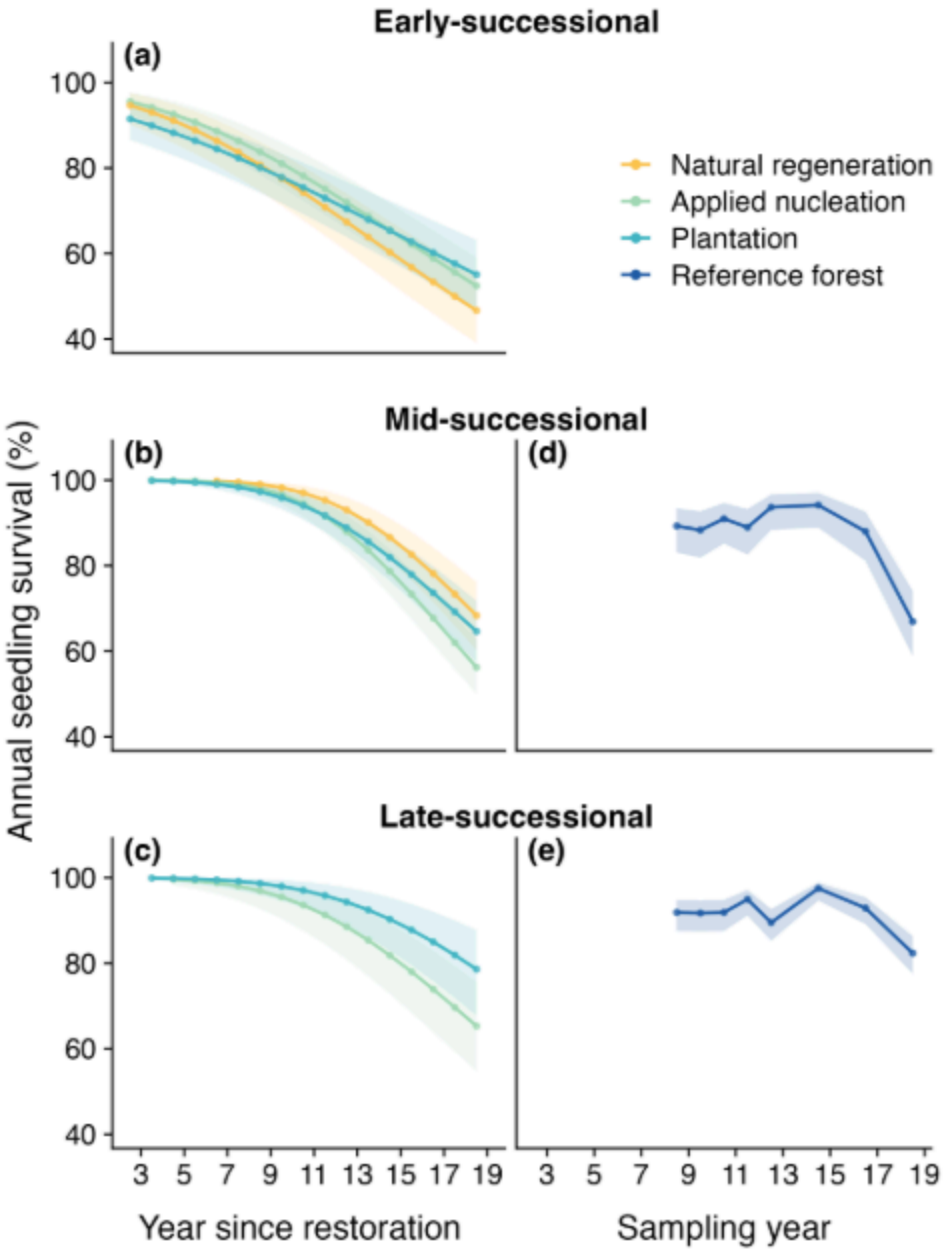


Figure 1

Annual survival (%) of seedlings by successional status over time. Left column shows estimated marginal means and 95% confidence intervals in restoration treatments for **(a)** early-successional (n = 8073 observations on 2663 seedlings), **(b)** mid-successional (n = 8223 observations on 2728 seedlings), and **(c)** late-successional species (n = 3170 observations on 1047 seedlings). Natural regeneration was omitted from late-successional seedling analysis due to low sample size in most years since restoration. Right column shows raw survival and Wilson confidence intervals for **(d)** mid-successional (n= 1,106 observations on 295 seedlings)

and **(e)** late-successional (n = 1958 observations on 506 seedlings) species in reference forest by absolute sampling year.

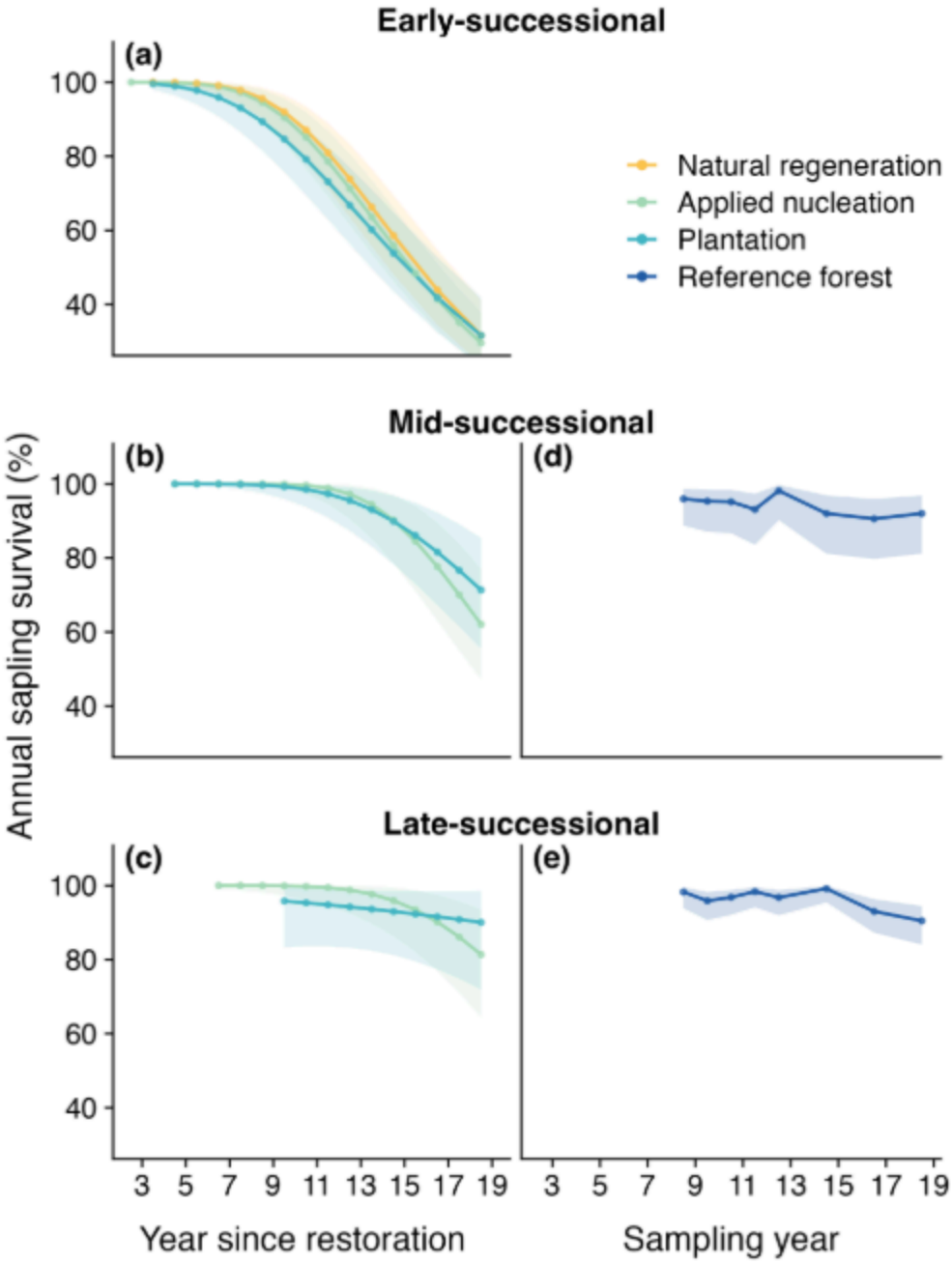


Figure 2

Annual survival (%) of sapling by successional status over time. Left column shows estimated marginal means and 95% confidence intervals in restoration treatments for **(a)**early-successional (n = 4970 observations on 1213 saplings), **(b)** mid-successional (n = 3149 observations on 939 saplings), and **(c)** late-successional species (n = 691 observations on 252 saplings). Natural regeneration was omitted from mid- and late-successional seedling analysis due to low sample size in most years since restoration. Right column shows raw survival and Wilson confidence intervals for **(d)** mid-successional (n= 465 observations on 94 seedlings) and **(e)** late-successional species (n = 983 observations on 185 seedlings) in reference forest by absolute sampling year.

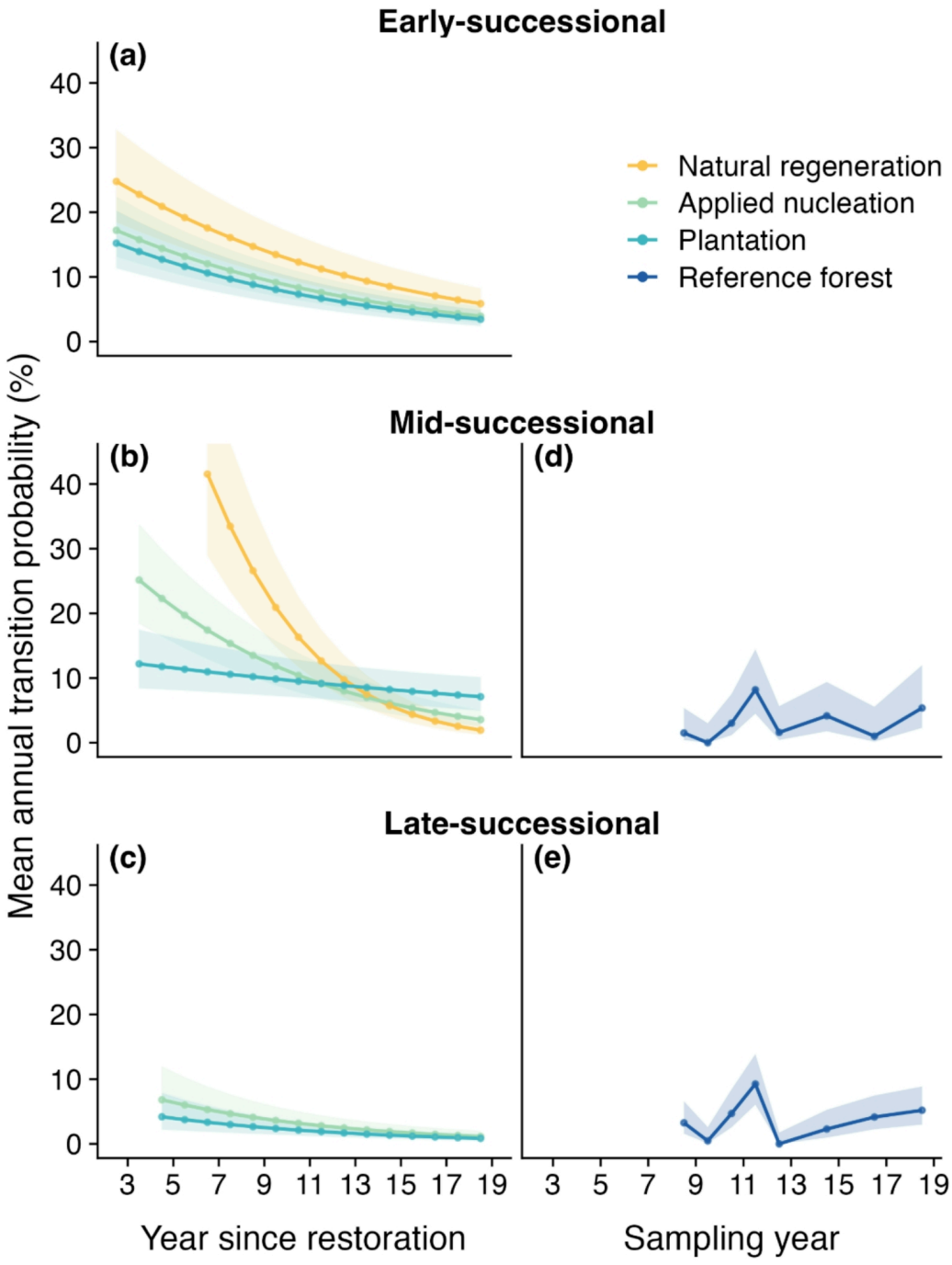


Figure 3

Mean annual probability (%) of seedling-to-sapling transitions by successional status over time. Left column shows estimated marginal means and 95% confidence intervals in restoration treatments for **(a)**early-successional (n = 7142 observations on 2391 recruits), **(b)** mid-successional (n = 7989 observations on 2750 recruits), and **(c)** late-successional species (n = 3206 observations on 1052 recruits). Natural regeneration was omitted from late-successional seedling analysis due to low sample

size in most years since restoration. Right column shows raw transition rates and Wilson confidence intervals for **(d)** mid-successional (n= 946 observations on 236 seedlings) and **(e)** late-successional species (n = 1765 observations on 426 seedlings) in reference forest by absolute sampling year.

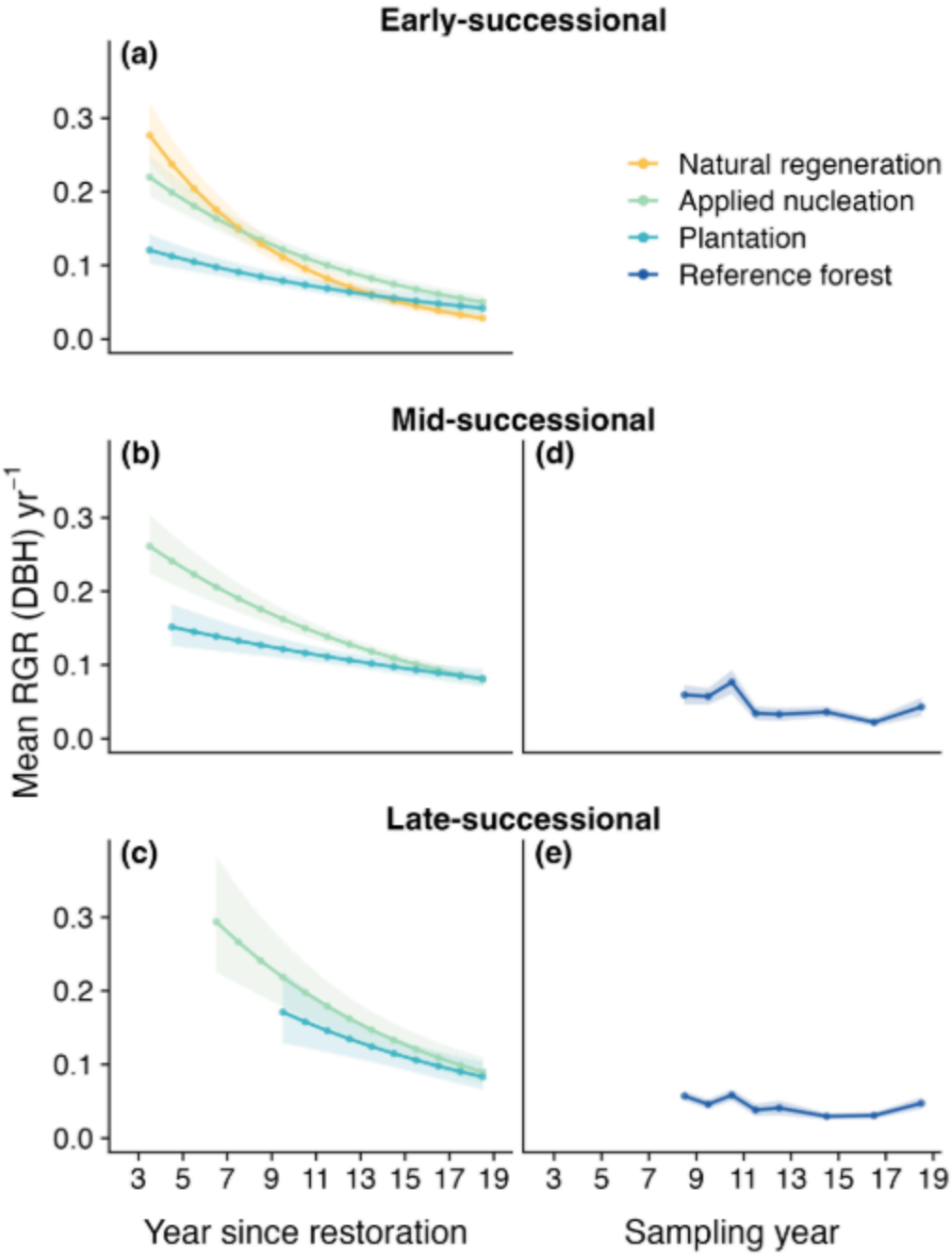


Figure 4

Mean annual relative growth rate (DBH) of saplings by successional status over time. Left column shows estimated marginal means and 95% confidence intervals in restoration treatments for **(a)** early-successional (n = 4166 observations on 1041 saplings), **(b)** mid-successional (n = 2797 observations on 854 saplings), and **(c)** late-successional species (n = 641 observations on 247 saplings). Natural regeneration was omitted from mid- and late-successional seedling analysis due to low sample size in

most years since restoration. Right column shows raw RGR and Wilson confidence intervals for **(d)** mid-successional (n= 406 observations on 85 seedlings) and **(e)**late-successional species (n = 900 observations on 172 seedlings) in reference forest by absolute sampling year.

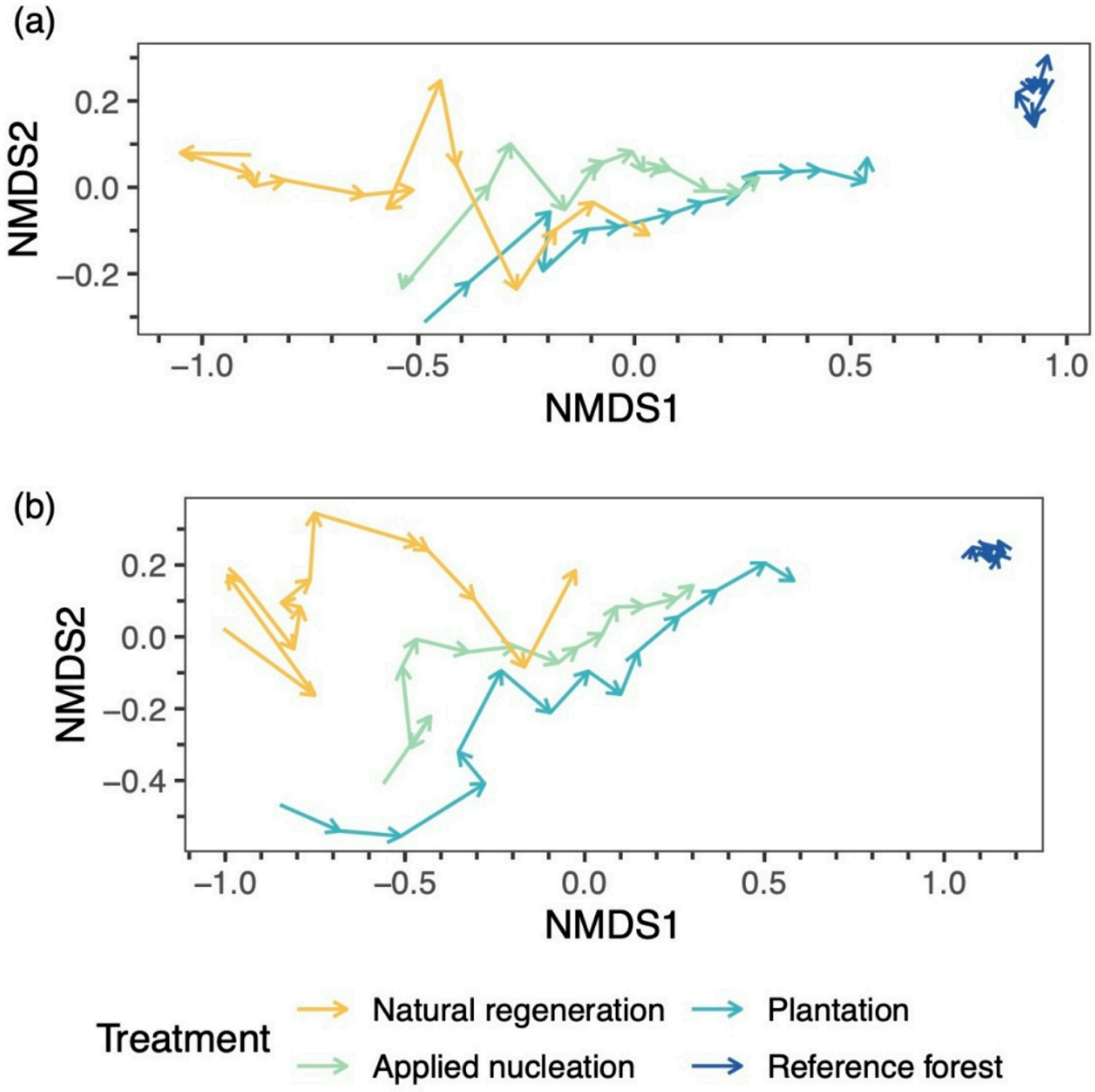


Figure 5

Community trajectories for tree recruits. NMDS plots based on Morisita-Horn dissimilarity matrices for **(a)** seedling (total n = 415, stress = 0.25) and **(b)** sapling (total n = 342, stress = 0.22) assemblages. Vertices represent the mean composition of treatment×year combinations (n plots = 4-11 for seedlings

and 2-11 for saplings) with segments connecting consecutive censuses and the direction of change indicated by arrowheads. Year range for reference forest plots is 2014-2025. Year range for restoration plots is 2009-2025 for seedlings and 2010-2025 for saplings. Plots were not sampled in 2020, 2022, or 2024.

Supplementary Files

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