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Authors

Werden, Leland K
Holl, Karen D
Chaves-Fallas, José Miguel
et al.

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RESEARCH ARTICLE

Degree of intervention affects interannual and within-plot heterogeneity of seed arrival in tropical forest restoration

Leland K. Werden[1] | Karen D. Holl[2] | José Miguel Chaves-Fallas [3,4] | Federico Oviedo-Brenes[5] | Juan Abel Rosales[5] | Rakan A. Zahawi[1,2]

[1]Lyon Arboretum and School of Life Sciences, University of Hawaii at Mānoa, Honolulu, HI, USA

[2]Environmental Studies Department, University of California, Santa Cruz, CA, USA

[3]Department of Biology and Whitney R. Harris World Ecology Center, University of Missouri–St. Louis, St. Louis, MO, USA

[4]Centro de Investigaciones en Productos Naturales (CIPRONA), Universidad de Costa Rica, San José, Costa Rica

[5]Las Cruces Biological Station, Organization for Tropical Studies, San Vito de Coto Brus, Costa Rica

Correspondence
Leland K. Werden
Email: lwerden@gmail.com

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Abstract

1. In degraded tropical landscapes, lack of seed dispersal can strongly limit recovery, and restoration interventions can overcome this barrier by attracting dispersers. However, seed dispersal patterns are typically studied over short time periods, thus the influences of temporal and spatial variability on seed arrival cannot be teased apart.

2. The choice of management approach can have important implications for restoration-mediated community reassembly. Accordingly, we used a 3.5-year record of seed deposition in pre-montane tropical wet forest in southern Costa Rica to examine how seed arrival differed between passive (natural regeneration) and active (applied nucleation, plantation) restoration after a decade of recovery, compared to remnant forest. We investigated: (a) how restoration treatments affected seed deposition rates and community composition; (b) how within-plot heterogeneity of animal-dispersed seed deposition varied by intervention; and (c) how interannual variation influenced animal-dispersed seed arrival across treatments.

3. Overall seed rain composition and diversity in restoration treatments was converging towards, but still differed substantially from, remnant forest (89.7%, 86.6% and 76.3% Shannon diversity recovered in applied nucleation, plantation and natural regeneration respectively).

4. Within-plot animal-dispersed seed heterogeneity was similar in applied nucleation and remnant forest, 27.0% more heterogeneous in applied nucleation than plantation, and equivalent when comparing natural regeneration to either applied nucleation or plantation.

5. In contrast to active interventions, animal-dispersed tree and shrub communities did not differ year to year in natural regeneration, which may promote the assembly of relatively homogeneous plant communities at this successional stage.

6. *Synthesis and applications.* Compared to natural regeneration, active restoration interventions: (a) catalysed the recovery of seed diversity (overall Shannon diversity 17.5% and 13.4% higher in applied nucleation and plantation respectively), (b) shifted seed community composition towards remnant forest more rapidly (overall Shannon diversity 13.4% and 10.2% closer), (c) almost doubled the proportion of later-successional tree species arriving, and (d) had seed communities

that differed year to year—a pattern not observed in natural regeneration. Finally, applied nucleation was the only intervention where seed arrival was as spatially heterogeneous as remnant forest, highlighting that this approach may facilitate the recovery of specific natural dispersal processes.

1 | INTRODUCTION

Human activities continue to drive a decline in forest cover globally (FAO, 2015), leading to the widespread loss of tropical biodiversity (Alroy, 2017). To counteract this trend, a suite of passive and active restoration approaches have been employed to facilitate the recovery of tropical forest ecosystem processes (Holl & Aide, 2011). However, the effectiveness of these techniques is highly variable and context dependent (Holl et al., 2017; Mesquita et al., 2015) and is influenced by the stochastic nature of forest successional trajectories (Norden et al., 2015). Hence, determining the relative influence of different restoration approaches, site-scale variation (e.g. land-use history, surrounding landscape cover, environmental heterogeneity) and ecological processes (e.g. seed dispersal, succession) on ecosystem recovery can improve the understanding of community reassembly. Long-term restoration experiments that directly compare how passive (i.e. natural regeneration) and active (e.g. tree planting) approaches influence the rates of recovery are critical to refine predictive frameworks for restoration outcomes (Brudvig et al., 2017).

Tropical forest regeneration on abandoned farmland is limited by dispersal and establishment processes (de la Peña-Domene et al., 2017; Holl, 1999; Werden et al., 2020), which are regulated by complex interactions between biotic and abiotic factors (Muscarella et al., 2013). The first step towards vegetation recolonization is for a seed to arrive, but dispersal is far from a simple process in tropical forests, given high temporal and spatial variability (Wright et al., 2005). As such, seed limitation is one of the strongest barriers to vegetation recovery in degraded tropical landscapes (Charles et al., 2017; Duncan & Chapman, 1999; Sangsupan et al., 2018). In abandoned tropical pastures, forest tree seeds are typically all but absent from the soil seed bank (Zahawi & Augspurger, 1999) and seed deposition rates are extremely low, even in the presence of adjacent remnant forest patches (Holl, 1999; Teegalapalli et al., 2010). Planting trees can attract dispersers by creating forest canopy structure when natural succession is slowed (Reid et al., 2014), thereby overcoming dispersal barriers and increasing deposition rates of animal-dispersed species (Cole et al., 2010; Reid et al., 2015; Wang et al., 2010).

The order and timing of species arrival (temporal priority effects; Fukami, 2015), coupled with the influences of site-level and interannual variability on vegetation dynamics (Stuble et al., 2017), are also important drivers of restoration recovery trajectories. Indeed, there is evidence that tropical forest restoration strategies can directly

modify biotic historical contingencies by differentially attracting animal dispersers, resulting in the arrival of distinct seed communities to actively planted versus passively regenerated plots (Reid et al., 2015). Moreover, different levels of restoration intervention can affect factors such as vegetation structural heterogeneity (Holl et al., 2013), potentially leading to divergent seed arrival patterns both within restoration plots and across restoration treatments. Whereas continuous multi-year records of seed deposition have been collected in mature (Muscarella et al., 2013; Wright et al., 2005) and secondary tropical forests (O'Brien et al., 2018), studies of primary seed dispersal in a restoration context are generally conducted on short temporal scales (~1–1.5 years), and during the first few years following land abandonment (e.g. Wang et al., 2010; Zahawi & Augspurger, 2006). This approach limits our ability to attribute differences in community composition of seeds arriving across restoration treatments to factors such as interannual variability in seed production (O'Brien et al., 2018) or heterogeneity in seed arrival due to avian dispersal preference (González-Castro et al., 2019).

We used a 3.5-year record of seed deposition (seed rain) in southern Costa Rica to examine how seed arrival differed between passive (natural regeneration) and active (applied nucleation, plantation) restoration treatments after a decade of recovery, as compared to adjacent remnant reference forests. This study is the first to examine how interannual and within-plot patterns of community-level seed dispersal differ across a gradient of restoration intervention. We addressed the following questions:

(Q1) How do restoration treatments affect seed deposition rates and community composition?
(Q2) How does within-plot spatial heterogeneity of animal-dispersed seed rain vary by restoration treatment?
(Q3) How does interannual variation influence animal-dispersed seed arrival across treatments?

Based on previous observations at our sites and others (Cole et al., 2010; de la Peña-Domene et al., 2014; Reid et al., 2015), we predicted that deposition rates and community composition (i.e. diversity and dissimilarity) would be similar in active restoration treatments where tree planting increases canopy cover and attracts animal dispersers, especially for larger seeded tree species. We also predicted that the diversity and composition of seed rain in active restoration treatments would be more similar to reference forests than

natural regeneration. We further expected that within-plot animal-dispersed seed arrival would be more spatially heterogeneous in the applied nucleation than in plantation plots, as the canopy in applied nucleation is more structurally variable (Holl et al., 2013; Zahawi, Dandois, et al., 2015; Zahawi, Duran, et al., 2015). Finally, we anticipated that seed composition in the natural regeneration treatment would have lower interannual variation for animal-dispersed seed arrival, as a previous study at our site indicated that seeds deposited within that treatment are predominantly from a small subgroup of species (Reid et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study sites

Data were collected at five ~1-ha sites in southern Costa Rica, located between the Las Cruces Biological Station (8°47′7″N, 82°57′32″W) and the town of Agua Buena (8°44′52″N, 82°56′39″W), part of a larger study initiated in 2004–2006 of the influence of restoration approaches on forest regeneration (Zahawi et al., 2013). Sites are at the boundary between Tropical Premontane Wet and Rain Forest zones with a mean annual precipitation of 3,500–4,000 mm (dry season December–March) and a mean annual temperature of ~21°C. They range from 1,100 to 1,290 m in elevation and are mostly steeply sloped (15%–30%). The soils are of volcanic origin with similar bulk density, high organic matter, low phosphorus concentrations and pH of ~5.5 (Holl et al., 2013). Forest cover in this region is <30% and highly fragmented, typical of most landscapes in Central America (Zahawi, Dandois, et al., 2015; Zahawi, Duran, et al., 2015). Forest cover with 500 m of the sites ranges widely from 9% to 80% (Jorge Amar, unpub. data). All sites are surrounded by a mixture of land uses, mostly agricultural with small remnant forest patches interspersed (see Appendix S1 and Table S1 for land-use history and initial site condition details).

2.2 | Experimental design

From 2004 to 2006, we established three 0.25-ha (50 × 50 m) treatment plots each separated by a ≥5 m buffer at each of the five sites. Within each site, all existing vegetation was cleared, including dominant exotic forage grasses, and one of three restoration treatments (natural regeneration, applied nucleation and plantation) was randomly applied to each plot (see Figure S1 for plot layouts). At three of the five sites we also established sampling plots in adjacent remnant forests (four 25 × 25 m plots per site) to serve as references. These remnants have been impacted to some extent by human disturbance, but, to our knowledge, have never been fully cleared.

In active restoration plots, we planted ~20- to 30-cm tall tree seedlings spaced ~2.8 m apart (planting distance: 4 m within rows and 2 m between rows, offset by 2 m every other row). In the applied nucleation treatment, we planted tree seedlings in six subplots (or clusters) of three sizes: two each of 4 × 4 (small), 8 × 8 (medium) and 12 × 12 m (large) subplots, spaced evenly in the four corners and centres of the treatment plots; applied nucleation subplots were randomly arranged in two planting rows (three subplots per row), each separated by ≥8 m. In the plantation treatment, seedlings were planted in uniform rows throughout each plot. In both active restoration plots, we planted two native species *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two naturalized softwoods, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae), in alternating rows of *Terminalia/Vochysia* and *Erythrina/Inga*.

2.3 | Quantifying seed rain across treatments

We measured seed rain twice monthly from May 2013 to November 2016 (3.5 years) in four subplots (separated by ≥10 m) within each treatment plot, referred to as sampling 'stations'. At each station, three 0.25-m² seed traps with 0.69-mm mesh were placed at randomly selected ≥1-m intervals (e.g. at 1.0, 2.5 and 4.5 m) along transects (see Appendix S2 and Figure S1 for details on seed trap design and placement). In total, 216 traps were monitored: each restoration treatment had 60 seed traps (5 sites × 4 stations × 3 traps) and reference forests had 36 seed traps (3 sites × 4 stations × 3 traps).

For each sampling period, seeds were collected from each trap, stored separately in paper envelopes and then dried at 65°C to preserve until processing. Seeds were counted and identified to species following Tropicos nomenclature (Missouri Botanical Garden, 2020) using a reference collection at Las Cruces Biological Station. We excluded grass seeds (Poaceae), as they are not a major component of mature forest flora. Less than 0.01% of seeds were identified to only family or morphospecies. Using local knowledge and literature reviews, we classified species' dispersal syndrome (ectozoochorous, endozoochorous, anemochorous, explosive or gravity), categorized species as early or later-successional, and grouped species into 10 growth forms: two herbaceous (forb and vine), and eight woody groups (liana, shrub, understorey palm, understorey tree, canopy tree, emergent tree) and epiphytes (both herbaceous and woody species).

We evaluated how biotic versus abiotic processes influenced dispersal patterns by grouping ectozoochorous with endozoochorous seeds (hereafter '*animal-dispersed*') and gravity- and explosively dispersed seeds with anemochorous seeds (hereafter '*wind-dispersed*'), as gravity- and explosively dispersed seeds were deposited at very low rates (<0.001% of observed seeds). For all animal-dispersed tree species, we quantified seed length and assigned each to one of three categories (<5 mm, 5–10 mm and >10 mm; hereafter '*seed size*' categories), based on the knowledge that dispersal of larger seeded animal-dispersed species is limited by frugivore gape width (Wheelwright, 1985). Due to the rarity of seeds observed in the >10-mm size class, we combined the larger two size classes for community composition analyses (see Section 2.4.1).

2.4 | Statistical analysis

2.4.1 | Data organization, focal groups and community composition calculations

For all analyses, we used seed sampling stations within treatments as the sampling unit ($n = 72$ stations across treatments), which assumes that sampling stations are independent within each treatment plot. Because seed dispersal in tropical forests is a highly variable process, many studies treat individual seed traps as true replicates (Wright et al., 2005). However, our seed traps within sampling stations were too close to each other to be considered replicates and even sampling stations may not be truly independent due to non-independent processes (e.g. restoration treatments, spatial autocorrelation). Therefore, to decrease the risk of Type I errors, we took a conservative approach when evaluating pairwise comparison between treatments by disregarding results at the margins of significance (i.e. those close to $\alpha = 0.05$).

For multivariate community composition analyses in *Qs* 1–3, we built a seed rain community composition matrix with species counts or presence–absence in columns and sampling stations in rows. We used a subset of this matrix to examine the categories of interest for each question: (Q1) abundance of all herbaceous and woody seeds, or tree seeds only grouped by seed sizes of <5 or ≥5 mm; (Q2) presence–absence of animal-dispersed tree and shrub seeds; and (Q3) abundance of animal-dispersed tree or shrub seeds. We focused on animal-dispersed species for *Qs* 2–3 to determine how animal vectors influenced dispersal patterns across treatments.

To quantify differences in seed rain community composition among treatments (Q1 and Q3), we calculated the abundance-based Chao–Jaccard dissimilarity index (VEGAN package) to account for undersampling and potential unseen shared rare species (Chao et al., 2004). Before computing Chao–Jaccard dissimilarity values, seed abundances were square root transformed to reduce the influence of species with high deposition rates (Borcard et al., 2011). When quantifying within-plot animal-dispersed seed rain heterogeneity (Q2), we used the presence–absence-based Jaccard index to focus on within-plot community similarity independent of deposition rates. All analyses were conducted in R 3.6.2 (R Development Core Team, 2020).

2.4.2 | Treatment-level deposition rates and species composition

To summarize woody seed deposition rates and species composition across treatments (Q1), we first calculated Shannon diversity (Hill order $q = 1$) and plotted sample size-based species accumulation curves and confidence intervals ($\alpha = 0.05$) for each treatment (iNEXT package; Hsieh et al., 2016). Then, we determined how station-level seed deposition rates (seeds m^{-2} $year^{-1}$) of trees and shrubs were influenced by treatments, seed size and their interaction (fixed effects), with site as a blocking factor (random effect), using mixed-effects two-way ANOVA (Equation 1; LME4 package). Because of

the limited number of sampling stations within treatment plots ($n = 4$), we could not include station nested within site as a random effect. Therefore, we visually assessed the scaled plot-level residuals (DHARMA package) and determined that model results were not influenced by spatial autocorrelation. Deposition rate was log transformed to meet normality assumptions. We performed two separate ANOVAs (Type III; to account for the unbalanced number of stations within treatments) for wind- and animal-dispersed species:

$$\log(\text{deposition rate})_{ij} = \beta_0 + \beta_1 \text{treatment}_{ij} + \beta_2 \text{seed size}_{ij} + \beta_3 \text{treatment} \times \text{seed size}_{ij} + b_{1,ij} + \epsilon_{ij}, \quad (1)$$

where i indexes observations (sampling stations) and j indexes sites; b_1 are the normally distributed random intercepts for sites; and ϵ are the normally distributed subject residuals. For these, and all following ANOVAs in our analyses, we used Likelihood-ratio chi-squared (χ^2) tests to detect significant model terms (CAR package), and Tukey's HSD post hoc tests to determine differences between groups (EMMEANS package). For this and subsequent analyses, we determined marginal (R^2_m; fixed effects) and conditional (R^2_c; fixed and random effects) R^2 values for each linear model produced (PERFORMANCE package; Nakagawa & Schielzeth, 2013). We also constructed rank abundance curves of animal- and wind-dispersed tree and shrub species to visualize patterns in species-specific seed arrival across treatments (BIODIVERSITYR package).

We used non-metric multidimensional scaling (NMDS) to visualize seed rain community composition across treatments, and permutational multivariate analysis of variance (PERMANOVA) to test for differences between treatment centroids (VEGAN package) on Chao–Jaccard distance matrices. For NMDS results, we report three-dimensional fits as two-dimensional fits were unreliable (stress > 0.2; Borcard et al., 2011). For PERMANOVAs, pseudo-F- and p-values for treatment effects were calculated from 10,000 permutations, stratified by site to control for site-level differences in species composition. Last, we used Bonferroni-corrected pairwise PERMANOVAs (BIODIVERSITYR package) to detect differences in seed community composition between treatment pairs.

2.4.3 | Within-plot spatial heterogeneity and proportion later-successional species arriving

We compared within-plot spatial heterogeneity of seed rain among treatments (Q2) by calculating Jaccard's similarity of animal-dispersed tree and shrub seeds arriving over the 3.5-year sampling period for all pairwise combinations of sampling stations within each treatment plot. This allowed us to test if within-plot seed rain composition was more spatially homogeneous (high similarity) or heterogeneous (low similarity) between stations. We tested for differences in mean within-plot seed rain spatial heterogeneity (Jaccard similarity) among treatments ('γ' in Equation 2) using a mixed-effects one-way ANOVA (Type II; Equation 2). Jaccard similarity values were square root transformed to meet normality assumptions, and ϵ are the normally distributed subject residuals in Equation 2.

Next, we assessed if within-plot spatial heterogeneity could be driven by differences in the proportions of animal-dispersed tree and shrub species classified by successional group. We calculated the 'proportion of later-successional species' arriving at each station: (total # later-successional species)/(total # species arriving) and tested for differences in proportions ('γ' in Equation 2) arriving across treatments using a one-way ANOVA (Type II) performed on a mixed-model zero-inflated beta regression with site as a random effect (Equation 2; GLMMTMB package):

$$y_{ij} = \beta_0 + \beta_1 \text{treatment}_{ij} + b_{1,ij} + \epsilon_{ij}, \qquad (2)$$

where i indexes observations (sampling stations) and j indexes sites, b_1 are the normally distributed random intercepts for sites and ϵ are the beta-distributed subject residuals for the proportion with a logit distribution for zero outcomes. Results were consistent using seed abundances rather than species numbers to calculate proportions.

2.4.4 | Effects of interannual variability on seed composition

We evaluated how interannual variability (temporal heterogeneity) influenced seed community composition across treatments using distance-based redundancy analysis (dbRDA). We performed separate dbRDAs (VEGAN package) with year (2013–2016) as the predictor on Chao–Jaccard distance matrices of tree or shrub seeds arriving in each treatment. Site was partialled out as a blocking variable. We used PERMANOVAs (10,000 permutations) to determine the significance of year for each growth form (tree or shrub) × treatment combination.

3 | RESULTS

3.1 | Seed rain summary

A total of 588,350 seeds, from 146 species and 55 families, were quantified at sampling stations over the 3.5-year survey period. Seeds were identified to species level for all but three taxa (*Desmodium* spp.,

Ficus sp. 1 and *Ficus* sp. 2; Table S2). Animal-dispersed seeds comprised 41.7% of all seeds and 72.6% of species (106 animal-dispersed vs. 40 wind-dispersed species). Seeds were predominantly early successional species (94.8% seeds; 74 of 146 species). Over half of all seed rain was composed of tree seeds (55.5%); shrub seeds were the second most common (34.1%; Table S3). An overwhelming majority of dispersed tree seeds (99.5%; 37 of 59 species) were small seeded (<5 mm long); 56.0% of all tree seeds were animal-dispersed (50 of 59 species; Table S2). Seed deposition by the four planted species was minimal (0.18% of all seeds) and did not influence any results (see Appendix S3).

3.2 | Seed deposition rates and community composition (Q1)

The Shannon diversity of arriving seed communities followed the same pattern across treatments for all species (Figure 1A) and for tree and shrub species (Figure 1B); reference forests had the highest diversity [*all*: 96.44 ± 2.73; *trees and shrubs*: 65.20 ± 1.85 (asymptotic estimate ± *SE*)], applied nucleation (86.52 ± 1.96; 58.57 ± 1.20) and plantation (83.48 ± 2.54; 56.26 ± 1.73) treatments were intermediate and equivalent, and natural regeneration was the most diversity poor (73.61 ± 2.02; 47.65 ± 1.20).

Tree and shrub seed deposition rates were strongly influenced by the interaction between restoration treatment and seed size for both animal- ($\chi^2_{df=8} = 53.9$; $p < 0.001$; $R^2_m = 0.75$, $R^2_c = 0.83$) and wind-dispersed seeds ($\chi^2_{df=6} = 48.1$; $p < 0.001$; $R^2_m = 0.72$, $R^2_c = 0.76$; Figure 2; see Table S4 for pairwise comparisons). Notably, the lowest deposition rate of animal-dispersed <5-mm tree seeds was observed in the plantation treatment [175.7 ± 53.4 m²/year (mean ± *SE*)], which was approximately three times lower than that in applied nucleation (552.7 ± 168.0; Figure 2); however, deposition rates only differed marginally between these two treatments ($p = 0.04$; Tukey's HSD). Reference forests had the highest deposition rate of animal-dispersed 5- to 10-mm tree seeds (10.3 ± 4.1); however, deposition rates for this size class did not differ among restoration treatments. Deposition rates of >10-mm animal-dispersed tree seeds were equivalently low in the reference (1.3 ± 0.7), applied nucleation (0.8 ± 0.4) and plantation (1.6 ± 0.7) treatments, but no seeds of this size were recorded in the natural regeneration treatment.
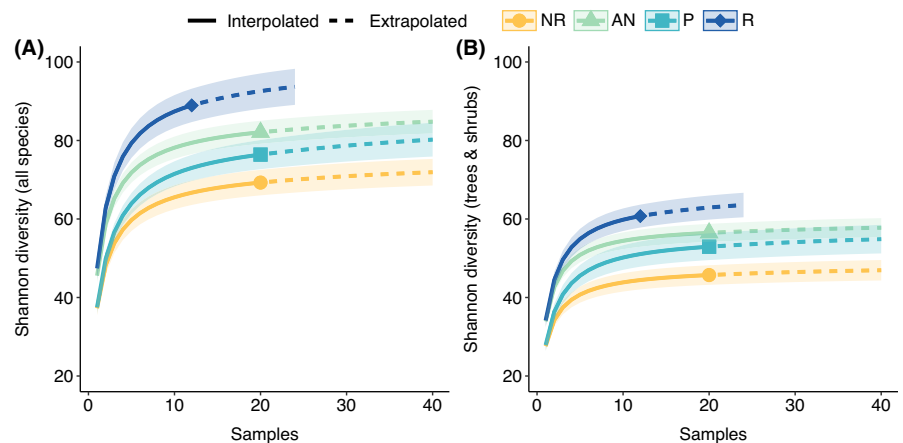

FIGURE 1 Rarefied species accumulation curves (solid line: rarefaction; dotted line: extrapolation) for Shannon diversity (Hill order $q = 1$) of seed rain of (A) all species and (B) trees and shrubs arriving in restoration treatments (NR =natural regeneration; AN =applied nucleation; P = plantation, R = reference). Shaded areas denote 95% confidence intervals
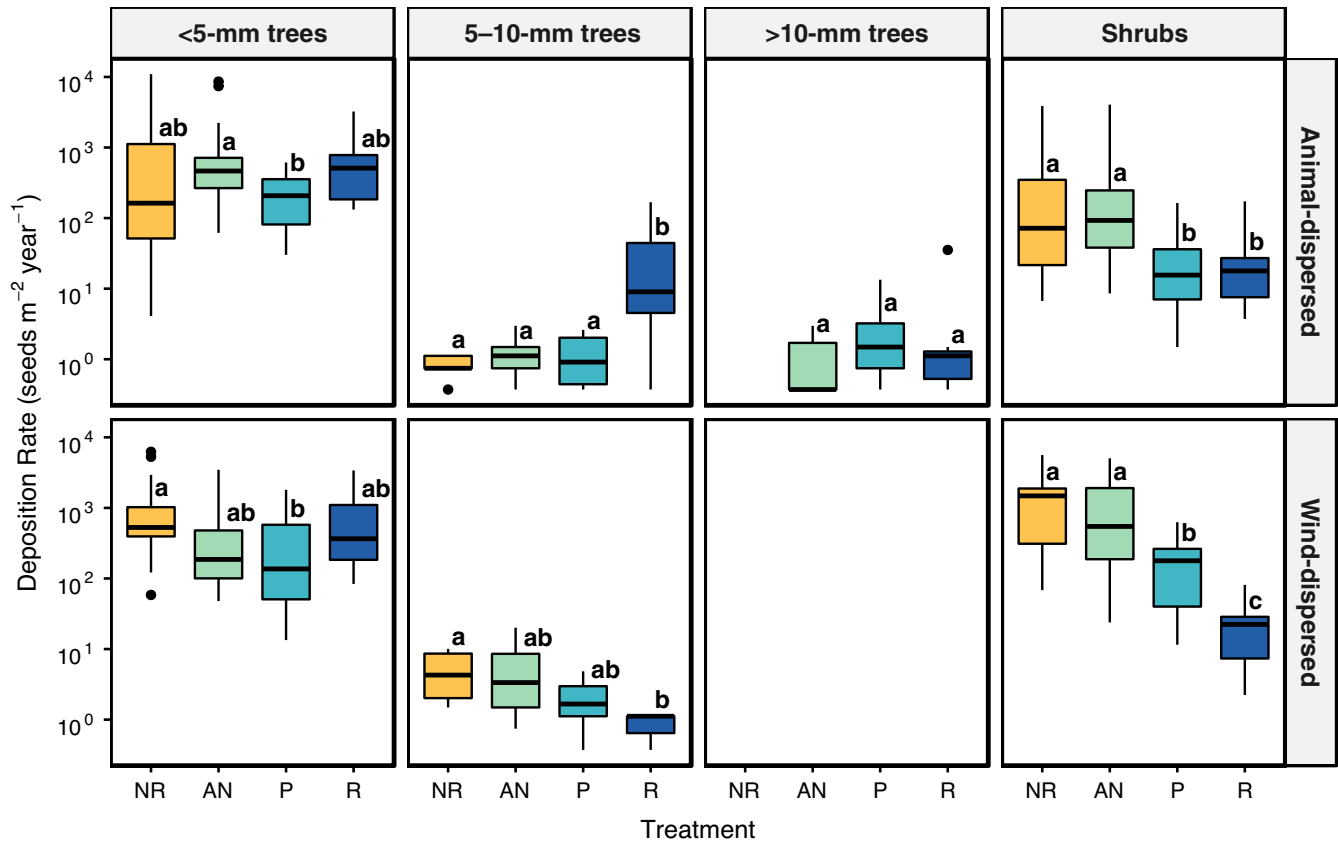
FIGURE 2 Log-scale seed deposition rates for trees and shrubs in the restoration treatments and reference forests (NR =natural regeneration; AN =applied nucleation; P = plantation; R = reference). Deposition rates are grouped by dispersal syndrome (animal- or wind-dispersed), and trees are separated by seed size. Centre line indicates the median and the top and bottom of boxes indicate upper and lower quartiles respectively. Letters above boxes indicate significant differences ($\alpha = 0.05$) in seed deposition rates among treatments for each dispersal mode and seed size group (pairwise Tukey's HSD tests on mixed-model ANOVAs). All test statistics for pairwise comparisons are reported in Table S4
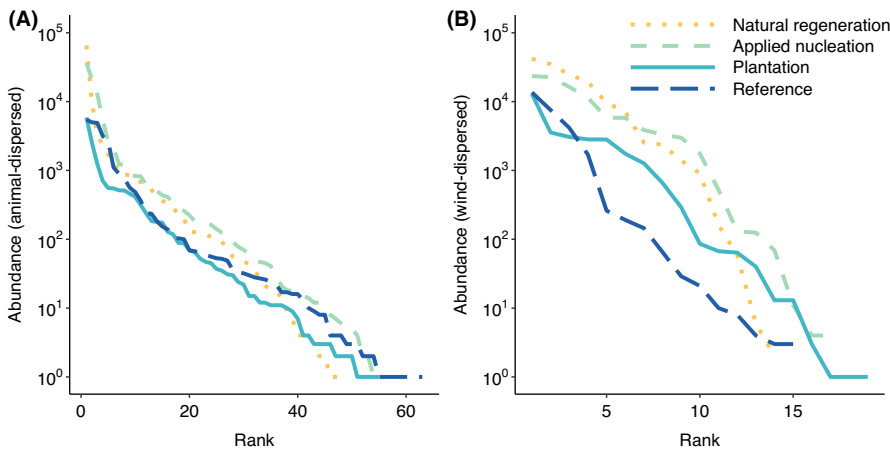

FIGURE 3 Rank-abundance curves (log-scale) of seed rain for all (A) animal- and (B) wind-dispersed tree and shrub seeds arriving in each treatment

Seed abundances of the most common tree species in the natural regeneration (*Conostegia xalapensis*, Melastomataceae) and applied nucleation treatments (*Cecropia obtusifolia*, Urticaceae) were an order of magnitude higher than in the other treatments (Figure 3A; Table S2); both are early successional, small-seeded trees. Likewise, shrub deposition rates were higher in natural regeneration and applied

nucleation than plantation and reference forest treatments (Figure 2) due to high deposition rates of one animal-dispersed (*Piper friedrichsthalii*; Piperaceae) and two wind-dispersed (*Vernonanthura patens* and *Vernonia arborescens*; Asteraceae) shrub(s) (Table S2; Figure 3B).

PERMANOVAs (Table 1) indicated differences in seed rain community composition of animal- and wind-dispersed species

TABLE 1 Differences in Chao–Jaccard dissimilarity of animal- and wind-dispersed seed rain communities among treatments. Letters indicate significant differences between treatments ($\alpha = 0.05$) for pairwise PERMANOVA (permutational multivariate analysis of variance) contrasts after Bonferroni correction. Pseudo-F, R^2 and p-values are reported for PERMANOVA tests across all treatments

Group	Natural regeneration	Applied nucleation	Plantation	Reference	Pseudo-F	R^2	p
All species	a	b	b	c	$F_{3,71} = 9.01$	0.28	0.001
Trees < 5 mm	a	a	a	b	$F_{3,71} = 3.73$	0.14	0.003
Trees ≥ 5 mm	a	b	b	c	$F_{3,62} = 4.66$	0.19	0.001

among treatments for all woody and herbaceous species (pseudo-$F_{3,71}$ = 9.01; p = 0.001), and both small- (<5 mm; pseudo-$F_{3,71}$ = 3.73; p = 0.003) and large-seeded tree species (≥5 mm; pseudo-$F_{3,62}$ = 4.66; p = 0.001). In all instances, seed rain in the reference forests was compositionally distinct from all restoration treatments. Moreover, for all but small-seeded tree species, pairwise PERMANOVAs indicated that applied nucleation and plantation treatments were compositionally equivalent and differed from the natural regeneration treatment (Table 1), and NMDS indicated that active restoration treatments were more similar to the reference forests than natural regeneration (Figure 4).

3.3 | Within-plot heterogeneity (Q2)

Within-plot spatial heterogeneity of animal-dispersed tree and shrub seed deposition ($\chi^2_{df=3}$ = 24.98; p < 0.001; R^2_m = 0.24, R^2_c = 0.43) and the respective proportion of later-successional species ($\chi^2_{df=3}$ = 42.09; p < 0.001; R^2_m = 0.59, R^2_c = 0.80) differed strongly among treatments. Within-plot animal-dispersed tree and shrub seed rain similarity was lower (i.e. more heterogeneous) in applied nucleation and reference forest plots, and higher (i.e. more homogeneous) in natural regeneration and plantation plots (Figure 5A; see Table S5 for pairwise comparisons). Moreover, the within-plot community composition of animal-dispersed tree and shrub species was 27.0% less similar on average, and therefore more spatially heterogeneous, in applied nucleation than plantation plots (p = 0.02; Tukey's HSD). The proportion of later-successional animal-dispersed species arriving was highest in reference forests, intermediate (and equivalent) between plantation and applied nucleation treatments (p = 0.99; Tukey's HSD) and lowest in the natural regeneration treatment (Figure 5B). As such, increased spatial heterogeneity of animal-dispersed seed deposition in the applied nucleation treatment was not due to differences in the proportion of later-successional species arriving within active restoration treatments.

3.4 | Interannual variability (Q3)

Interannual variation in seed arrival (i.e. which species arrived year-to-year, and at what abundance) significantly influenced the composition of animal-dispersed tree and shrub species deposited in all but the natural regeneration treatment (Table 2). However, the composition of animal-dispersed tree seeds arriving was less strongly affected by interannual variability in seed arrival in plantations ($F_{3,71}$ = 1.89), when compared to applied nucleation ($F_{3,71}$ = 3.01) and reference treatments ($F_{3,41}$ = 3.57).

4 | DISCUSSION

Our results show that seed rain species diversity and composition, as well as the proportion of later-successional species arriving, generally had greater convergence towards remnant forest in applied nucleation and plantation treatments than in natural regeneration. Additionally, tree and shrub communities arriving in the natural regeneration treatment did not differ interannually, indicating that dispersal patterns in this treatment may lead to the development of relatively homogeneous plant communities at this stage of succession. Moreover, our findings highlight that applied nucleation was the only restoration approach where spatial patterns of seed arrival were as heterogeneous as those observed in remnant forest, suggesting that applied nucleation may more quickly recuperate natural dispersal processes.

4.1 | Tree planting facilitates convergence of seed dispersal processes towards remnant forest

Whereas many studies show that tropical wet forest regeneration can be highly constrained in the first decade by a lack of seed dispersal, and especially for larger animal-dispersed species (de la Peña-Domene et al., 2014; Holl, 1999; Sangsupan et al., 2018), tree planting can alleviate this limitation (Reid et al., 2015). While we did not observe differences in overall seed rain community composition among restoration treatments 6–8 years into our experiment (Reid et al., 2015), current results demonstrate shifts in the diversity and composition of seeds arriving in restored sites as succession proceeds. By the second decade, results for both Shannon diversity (Figure 1) and the proportion of later-successional species arriving (Figure 5B) highlight that seed rain community composition in active restoration treatments is shifting towards that of remnant reference forests for all but small-seeded (<5 mm) tree species (Figure 4; Table 1). Additionally, while the deposition rates of small (<5 mm) and medium (5–10 mm) tree seeds are similar in active versus passive treatments, active restoration decreases seed limitation for the largest seeded (>10 mm), animal-dispersed tree species (Figure 2).
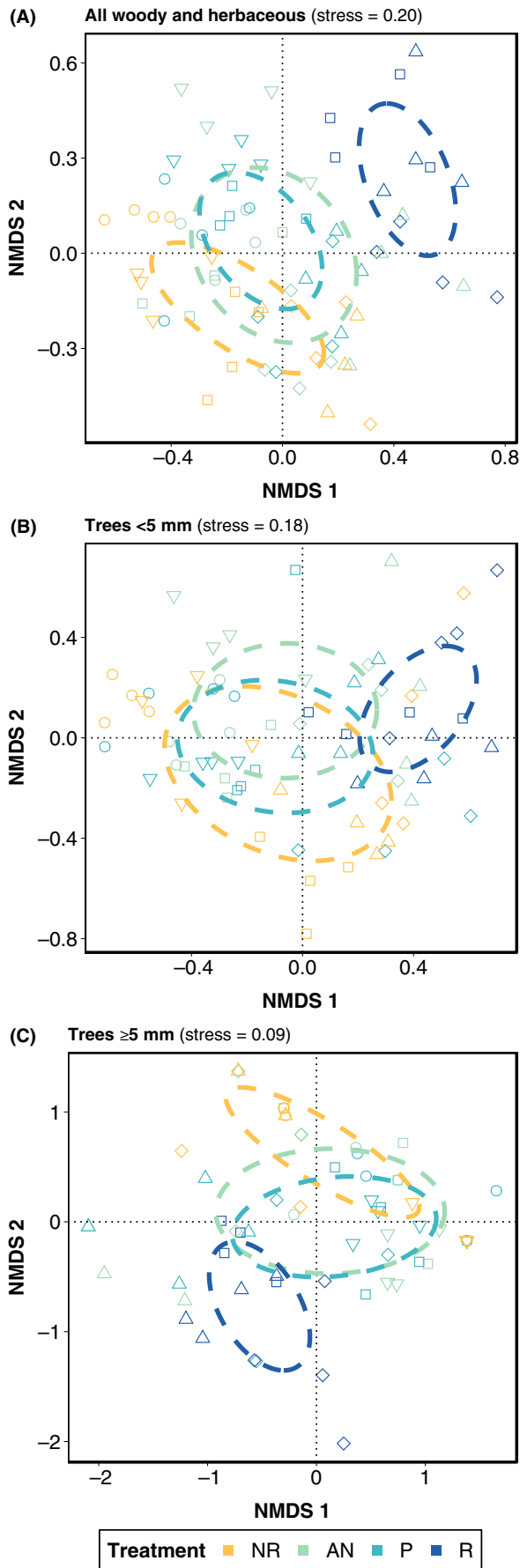
(A)   **All woody and herbaceous** (stress = 0.20)

(B)   **Trees <5 mm** (stress = 0.18)

(C)   **Trees ≥5 mm** (stress = 0.09)

Treatment   ■ NR   ■ AN   ■ P   ■ R

FIGURE 4 Non-metric multidimensional scaling (NMDS) fits based on Chao–Jaccard dissimilarity of seed rain community composition in forest restoration treatments and reference forests (NR = natural regeneration; AN = applied nucleation; P = plantation; R = reference) for (A) all woody and herbaceous species; (B) trees with <5-mm seeds; and (C) trees with ≥5-mm seeds. The first two axes of three-dimensional fits are shown as two-dimensional fits were unreliable (high stress). Points indicate species composition at sampling stations, with each site represented by a different symbol. Dashed ellipses are 95% standard deviation confidence intervals

Seeds in this category represented seven tree species (~12% of observed trees species) all of which were absent from the natural regeneration treatment. Whereas deposition rates of >10-mm animal-dispersed tree seeds were very low (0.8–1.6 seeds m^{-2} $year^{-1}$ across treatments), data on seedling recruitment in our plots suggest that these rare dispersal events do result in increased establishment (Holl et al., 2017). Taken together, results suggest that accelerating forest canopy development by planting trees shifts seed rain composition towards that of remnant forest (Table 1; Figure 4) with important implications for community reassembly trajectories in restored tropical forest.

Priority effects can have a lasting impact on restoration projects (Young et al., 2017), and this has been well-demonstrated in grasslands (Stuble et al., 2017). Our results emphasize that forest restoration treatments can modify temporal priority effects by attracting divergent seed rain communities over time (Table 1; Figure 4). It is also important to consider how differences in seed deposition rates across treatments could affect recovery trajectories. For example, although the overall composition of <5 mm animal-dispersed tree species did not differ among restoration treatments (Table 1; Figure 4B), deposition rates of these species were three times higher in the applied nucleation than the plantation treatment (Figure 2), and were mainly driven by two early successional tree species (*Cecropia obtusifolia* and *Miconia schlimii*; Table S2). Additionally, shrub deposition rates were equivalent and highest in the natural regeneration and applied nucleation treatments (Figure 2). Such deposition patterns may influence tree and shrub recruitment patterns, contributing to different vegetation recovery dynamics across treatments. That said, higher seed deposition does not necessarily lead to increased recruitment because of establishment filters (Reid & Holl, 2013), and seed-to-seedling transitions are similarly low across restoration treatments at our sites (Werden et al., 2020).

To develop a more complete picture of how seed rain is shifting over time, we could examine how seed dry mass differs across treatments. This would enable a more continuous comparison of seed deposition rates across treatments and reference forest, which likely have a higher ratio of seed mass/number of seeds deposited due to disproportionally higher rates of large-seeded tree deposition. These patterns are likely also affected by within-plot tree and shrub reproductive rates, which were notably higher in
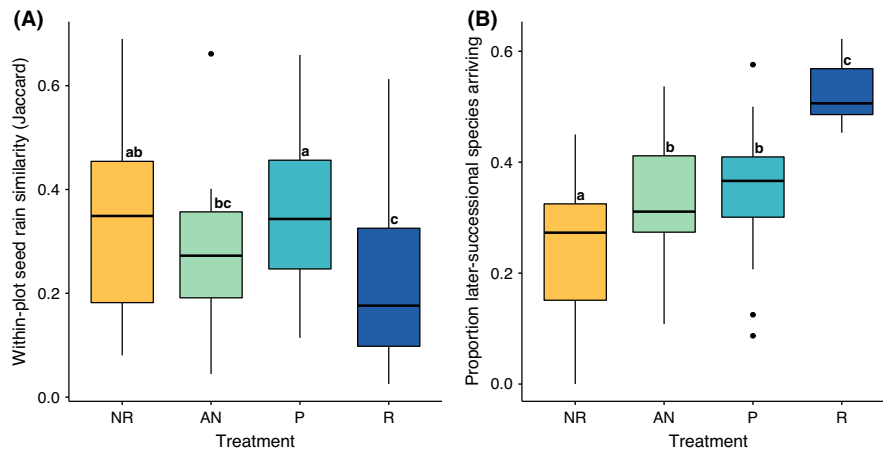
FIGURE 5 (A) Within-plot Jaccard's similarity of animal-dispersed tree and shrub species, and (B) proportion of later-successional animal-dispersed tree and shrub species arriving across restoration treatments (NR = natural regeneration; AN = applied nucleation; P = plantation) and reference forests (R). In (A) values closer to 0 indicate low similarity (higher within-plot heterogeneity) of species arriving, and in (B) values closer to 0 indicate a lower proportion of later-successional species arriving (n = 20 stations for NR, AN, P; n = 12 stations for R). In both panels, the centre line indicates the median and the top and bottom of boxes indicate upper and lower quartiles respectively. Letters above boxes indicate significant differences ($\alpha = 0.05$) between treatments (pairwise Tukey's HSD tests on mixed-model ANOVAs) and responses were back-transformed for plotting. All test statistics for pairwise comparisons are reported in Table S5

TABLE 2 Distance-based redundancy analyses (dbRDAs) with year as a predictor of animal-dispersed tree or shrub community composition in each treatment (Chao–Jaccard distances matrices). Pseudo-F and p-values (in parentheses; bold at $\alpha = 0.05$) are reported for PERMANOVAs testing for the significance of year

Treatment	Trees	Shrubs
Natural regeneration	$F_{3,70} = 1.22$ (0.16)	$F_{3,65} = 1.38$ (0.07)
Applied nucleation	$F_{3,71} = 3.01$ (**<0.001**)	$F_{3,71} = 1.70$ (**0.01**)
Plantation	$F_{3,71} = 1.89$ (**0.001**)	$F_{3,56} = 1.71$ (**0.01**)
Reference	$F_{3,41} = 3.57$ (**<0.001**)	$F_{3,39} = 2.16$ (**0.001**)

natural regeneration than active restoration treatments in Mexican wet forest (Caughlin et al., 2018). Additionally, the composition of reproductive trees in the surrounding landscape matrix likely has an important impact on these dynamics (R. Zahawi, unpubl. data), though we observed that treatment-level effects always explained more of the response variation than site-level effects (difference between R^2_m and R^2_c).

4.2 | Active restoration approaches can increase the heterogeneity of seed arrival

Our results demonstrate that active tree planting increases the interannual heterogeneity of animal-dispersed seed arrival. However, interannual composition of animal-dispersed tree and shrub seeds in the natural regeneration treatment was very homogeneous (Table 2). This finding aligns with a study in naturally regenerating

Mexican tropical dry forest that showed little interannual variation in seed rain species richness (Martínez-Garza et al., 2011). Such patterns are likely driven by the limited number of primarily early successional species deposited in the natural regeneration treatment (Table S2), and low visitation rates of animal dispersers of larger seeds (Reid et al., 2014). Moreover, bird-mediated dispersal has been directly linked to increased seed dispersal heterogeneity in early successional tropical wet forest (González-Castro et al., 2019) and the interannual seed dispersal patterns we observed support the importance of this mechanism in directing community reassembly in regenerating tropical forest. Specifically, the increased probability of rare dispersal events of larger seeded late-successional seeds to applied restoration and reference forest plots appears to contribute to the strong interannual variability of seed arrival in those treatments.

Interestingly, results suggest that applied nucleation increased within-plot spatial heterogeneity of animal-dispersed tree and shrub seed arrival compared to tree plantations (Figure 5A), which could lead to spatially distinct recruitment patterns. This is consistent with our initial expectation and may be due to the greater structural complexity of niche-space observed in applied nucleation plots (Holl et al., 2013; Zahawi, Dandois, et al., 2015; Zahawi, Duran, et al., 2015), which may attract a more diverse assemblage of dispersers. For example, increased heterogeneity of tall tree canopy cover can be associated with an increase in bird species richness (Stirnemann et al., 2015). Collectively, results suggest that the slower succession observed in the natural regeneration treatment is likely perpetuated by a lack of interannual variation in the seed community deposited, but not by within-plot spatial patterns of seed arrival.

4.3 | Implications for restoration design and outcomes

While tropical forest successional dynamics can be highly context dependent (Norden et al., 2015), our results indicate that restoration treatments can be strong deterministic predictors of the composition and diversity of seed rain. Moreover, these dispersal dynamics appear to be strongly linked to differential patterns of tree recruitment across active and passive restoration approaches (Holl et al., 2017; de la Peña-Domene et al., 2017). When compared to natural regeneration, we observed that targeted tree planting in this ecosystem is a reliable approach to:

1. Catalyse the recovery of seed rain biodiversity: Shannon diversity of arriving seed communities recovered more rapidly in active restoration treatments than natural regeneration (*all species*: 17.5% and 13.4% higher in applied nucleation and plantation treatments than natural regeneration respectively; *trees and shrubs*: 22.9% and 18.1% higher in applied nucleation and plantation treatments respectively; Figure 1).
2. Shift the species composition of arriving seeds towards that of remnant forest: Shannon diversity of arriving seeds more closely resembled reference forests in active restoration versus natural regeneration on average (*all species*: 89.7, 86.6 and 76.3 of reference forest diversity recovered in applied nucleation, plantation and natural regeneration treatments respectively; *trees and shrubs*: 89.8%, 86.3% and 73.1% recovered in applied nucleation, plantation and natural regeneration treatments respectively; Figure 1).
3. Increase the arrival of later-successional seeds: The proportion of later-successional species arriving almost doubled in active restoration (87.9% and 89.0% higher in applied nucleation and plantation respectively) versus natural regeneration (Figure 5B).
4. Ensure that arriving seed communities are sufficiently temporally heterogeneous to overcome successional barriers observed in many abandoned tropical pastures (Zahawi & Augspurger, 1999): Interannual variation in seed arrival was highly influential on seed community composition in the active restoration treatments, which may catalyse the reassembly of more heterogeneous plant communities over a shorter time period. The opposite was true in the natural regeneration treatment (Table 2).

All these factors may contribute to more rapid reassembly of diverse communities in active restoration treatments over natural regeneration, in addition to increasing seed availability necessary to overcome low seed-to-seedling transition rates prevalent in other degraded tropical wet forests (de la Peña-Domene et al., 2017). Moreover, rapidly overcoming dispersal limitation is especially important given that natural regeneration may take >100 years to match the species richness of mature tropical forests (Rozendaal et al., 2019).

Finally, we found evidence that applied nucleation may facilitate the recovery of certain natural dispersal processes over plantation forestry, as spatial heterogeneity of animal-dispersed seeds arriving within applied nucleation plots reached the levels observed in remnant forest, whereas plantations did not. This result is one of the first to indicate that increasing habitat spatial heterogeneity, an important potential benefit of the applied nucleation technique (Corbin & Holl, 2012), may speed the recovery of natural ecological processes over other active restoration interventions. Overall, results highlight that tree planting can promote the recovery of many seed dispersal processes, which can speed the recuperation of plant biodiversity in degraded tropical landscapes.

AUTHORS' CONTRIBUTIONS

K.D.H. and R.A.Z. created and implemented the experiment; K.D.H., J.M.C.-F., F.O.-B., J.A.R. and R.A.Z. collected the data; L.K.W. performed statistical analyses and wrote the first draft, K.D.H., R.A.Z. and J.M.C.-F. contributed to revisions.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3xsj3txgc (Werden et al., 2021).

ORCID

Leland K. Werden https://orcid.org/0000-0002-3579-4352
Karen D. Holl https://orcid.org/0000-0003-2893-6161
José Miguel Chaves-Fallas https://orcid.org/0000-0001-9049-9383
Rakan A. Zahawi https://orcid.org/0000-0002-5678-2967

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