Restoration interventions mediate tropical tree recruitment dynamics over time

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Abstract

Forest restoration is increasingly heralded as a global strategy to conserve biodiversity and mitigate climate change, yet long-term studies that compare the effects of different restoration strategies on tree recruit demographics are lacking. We measured tree recruit survival and growth annually in three restoration treatments – natural regeneration, applied nucleation, and tree plantations – replicated at 13 sites in southern Costa Rica, and evaluated the changes over a decade. Early-successional seedlings had 14% higher survival probability in the applied nucleation than natural regeneration treatments. Early-successional sapling growth rates were initially 227% faster in natural regeneration and 127% faster in applied nucleation than plantation plots but converged across restoration treatments over time. Later-successional seedling and sapling survival were similar across treatments but later-successional sapling growth rates were 39% faster in applied nucleation than in plantation treatments. Results indicate that applied nucleation was equally or more effective in enhancing survival and growth of naturally recruited trees than the more resource intensive plantation treatment, highlighting its promise as a restoration strategy. Finally, tree-recruit dynamics changed quickly over the 10-yr period,

underscoring the importance of multi-year studies to compare restoration interventions and guide ambitious forest restoration efforts planned for the coming decades.

Introduction

Ambitious efforts are underway to restore forests across the globe [1], yet restoration experiments at the temporal and spatial scale needed to guide these efforts are largely lacking [2]. Most tropical forest restoration studies and on-the-ground projects monitor only the first few years of recovery [3], despite the fact that achieving desired biodiversity and carbon sequestration benefits will take decades if not centuries [4]. Moreover, most past studies focus on measuring survival and growth of planted trees, whereas long-term success of forest restoration, particularly in highly diverse tropical forest, depends on the establishment, survival, and growth of naturally recruiting trees. An extensive body of literature demonstrates the importance of quantifying demographic processes to understand community dynamics and successional trajectories in naturally regenerating [e.g., 5, 6], actively planted [7], and intact forests [e.g., 8, 9]. However, rarely have survival and growth of recruiting tree seedlings and saplings been compared over time across different restoration approaches [but see 10] ranging from passively (i.e., natural regeneration) to actively (most commonly planting trees) restored forests [11].

As politicians, investors, practitioners, and the general public jump on the global bandwagon to plant a trillion trees worldwide, a repeated question has been whether investing resources in tree planting actually accelerates forest recovery over the long-term [12, 13], given that large areas of forests across the globe have regenerated naturally without human intervention [14]. In fact, recent meta-analyses suggest that overall recovery of biodiversity, carbon sequestration, and nutrient cycling are similar or may even be faster in passively compared to actively (restoration plantings) restored forests [15, 16]. Given the paucity of long-term studies that directly compare multiple forest restoration approaches at the same site [3, 16], however, syntheses primarily rely on data from active and passive restoration from different locations and studies. Moreover, these

meta-analyses are biased towards more successful naturally-regenerated sites; i.e., studies of passively restored sites are typically conducted where forest naturally regenerated with minimal intervention, whereas actively restored sites span a broader range of conditions, including locations where recovery is slow or non-existent [17]. Finally, despite calls for replication of restoration sites across a landscape, most studies focus on a single or a few sites [2, 3].

Long-term studies that directly compare active and passive restoration approaches at multiple sites are critical to guide investments and to gauge expectations in large-scale forest landscape restoration initiatives. Here, we compared annual survival of yearly updated cohorts and growth of naturally recruiting tree seedlings and saplings under three restoration treatments (natural regeneration, applied nucleation, and tree plantations) replicated at 13 sites distributed across the landscape. We asked how recruit demography changed over a decade. Natural regeneration and plantation-style planting have been widely employed as forest restoration approaches, whereas applied nucleation (i.e., planting trees in clusters or islands) has been suggested as an intermediate intervention strategy that helps to overcome common barriers to natural regeneration while simultaneously promoting a more heterogeneous ecosystem [18]. Our prior research shows that applied nucleation and plantations are similarly effective in increasing the abundance and diversity of tree recruits, as compared to natural regeneration [19]. But quantifying how patterns of survival and growth of these recruiting individuals change over time is key to predicting future successional trajectories [10].

We used our decade-long demographic data to disentangle the effects of restoration treatment and recruit size on seedling and sapling survival, as well as sapling growth, of both early- and later-successional species. We also explored how seedling survival and sapling growth changed as succession progressed. We hypothesized that survival and growth of early-successional recruits would be highest in the applied nucleation treatment due to intermediate canopy and understory cover and, in turn light availability [20]. The plantation treatments had high canopy cover through

most of the study period, and low light availability is a key factor limiting seedling survival and growth in tropical forests, particularly for early-successional species [6, 21]. By contrast, recruits in the natural regeneration plots must overcome strong competition from 1-3 m-tall pasture grasses [22]. We therefore expected lower early-successional survival in natural regeneration, but faster recruit growth rates than actively planted treatments due to the high light environment once recruits overtopped competitive grasses [10, 23], particularly early in the recovery process. In contrast, we anticipated that survival of later-successional species would be similar across treatments and change less over time, given that later-successional species are adapted to tolerate variable light environments [24]. Finally, we hypothesized that growth and survival rates across treatments would converge over time due to increasing canopy cover in natural regeneration and applied nucleation plots [18].

Methods

STUDY REGION

This study was conducted at 13 ~1-ha sites spread across an ~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 (Figure S1). The forests in this region are at the boundary between Tropical Premontane Wet and Rain Forest zones (Holdridge et al. 1971), range in elevation from 1100-1430 m asl, and receive mean annual rainfall of 3500-4000 mm, with a dry season from December to March. Mean annual temperature is ~21°C. All sites are separated by ≥700 m, and most are steeply sloped (15-35º). Soils are volcanic in origin, mildly acidic, low in P, and high in organic matter [25]. The landscape surrounding the plots is dominated by cattle pastures and low-intensity, sun-coffee plantations, with old-growth and secondary forest fragments of varying sizes covering 28% of the study region [26]. All sites were farmed for ≥18 years, and most were burned once or twice after clearing, but not thereafter. Most sites had been used for a mixture of cattle grazing and coffee farming and, at the start of the study, were either dominated by one or a combination of three forage grasses, *Axonopus scoparius* (Flüggé) Kuhlm.

Pennisetum purpureum Schumach., and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R.D. Webster; or hosted a mixture of grasses, forbs, and the fern *Pteridium arachnoideum* (Kaulf.) Maxon.

EXPERIMENTAL DESIGN

Five sites were established in 2004, five in 2005, and three in 2006. At each site we established three 0.25-ha (50×50 m) plots, each separated by a ≥5-m buffer. Each plot received one of three randomized treatments: natural regeneration (NR), applied nucleation (AN), or plantation (PL). Plantations were uniformly planted with tree seedlings, whereas the applied nucleation treatment was planted with six tree clusters (or islands) of three sizes: two each of 4×4, 8×8 and 12×12 m (Figure S2). Tree island sizes were randomly arranged within each row and were separated by ≥8 m. Planting density was kept constant (~2.8 m between seedlings); 313 trees were planted in plantation, 86 in applied nucleation, and none in natural regeneration plots. We planted seedlings (20-30 cm tall) of four tree species that have high survival and extensive canopy development [27]. These included two natives, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), and two naturalized softwoods, *Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. (Fabaceae) that are used widely in intercropping systems in Central America. In all plots (including natural regeneration) all herbaceous and woody vegetation was cleared to ground level at ~3-mo intervals for the first 2.5 years to allow planted tree seedlings to grow above existing vegetation. Vegetation clearing ceased between 2007 and 2009 depending on when the site was initially planted. By the end of the study, tree canopy cover (based on densiometer measurements) had increased substantially in all treatments to >60% in natural regeneration and >90% in applied nucleation and plantations (Fig. S3a).

DATA COLLECTION

We surveyed tree seedlings (≥20 cm tall and <1 cm DBH) and saplings (≥1 cm and <5 cm DBH) annually during late June-early July of each year in all restoration plots. We did not record

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recruits <20 cm in height because it was impossible to reliably detect them amongst the dense understory cover of grasses and ruderal forbs in many plots. We started sampling in 2007-2009 (3 years after a plot was established and 6 months after understory clearing ceased) and continued through 2019. 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 quadrant of the plot in natural regeneration and plantations, and six associated with each of the tree islands in applied nucleation (n = 16 natural regeneration/plantation, n = 30 applied nucleation, Fig. S2). The applied nucleation treatment was sampled more intensively to quantify potential differences in recruitment between planted and unplanted areas (Fig. S2). Since survival and growth analyses were focused at the plant level and hence not dependent on abundances, we did not standardize for sampling area differences between applied nucleation and other treatments. Each recruit was permanently tagged and survival was recorded annually in subsequent years. Height was recorded for seedlings ≥20-cm tall and <1-cm diameter-at-breast height (DBH). DBH of the largest stem was recorded for saplings with ≥1-cm and <5-cm DBH. For seedlings that transitioned to saplings, survival observations were included in the seedling dataset until recruits reached ≥1-cm DBH. Thereafter, observations were included only in the sapling dataset. The sapling dataset did not include survival observations for saplings that transitioned to small trees (> 5-cm DBH).

DATA ANALYSIS

We focused analyses on naturally established tree recruits that dispersed into plots from the landscape. Given our emphasis on forest succession, we omitted recruits from planted species, three of which had very low recruitment; the fourth (*Erythrina poeppigiana*) frequently recruited but recruits suffered >95% mortality within the first year [28]. We also omitted individuals that resprouted following previous agricultural activities (primarily *Citrus* spp. and *E. poeppigiana*).

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We modeled seedling survival and sapling growth separately for early- and later-successional species. Tree successional stage (early or later) was determined using local knowledge and literature references. We consider later-successional species as those that are found either in the understory of mature forests or in a mix of mature and secondary forests, but that do not establish during the earliest stages of succession. Natural regeneration plots were excluded from later-successional recruit models due to very low numbers of later-successional recruits (42 total). We pooled all recruits for sapling survival models as the separate model for later-successional saplings did not converge due to sample size constraints (early successional saplings: n = 502, later-successional saplings: n = 221).

To examine the effects of restoration treatment and year since restoration on seedling (n=1286) and sapling (n=723) survival of annually updated cohorts, we used generalized linear mixed-effects models (GLMMs) with a binomial distribution [lme4 package, 29]. We define year since restoration as the time a seedling recruited after vegetation clearing ceased at a given site. We included size measurements of recruits from the preceding year (height for seedlings, DBH for saplings) as recruit size has been shown to strongly affect survival [30, 31]. We initially included the following random intercepts in all models: restoration site as a blocking factor, tree species to account for species-specific variation, and plant identity to account for repeated measures on each recruit. We used intraclass correlation coefficients (ICC) to assess the level of within-group similarity and determine the influence of random effects on model estimates [32, performance package, 33]. For all survival models, intraclass correlation was small for site and plant identity random effects (ICC < 0.10). These random effects were therefore omitted from models making tree species (ICC > 0.10) the only random effect included. These omissions did not change trends compared to models including all random effects but aided in model fit to test hypotheses.

Whereas we collected recruit data from 2007-2019, there was an insufficient number of recruits in 2007 to include those data in models. Moreover, an examination of seedling age and mortality

showed that >75% of seedlings that died did so by age three. We therefore omitted recruits that established at the end of the study (between 2017-2019) from survival models as these seedlings may not have had sufficient time to die and would have biased our temporal comparisons. Both conspecific and overall density dependence based on total stem abundance per quadrat (early- and later-successional species pooled) were poor predictors of recruit survival in our preliminary models, so we did not include negative density dependence in any final models.

We modeled sapling (n=1203) growth as absolute change in DBH between each annual sampling period (DBH_t - DBH_{t-1}) predicted by restoration treatment, year since restoration, their interaction, and sapling size (DBH_{t-1}) using GLMMs with Tweedie (compound Poisson-Gamma) distributed errors [package glmmTMB, 34]. Tweedie distributions are generalized power law distributions for modelling continuous data with many zeros and provided a better fit and convergence than other distributions. For both growth models, intraclass correlation was small for site- and tree species-level random effects (ICC <0.05) which were omitted leaving individual plant identity (ICC >0.075) as the only random effect. Our sapling growth data span from 2010-2019 as the number of recruits was too small for analysis in the first three years since restoration. We did not analyze seedling growth (height) due to our sampling design; we transitioned from height to DBH growth measures at >1-cm DBH so a seedling height analyses would be biased towards recruits with slow growth.

We assessed model performance and assumptions in the R package DHARMa [35], which uses a simulation-based approach to create standardized residuals for GLMMs. We then examined plots of standardized residuals vs. predicted values and quantile-quantile plots of deviation from a uniform distribution [see 35 for details], which both indicated reasonable fit for all models. We report marginal and conditional pseudo-R^2 ($R2_M$ and $R2_C$ respectively) following Nakagawa and Schielzeth [36] [performance package, 33] as an analogue of goodness of fit appropriate for GLMMs. Collinearity was assessed using variance inflation factor (VIF) values among fixed

effects. No collinearly was found (VIF <10) in any model. We tested the effects of predictor variables and their interactions using likelihood ratio tests based on comparisons of $\chi 2$ distributions between full and reduced models. We assessed the effects of treatment levels as well as their interaction with time since restoration using bias adjusted, estimated marginal means (predicted survival probability and predicted Δ DBH; hereafter referred to as "survival probability" and "growth" respectively) and estimated slopes for interactions [package emmeans, 37]. When appropriate, we used Tukey post-hoc multiple comparisons [package emmeans, 37] to determine significant differences ($p < 0.05$) between restoration treatment levels. When needed, continuous variables were scaled using z-scores to improve model convergence. All analyses were conducted in R v.3.6.3 [38].

Results

RECRUIT SURVIVAL

Early-successional seedlings had greater annual survival probability in applied nucleation than natural regeneration treatments (Table S1, $z = 3.48$, $p = 0.001$, $R2_C = 0.22$, $R2_M = 0.12$) but there was no significant difference between plantations and the other two treatments (Figure 1a, Table S1, $p > 0.19$). As year since restoration increased, early-successional seedlings experienced marginally greater survival (Figure S3a, $p = 0.07$), but the treatment × year since restoration interaction was not significant ($p = 0.86$, Table S1). Later-successional seedling survival probability was similarly high (> 0.94) in applied nucleation and plantation treatments (Figure 1b, Table S1, $p = 0.44$) and did not differ between treatments over time (Figure S3b, Table S1, $R2_C = 0.50$, $R2_M = 0.16$). Taller seedlings of both early- (Figure S4a) and later- (Figure S4b) successional seedlings had higher survival ($p < 0.001$).

Sapling survival probability was very high for all three restoration treatments (Figure 1c, Table S1, $R2_C = 0.42$, $R2_M = 0.12$), with slightly but significantly higher survival probability in applied nucleation compared to plantation treatments ($z = 2.48$, $p = 0.04$). Sapling survival probability

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decreased significantly with time since restoration (Figure S3c, p < 0.001) but stayed at high levels (> 0.96) throughout the study. Larger seedlings experienced higher survival (p < 0.001). By the end of the study, 87.2% of saplings had survived compared to 58.6% of seedlings.

SAPLING GROWTH

Treatment and year since restoration had an interactive effect on early-successional sapling growth (Figure 2a, Figure S5a, p <0.001) which reflects significant differences in estimated slopes of survival over year since restoration between all combinations of treatments (Table S1, $R2_C$ = 0.79, $R2_M$ = 0.14). In the first few years immediately following restoration, growth rates were much faster in natural regeneration and applied nucleation than plantation treatments. By the end of the sampling period, however, early-successional sapling growth had slowed substantially in applied nucleation and even more in natural recruitment plots, such that sapling growth rates had converged across treatments after nearly a decade (Figure 2a, Figure S5a). By contrast, later-successional sapling growth remained relatively constant across the entire sampling period (Figure 2b, Figure S5b, p = 0.46), but was significantly higher in applied nucleation than plantation treatments (Figure 3, Figure S6, p < 0.001, $R2_C$ = 0.63, $R2_M$ = 0.04). Larger early-successional saplings grew faster (p < 0.001), whereas later-successional sapling growth showed no association with size (p = 0.57).

Discussion

Ours is the first long-term (10 yr), multi-site study that compares survival and growth of naturally recruiting trees across a gradient of restoration interventions. Whereas many short-term studies (typically 1-5 yr) comparing survival and growth of recruits show strong differences across restoration treatments [e.g., 39, 40], our results suggest that some differences among treatments may converge rapidly, even within the first decade. Nonetheless, we documented multiple differences in survival and growth of recruits across restoration treatments that could result in different rates of recovery, and possibly plant community composition, well into the future.

Lower survival of early-successional seedlings in natural regeneration plots (Figure 1a) is likely explained by strong competition with non-native pasture grasses which many previous studies have shown is a strong barrier to tree recruitment and survival [e.g., 22, 41, 42]. Indeed, grass cover was consistently higher in natural regeneration compared to other treatments after active management ceased, although it decreased over time (Figure S7b). Across all treatments, early-successional seedlings that established soon after restoration experienced marginally higher mortality than those arriving later in succession, suggesting that even modest levels of grass cover present before canopies close can affect early-successional seedling survival (Figure S3a).

Once seedlings survived to the sapling stage and hence overtopped non-native pasture grasses, survival was generally high, although slightly lower in the plantations than other treatments [Figure 1c, 10]. Moreover, early-successional saplings grew faster in natural regeneration and applied nucleation treatments soon after restoration but growth rates declined and converged substantially a decade post-restoration (Figure 2a). This result is consistent with many other studies showing that early-successional tree growth rates decline as light limitation increases [43, 44]. Likewise, Caughlin, de la Peña-Domene [10] who monitored growth 7 years post-restoration reported that recruits reached reproductive maturity sooner in natural regeneration than plantation plots in Mexico. These patterns are likely due to the lower canopy cover and associated shading in the natural regeneration compared to plantation treatments (Figure S7a). Whereas other tropical forest succession studies have shown that seedling growth may be nutrient limited [e.g., 30, 45, 46], surface soil nutrients in our sites were similar across treatments during the study [25, unpub. data]. Additionally, litterfall inputs of nutrients most limiting to plant growth were highest in the plantation treatments early in this study [47], contrasting with lower growth rates in plantations compared to other treatments. Together these results suggest that sapling growth patterns in our sites are more driven by light than nutrient limitation.

Later-successional species showed similar seedling survival rates in applied nucleation and plantation treatments (Figure 1b). This pattern is consistent with many prior studies demonstrating that later-successional, shade tolerant recruits have higher survival overall and are less sensitive to light availability [24, 48, 49]. Moreover, seedling herbivory and subsequent mortality tends to be lower when comparing later-successional to early-successional seedlings [28], likely due to higher levels of secondary chemicals and mechanical defenses [50]. These results, as well as the fact that recruitment of later-successional seedlings in natural regeneration plots was so low that we could not compare survival, are consistent with past work of our group and others showing that dispersal-limitation is stronger than establishment-limitation for later-successional species in secondary tropical forests, particularly for the many species with large, animal-dispersed seeds [51-53].

We were surprised that neither the density of conspecific nor heterospecific species were significant explanatory factors in our initial models, given that many studies have shown NDD to be an important factor affecting seedling survival in both naturally regenerating and intact natural forests [6, 8, 31]. We suspect that NDD was weak in our plots due to the fact that (1) we did not analyze recruit data from planted tree species, and (2) few recruited species fruited during the study period, so nearly all recruits came from outside the plots rather than falling in high density below fruiting trees. We anticipate that NDD will become more important over time as species within the plots become reproductively mature and note that further study of the role of NDD in seedling recruitment in a restoration context is needed.

A large body of literature shows that both recruit survival and growth rates typically increase with plant size and that the strongest filters to forest recovery act more strongly on smaller recruit size classes [9, 10, 54, 55]. Our results are generally consistent with these patterns, with the exception of later-successional sapling growth rates which showed no correlation with initial sapling size (Table S1). Others have shown that late-successional saplings in the understory invest more in

leaf replacement than other forms of growth [56]. Since all of our later-successional growth data come from plantation and applied nucleation treatments, high canopy cover in these treatments could explain the lack of a size effect on sapling growth [48, 57].

Our results suggest that applied nucleation promotes an intermediate and more heterogeneous canopy cover [20, 58], which in turn creates a light environment that facilitates survival and growth of both early- and later-successional tree recruits. Survival of both seedlings and saplings was similar in applied nucleation plots when compared to the more resource-intensive plantation forestry approach. Interestingly, later-successional sapling survival and growth were higher in applied nucleation than in the plantation treatment, which is supported by other studies showing that small-scale heterogeneity in light environments within closed canopy forests can drive growth dynamics of recruits in the understory [6, 59]. In addition, previous studies of natural recruitment into older tree plantations show that medium-size classes of recruiting trees are underrepresented [60, 61], whereas faster later-successional sapling growth in applied nucleation plots may ultimately lead to more heterogeneity in tree size classes. Together, these findings suggest that over the longer-term, later-successional species may come to dominate our applied nucleation plots sooner than plantation plots with implications for more rapid reassembly of mature tropical forest communities. However, we hasten to note that we only planted four species of trees, since our goal was to rapidly achieve canopy cover that enhanced the rate of succession by attracting dispersers and providing more favorable conditions for seedling establishment. The results of both applied nucleation and plantation restoration strategies would differ if later-successional species were included as part of the initial planting mix or actively planted after the initial canopy established. Indeed, the effect of species composition on the relative effects of applied nucleation and plantation planting strategies is an important area for future research [18, 62].

The results presented here, combined with our prior work showing that applied nucleation facilitates later-successional seed dispersal to a similar degree as tree plantations [51], suggest that

applied nucleation not only provides a promising and cost-effective approach towards overcoming initial barriers to tree establishment, but also facilitates the recovery of the forest composition beyond the first decade. However, most appropriate restoration approach for a given site depends critically on the project goals and the ecological and social conditions [63]. Applied nucleation is likely to be an effective strategy to facilitate forest recovery in cases where there are sufficient sources of a diversity of tree seeds and seed-dispersing animals in the surrounding landscape; woody vegetation nuclei are lacking in the restoration site; spread of tree nuclei is not inhibited by herbivory, invasive species competition, or fire; and it is compatible with landowner preferences [18]. In regions with small landholders who depend heavily on income from their land, extensive planting of native species that provide fruit, firewood, or timber resources will often be more appropriate. Likewise, extensive planting of a diversity of trees may be necessary in highly degraded sites that lack nearby seed sources. The next step is to implement the applied nucleation approach in on-the-ground restoration projects [62] at the scale of tens to hundreds of hectares and monitor outcomes [62], such as a new 500-ha project being undertaken by Conservation International in the Brazilian Amazon region [D. Celentano, pers. comm.]. Long-term, multi-site studies are key to determining under what conditions different restoration strategies are most effective to achieve the biodiversity and carbon sequestration goals of the ambitious forest restoration efforts planned for the coming decades.

Author contributions

KH and RZ initially designed the experiment; AK, KH, RZ, and LW collected the data; AK analyzed the data with feedback from KH, KZ, and LW; AK and KH co-wrote the first draft of the manuscript and all other authors provided editorial feedback on multiple drafts of the manuscript.

Data availability

Data will be posted on Dryad after acceptance of the paper.

References

1.   Chazdon R.L., Brancalion P.H.S., Lamb D., Laestadius L., Calmon M., Kumar C. 2017. A policy-driven knowledge agenda for global forest and landscape restoration. *Conservation Letters* **10**, 125-132. (doi:10.1111/conl.12220).
2.   Holl K.D. 2017. Research directions in tropical forest restoration. *Ann Mo Bot Gard* **102**, 237-250. (doi:10.3417/2016036).
3.   Shoo L.P., Catterall C.P. 2013. Stimulating natural regeneration of tropical forest on degraded land: approaches, outcomes, and information gaps. *Restor Ecol* **21**, 670-677. (doi:10.1111/rec.12048).
4.   Curran M., Hellweg S., Beck J. 2014. Is there any empirical support for biodiversity offset policy? *Ecol Appl* **24**, 617-632.
5.   Muscarella R., Lohbeck M., Martínez-Ramos M., Poorter L., Rodríguez-Velázquez J.E., van Breugel M., Bongers F. 2017. Demographic drivers of functional composition dynamics. *Ecology* **98**, 2743-2750. (doi:10.1002/ecy.1990).
6.   Uriarte M., Muscarella R., Zimmerman J.K. 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology* **24**, e692-e704. (doi:10.1111/gcb.14000).
7.   Werden L.K., Averill, C., Crowther, T.W., Calderón-Morales, E., Toro, L., Alvarado J., P., Gutiérrez L., M., Mallory, D.E., Powers, J.S. In review. Belowground traits mediate tree survival in a tropical dry forest restoration. *Proceedings of the Royal Society B*.
8.   Record S., Kobe R.K., Vriesendorp C.F., Finley A.O. 2016. Seedling survival responses to conspecific density, soil nutrients, and irradiance vary with age in a tropical forest. *Ecology* **97**, 2406-2415. (doi:10.1002/ecy.1458).
9.   Zhu Y., Queenborough S.A., Condit R., Hubbell S.P., Ma K.P., Comita L.S. 2018. Density-dependent survival varies with species life-history strategy in a tropical forest. *Ecol Lett* **21**, 506-515. (doi:10.1111/ele.12915).
10.   Caughlin T.T., de la Peña-Domene M., Martínez-Garza C. 2019. Demographic costs and benefits of natural regeneration during tropical forest restoration. *Ecol Lett* **22**, 34-44. (doi:10.1111/ele.13165).
11.   Holl K.D., Aide T.M. 2011. When and where to actively restore ecosystems? *For Ecol Manag* **261**, 1558-1563. (doi:10.1016/j.foreco.2010.07.004).
12.   Holl K.D., Brancalion P.H.S. 2020. Tree planting is not a simple solution. *Science* **368**, 580-581. (doi:10.1126/science.aba8232).
13.   Di Sacco A., Hardwick K.A., Blakesley D., Brancalion P.H.S., Breman E., Cecilio Rebola L., Chomba S., Dixon K., Elliott S., Ruyonga G., et al. 2021. Ten golden rules for reforestation to

optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global Change Biology* **n/a**. (doi:10.1111/gcb.15498).

14.   Chazdon R.L., Lindenmayer D., Guariguata M.R., Crouzeilles R., Rey Benayas J.M., Lazos Chavero E. 2020. Fostering natural forest regeneration on former agricultural land through economic and policy interventions. *Environmental Research Letters* **15**, 043002. (doi:10.1088/1748-9326/ab79e6).

15.   Crouzeilles R., Ferreira M.S., Chazdon R.L., Lindenmayer D.B., Sansevero J.B.B., Monteiro L., Iribarrem A., Latawiec A.E., Strassburg B.B.N. 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances* **3**. (doi:10.1126/sciadv.1701345).

16.   Meli P., Holl K.D., Benayas J.M.R., Jones H.P., Jones P.C., Montoya D., Mateos D.M. 2017. A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLOS One* **12**, e0171368.

17.   Reid J.L., Fagan M.E., Zahawi R.A. 2018. Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. *Science Advances* **4**, eeas9143. (doi:10.1126/sciadv.aas9143).

18.   Holl K.D., Reid J.L., Cole R.J., Oviedo-Brenes F., Rosales J.A., Zahawi R.A. 2020. Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. *J Appl Ecol* **57**, 2316-2328. (doi:10.1111/1365-2664.13684).

19.   Holl K.D., Reid J.L., Chaves-Fallas J.M., Oviedo-Brenes F., Zahawi R.A. 2017. Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. *J Appl Ecol* **54**, 1091-1099. (doi:10.1111/1365-2664.12814).

20.   Holl K.D., Stout V.M., Reid J.L., Zahawi R.A. 2013. Testing heterogeneity-diversity relationships in tropical forest restoration. *Oecologia* **173**, 569–578. (doi:10.1007/s00442-013-2632-9).

21.   Chazdon R.L., Pearcy R.W., Lee D.W., Fetcher N.E.D. 1996 Photosynthetic responses of tropical forest plants to contrasting light environments. In *Tropical forest plant ecophysiology* (eds. Mulkey SS, RL C., AP S.), pp. 5-55. New York, Chapman and Hall.

22.   Hooper E., Legendre P., Condit R. 2005. Barriers to forest regeneration of deforested and abandoned land in Panama. *J Appl Ecol* **42**, 1165-1174.

23.   Werden L.K., Calderón-Morales E., Alvarado J. P., Gutiérrez L. M., Nedveck D.A., Powers J.S. 2020. Using large-scale tropical dry forest restoration to test successional theory. *Ecol Appl* **30**, e02116. (doi:10.1002/eap.2116).

24.   Kitajima K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**, 419-428.

25.   Holl K.D., Zahawi R.A. 2014. Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. *For Ecol Manag* **319**, 36-43. (doi:10.1016/j.foreco.2014.01.024).

26.   Zahawi R.A., Duran G., Kormann U. 2015. Sixty-seven years of land-use change in southern Costa Rica. *PloS one* **10**, e0143554. (doi:10.1371/journal.pone.0143554).

27.   Holl K.D., Zahawi R.A., Cole R.J., Ostertag R., Cordell S. 2011. Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restor Ecol* **19**, 470-479. (doi:10.1111/j.1526-100X.2010.00674.x).

28.   Kulikowski A.J., II. 2020 The influence of plant-insect interactions and incentive-based environmental policy on tropical forest restoration. University of California, Santa Cruz.

29.   Bates D., Mächler M., Bolker B., Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1-48. (doi:10.18637/jss.v067.i01).

30.   van Breugel M., Hall J.S., Craven D.J., Gregoire T.G., Park A., Dent D.H., Wishnie M.H., Mariscal E., Deago J., Ibarra D., et al. 2011. Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. *For Ecol Manag* **261**, 1580-1589. (doi:10.1016/j.foreco.2010.08.019).

31.   Johnson D.J., Condit R., Hubbell S.P., Comita L.S. 2017. Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. *Proceedings of the Royal Society B-Biological Sciences* **284**. (doi:10.1098/rspb.2017.2210).

32.   Hox J. 2002 *Multilevel analysis: techniques and applications*. Multwah, NJ, USA, Lawrence Erlbaum Associates.

33.   Lüdecke D., Ben-Shachar M.S., Patil I., Waggoner P., Makowski D. 2021. Assessment, testing and comparison of statistical models using R. *Journal of Open Source Software* **6**, 3112. (doi:10.31234/osf.io/vtq8f).

34.   Brooks M.E., Kristensen K., Van Benthem K.J., Magnusson A., Berg C.W., Nielsen A., Skaug H.J., Machler M., Bolker B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal* **9**, 378-400. (doi:20.500.11850/242692).

35.   Hartig F. 2021. Diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.1. http://florianhartig.github.io/DHARMa/.

36.   Nakagawa S., Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**, 133-142.

37.   Lenth R.V. 2021. emmeans: Estimated marginal means, aka least-squares means. R package version 1.5.5-1. https://CRAN.R-project.org/package=emmeans.

38.   R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

39.   Méndez-Toribio M., Benítez-Malvido J., Zermeño-Hernández I.E., Castillo-Mandujano J. 2019. Removal of climbing plants and soil plowing as a strategy to enhance forest recovery in tropical dry forests old fields. *Ecological Restoration* **37**, 113-122.

40.   Zahawi R.A., Augspurger C.K. 2006. Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. *Ecol Appl* **16**, 464-478. (doi:10.1890/1051-0761).

41.   Griscom H.P., Griscom B.W., Ashton M.S. 2009. Forest regeneration from pasture in the dry tropics of Panama: effects of cattle, exotic grass, and forested riparia. *Restor Ecol* **17**, 117-126. (doi:10.1111/j.1526-100X.2007.00342.x).

42.   Roman-Danobeytia F.J., Castellanos-Albores J., Levy-Tacher S.I., Aronson J., Ramirez-Marcial N., Rodrigues R.R. 2012. Responses of transplanted native tree species to invasive alien grass removals in an abandoned cattle pasture in the Lacandon region, Mexico. *Tropical Conservation Science* **5**, 192-207.

43.   Wright S.J., Kitajima K., Kraft N.J.B., Reich P.B., Wright I.J., Bunker D.E., Condit R., Dalling J.W., Davies S.J., Diaz S., et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **91**, 3664-3674. (doi:10.1890/09-2335.1).

44.   Kitajima K., Poorter L. 2008 Functional basis for resource niche partitioning by tropical trees. In *Tropical forest community ecology* (eds. Carson W.P., Schnitzer S.A.), pp. 160-181, Blackwell Science.

45.   Santiago L.S., Wright S.J., Harms K.E., Yavitt J.B., Korine C., Garcia M.N., Turner B.L. 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. *J Ecol* **100**, 309-316. (doi:10.1111/j.1365-2745.2011.01904.x).

46.   Estrada-Villegas S., Bailón M., Hall J.S., Schnitzer S.A., Turner B.L., Caughlin T., van Breugel M. 2020. Edaphic factors and initial conditions influence successional trajectories of early regenerating tropical dry forests. *J Ecol* **108**, 160-174. (doi:10.1111/1365-2745.13263).

47.   Celentano D., Zahawi R.A., Finegan B., Ostertag R., Cole R.J., Holl K.D. 2011. Litterfall dynamics under different tropical forest restoration strategies in Costa Rica. *Biotropica* **43**, 279-287. (doi:10.1111/j.1744-7429.2010.00688.x).

48.   Davies S.J. 2001. Tree mortality and growth in 11 sympatric Macaranga species in Borneo. *Ecology* **82**, 920-932.

49.   Lasky J.R., Uriarte M., Boukili V.K., Chazdon R.L. 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proc Natl Acad Sci U S A* **111**, 5616-5621. (doi:10.1073/pnas.1319342111).

50.   Poorter L., van de Plassche M., Willems S., Boot R.G.A. 2004. Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology* **6**, 746-754. (doi:10.1055/s-2004-821269).

51.   Werden L.K., Holl K.D., Rosales J.A., Sylvester J.M., Zahawi R.A. 2020. Effects of dispersal- and niche-based factors on tree recruitment in tropical wet forest restoration. *Ecol Appl* **30**, e02139. (doi:10.1002/eap.2139).

52.   Muscarella R., Uriarte M., Forero-Montaña J., Comita L.S., Swenson N.G., Thompson J., Nytch C.J., Jonckheere I., Zimmerman J.K. 2013. Life-history trade-offs during the seed-to-seedling transition in a subtropical wet forest community. *J Ecol* **101**, 171-183. (doi:10.1111/1365-2745.12027).

53.   de la Peña-Domene M., Martínez-Garza C., Howe H.F. 2013. Early recruitment dynamics in tropical restoration. *Ecol Appl* **23**, 1124-1134. (doi:10.1890/12-1728.1).

54.   Comita L.S., Uriarte M., Thompson J., Jonckheere I., Canham C.D., Zimmerman J.K. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J Ecol* **97**, 1346-1359. (doi:10.1111/j.1365-2745.2009.01551.x).

55.   Yan Y., Zhang C., Wang Y., Zhao X., von Gadow K. 2015. Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. *Ecology and Evolution* **5**, 4287-4299. (doi:10.1002/ece3.1688).

56.   King D.A. 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Funct Ecol* **5**, 485-492.

57.   Valladares F., Niinemets Ü. 2008. Shade Tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics* **39**, 237-257. (doi:10.1146/annurev.ecolsys.39.110707.173506).

58.   Zahawi R.A., Dandois J.P., Holl K.D., Nadwodny D., Reid J.L., Ellis E.C. 2015. Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. *Biol Conserv* **186**, 287-295. (doi:10.1016/j.biocon.2015.03.031).

59.   Montgomery R., Chazdon R. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* **131**, 165-174. (doi:10.1007/s00442-002-0872-1).

60.   de Oliveira C.D.C., de Oliveira I.R.C., Suganuma M.S., Durigan G. 2019. Overstory trees in excess: A threat to restoration success in Brazilian Atlantic forest. *For Ecol Manag* **449**, 117453. (doi:10.1016/j.foreco.2019.117453).

61.   César R.G., Moreno V.S., Coletta G.D., Chazdon R.L., Ferraz S.F.B., de Almeida D.R.A., Brancalion P.H.S. 2018. Early ecological outcomes of natural regeneration and tree plantations for restoring agricultural landscapes. *Ecol Appl* **28**, 373-384. (doi:10.1002/eap.1653).

62.   Wilson S.J., Alexandre N.S., Holl K.D., Reid J.L., Zahawi R.A., Celentano D., Sprenkle-Hyppolite S.D., Werden L.K. 2021 *Applied nucleation guide for tropical forests*, Conservation International.

63.   Holl K.D. 2020 *Primer of ecological restoration*. Washington, D.C., Island Press.

Figure captions

Figure 1: Predicted survival probabilities for **a)** early-successional seedlings, **b)** later-successional seedlings, and **c)** all saplings by restoration treatment. NR = natural regeneration (omitted for later-successional seedlings), AN = applied nucleation, and PL = plantation restoration treatments. Error bars are estimated 95% upper and lower asymptotic confidence levels around estimated marginal means. Means with the same letter do not differ significantly using Tukey's multiple comparison test among treatments.

Figure 2: Predicted increase in growth (DBH) by year since restoration for **a)** early- and **b)** later-successional saplings in each restoration treatment. NR = natural regeneration, AN = applied nucleation, and PL = plantation restoration treatments. Error bands are 95% confidence intervals around the estimated trend.

Figure 3: Predicted annual increase in later-successional sapling growth (DBH) in applied nucleation (AN) and plantation (PL) treatments. Error bars are 95% confidence intervals around estimated marginal means. Different letters represent a significant difference between treatments at the $\alpha = 0.05$ level.
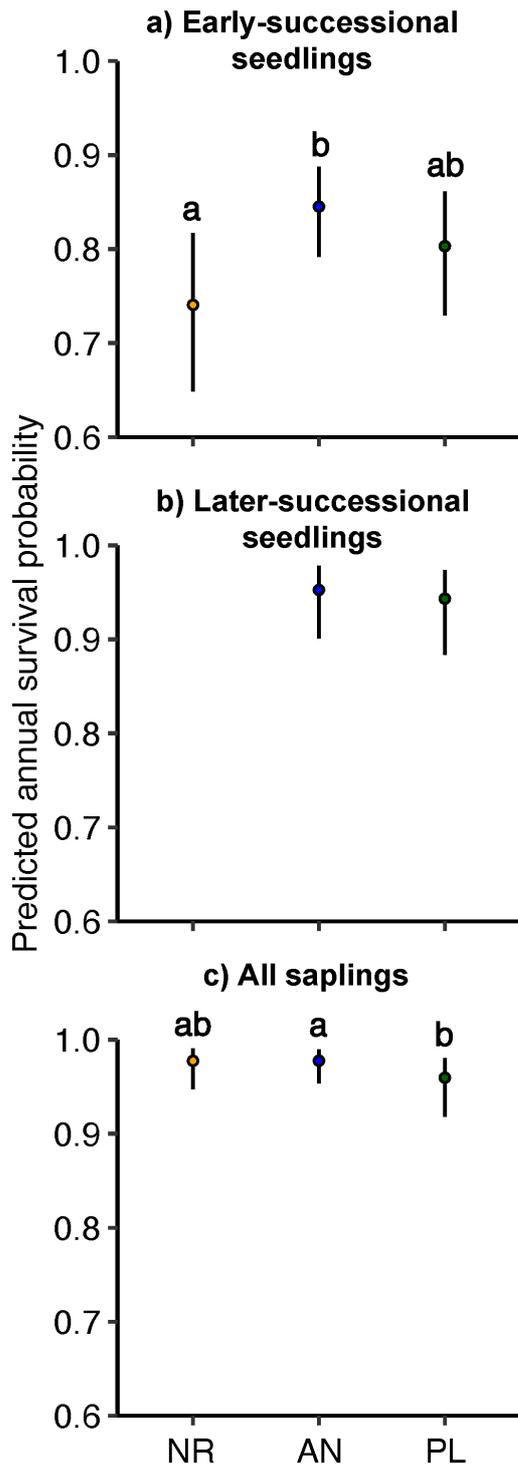
Figure 1

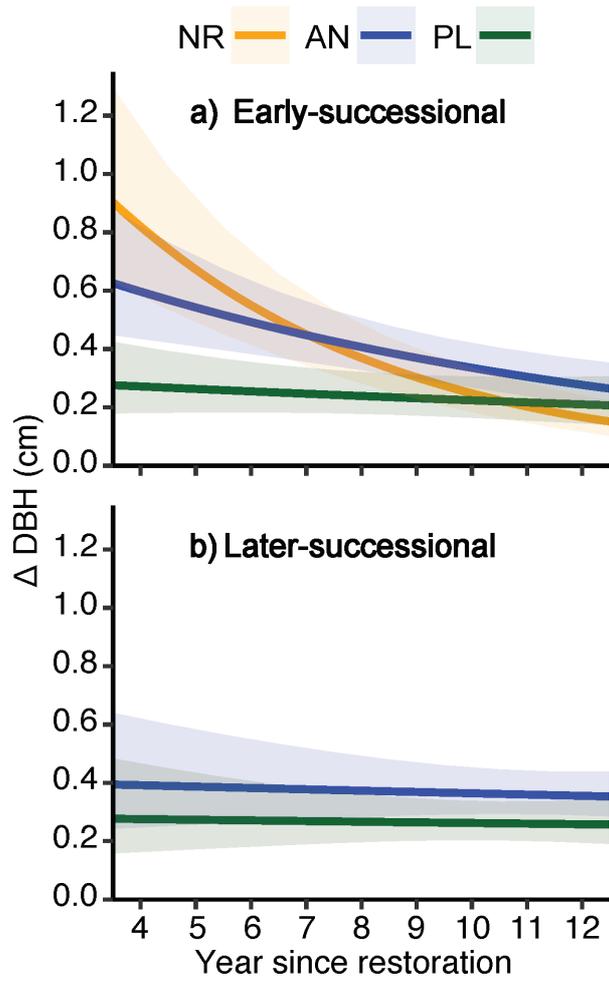a) Early-successional seedlings

b) Later-successional seedlings

c) All saplings

Predicted annual survival probability

NR   AN   PL

Figure 2

Figure 3