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Authors

Reid, J Leighton
Holl, Karen D
Zahawi, Rakan A

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Seed dispersal limitations shift over time in tropical forest restoration

J. Leighton Reid,[1,2,4] Karen D. Holl,[1] and Rakan A. Zahawi[3]

[1]*Environmental Studies Department, University of California, 1156 High St., Santa Cruz, California 95064 USA*
[2]*Center for Conservation and Sustainable Development, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299 USA*
[3]*Las Cruces Biological Station, Organization for Tropical Studies, Apartado 73-8257, San Vito, Costa Rica*

Abstract. Past studies have shown that tropical forest regeneration on degraded farmlands is initially limited by lack of seed dispersal, but few studies have tracked changes in abundance and composition of seed rain past the first few years after land abandonment. We measured seed rain for 12 months in 10 6–9-year-old restoration sites and five mature, reference forests in southern Costa Rica in order to learn (1) if seed rain limitation persists past the first few years of regeneration; (2) how restoration treatments influence seed community structure and composition; and (3) whether seed rain limitation is contingent on landscape context. Each restoration site contained three 0.25-ha treatment plots: (1) a naturally regenerating control, (2) tree islands, and (3) a mixed-species tree plantation. Sites spanned a deforestation gradient with 9–89% forest area within 500 m around the treatment plots. Contrary to previous studies, we found that tree seeds were abundant and ubiquitous across all treatment plots (585.1 ± 142.0 seeds·m^{-2}·yr^{-1} [mean ± SE]), indicating that lack of seed rain ceased to limit forest regeneration within the first decade of recovery. Pioneer trees and shrubs comprised the vast majority of seeds, but compositional differences between restoration sites and reference forests were driven by rarer, large-seeded species. Large, animal-dispersed tree seeds were more abundant in tree islands (4.6 ± 2.9 seeds·m^{-2}·yr^{-1}) and plantations (5.8 ± 3.0 seeds·m^{-2}·yr^{-1}) than control plots (0.2 ± 0.1 seeds·m^{-2}·yr^{-1}), contributing to greater tree species richness in actively restored plots. Planted tree species accounted for <1% of seeds. We found little evidence for landscape forest cover effects on seed rain, consistent with previous studies. We conclude that seed rain limitation shifted from an initial, complete lack of tree seeds to a specific limitation on large-seeded, mature forest species over the first decade. Although total seed abundance was equal among restoration treatments, tree plantations and tree islands continued to diversify seed rain communities compared to naturally regenerating controls. Compositional differences between regenerating plots and mature forests suggest that large-seeded tree species are appropriate candidates for enrichment planting.

Key words: *applied nucleation; Costa Rica; forest regeneration; secondary forest; succession; tree plantation.*

Introduction

In most tropical countries, the majority of forests are second growth (Chazdon 2014). As deforestation progresses, these young forests will be increasingly important for biodiversity conservation (Wright and Muller-Landau 2006, but see Gibson et al. 2011), hydrological regulation (Hölscher et al. 1997, Hassler et al. 2011), and carbon sequestration (Silver et al. 2000, Gilroy et al. 2014, but see Mackey et al. 2013). In Latin America, forest regeneration frequently occurs when marginal farmlands are taken out of cultivation (Aide et al. 2013). However, recovery rates on these farmlands are highly variable due to differences in land-use history, landscape context, and the completeness of regional

assemblages (Chazdon et al. 2009). Moreover, the benefits of forest regeneration will accrue over decades (Finegan 1996, Martin et al. 2013), highlighting the need for long-term studies.

Tropical forest regeneration on degraded farmlands is limited by a suite of local processes (Holl 2012). Soil seed banks are typically depleted after a few years of agricultural use (Cubiña and Aide 2001, López-Toledo and Martínez-Ramos 2011), so recolonization is initially contingent upon seed dispersal by birds, bats, and wind (Nepstad et al. 1990, Duncan and Chapman 1999, Ingle 2003). Seed arrival is scarce in open areas outside of forests (Wijdeven and Kuzee 2000, Dosch et al. 2007, Barnes and Chapman 2014), and the few dispersed seeds that do not succumb to desiccation, predators, or rot (Cole 2009) are typically outcompeted by aggressive pasture grasses or other ruderal vegetation (Holl 1998, Ferguson et al. 2003). These initial, rate-limiting

[4] E-mail: j.leighton.reid@gmail.com

processes are well-understood, but few studies have tracked their relative importance beyond the first few years of succession.

Mixed-species tree plantations are a common strategy for accelerating forest succession (Chazdon 2008, Lamb 2011). Tree plantations attract seed dispersers and shade competitive grasses (Kanowski et al. 2003, Lindell et al. 2013), facilitating both seed arrival and seedling survival. However, tree plantations are relatively expensive to establish and even-aged plantations can have homogeneous structure, potentially limiting their capacity to support diverse communities (Holl et al. 2011, 2013). Tree species selection can also have unintended consequences, for example, on nutrient cycling (Siddique et al. 2008, Celentano et al. 2011) and future seedling recruitment (Murcia 1997, Cusack and Montagnini 2004, Schweizer et al. 2013).

An alternative restoration strategy is to plant small patches or "islands" of trees with the expectation that these islands will expand and coalesce over time (Robinson and Handel 2000). Tree islands may also promote seed dispersal into adjacent areas (Rey Benayas et al. 2008). This method builds on the nucleation model of succession, in which woody vegetation initially establishes in patches and expands outwards clonally or through facilitation (Yarranton and Morrison 1974). The promise of applied nucleation (sensu Corbin and Holl 2012) is that it will accelerate succession less deterministically than tree plantations, and for a lower cost. Previous experiments have found that applied nucleation enhances seed rain and seedling establishment compared to natural regeneration (Zahawi and Augspurger 2006) and does so to a similar degree as tree plantations (Cole et al. 2010, Zahawi et al. 2013). However, changes in the relative costs and benefits of these different strategies have not been studied over time.

Restoration treatment effects are also contingent upon the surrounding landscape, which serves as a source of propagules as well as disturbances (e.g., invasive species or movement of agricultural chemicals). Previous studies show that forest amount and proximity are positively correlated with bird abundance and composition (Lindenmayer et al. 2010, Van Bael et al. 2013), and many authors suppose that seed rain and seedling recruitment should respond similarly (Chazdon et al. 2009, Rodrigues et al. 2009, Tambosi et al. 2013). However, empirical evidence has been mixed with some studies finding landscape effects on forest regeneration (Purata 1986, Teegalapalli et al. 2010) and others not (Howe et al. 2010, Zahawi et al. 2013).

Here we present seed rain measurements from 10 6–9-year-old restoration sites and five mature forests to address the following questions: (1) Does seed rain limitation persist beyond the first few years of succession in tropical farmlands? (2) How do different restoration strategies affect the structure and composition of seed rain relative to a reference community? (3) What is the influence of the surrounding landscape on seed community structure and composition? Based on our earlier results (Cole et al. 2010), we anticipated that seed rain abundance and diversity would be greater in tree plantations and applied nucleation treatments than in naturally regenerating controls. We also expected that seed rain composition would better resemble seed rain in reference communities when restoration sites were embedded in landscapes with high surrounding forest cover, consistent with patterns of bird communities in the sites (Reid et al. 2014). Understanding the effects of restoration strategies and landscape context on plant colonization will help practitioners and decision makers decide how and where to restore tropical forests.

Methods

Study area

This work was conducted in the landscape surrounding Las Cruces Biological Station (8°47′ N, 82°57′ W) and the town of Agua Buena (8°44′ N, 82°56′ W) in Coto Brus Canton, Costa Rica. The study area encompasses ~100 km^2 of hilly terrain with elevations ranging from 1100 to 1290 m (Appendix A: Table A1). Annual precipitation ranges from 3000–4000 mm throughout the study area with most rain falling between April and November. Mean annual temperature at Las Cruces is 21°C. The primary native ecosystem is tropical premontane humid forest (Holdridge et al. 1971), but most of this forest was cleared for coffee cultivation between 1960 and 1980. Currently the study area is a mixed, agricultural mosaic of cattle pastures, coffee plantations, various vegetable crops, small forest fragments, and riparian corridors. Forest elements comprise ~35% of the study area (Mendenhall et al. 2011).

Experimental design

We monitored seed rain at 10 restoration sites and five mature, reference forests (Table A1). Restoration sites were established in 2004–2006 on post-agricultural lands (mostly cattle pastures; Holl et al. 2011) that were farmed for ≥18 years. Each restoration site contained three 0.25-ha treatments (Fig. A1). Control plots were allowed to regenerate naturally, plantations were planted with tree seedlings throughout the entire 0.25-ha plot, and island plots were planted with six patches of trees, two each of 4 × 4, 8 × 8, and 12 × 12 m. Planted tree spacing was equivalent (2.8 m between seedlings) in islands and plantation plots, but island plots had 86 total seedlings whereas plantations had 313. Islands and plantations were planted with seedlings of four tree species used locally in agroforestry systems. *Erythrina poeppigiana* (Walp.) Skeels (Fabaceae), *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae), and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae) produce wind-dispersed seeds, whereas *Inga edulis* Mart. (Fabaceae) produces an indehiscent fruit with an edible pulp consumed by primates and, to a lesser degree, bats

(Lobova et al. 2009). *I. edulis* and *E. poeppigiana* are fast-growing nitrogen-fixers whereas *T. amazonia* and *V. guatemalensis* are slower growing. All plots were hand-cleared by machete for 2.5 yr following planting to allow seedlings to grow above the height of the pasture grasses. Plots within a site were separated by ≥5 m, and sites were separated by ≥0.7 km.

At the time of seed rain measurement, canopy height of planted trees was 9–14 m in plantations and 2–8 m in islands. The canopy of the planted tree islands covered a mean of 42% of the plot (range 15–65%). Canopy cover was >80% in plantations. Individual tree island sizes within each island treatment plot varied due to differences in growth and survival of planted trees as well as recruitment at the island edges. In 2012, island sizes were was 305 ± 122 m² (large islands [mean ± SD]), 180 ± 74 m² (medium islands), and 77 ± 46 m² (small islands).

Remnant and regrowth forest cover within a 500 m radius around each restoration plot's centroid ranged from 9% to 89% (Table A1). We selected 100- and 500-m spatial scales for forest cover analyses to account for different processes that promote short-distance dispersal (10–100 m; e.g., wind, gravity) and longer-distance dispersal (100–1000 m; e.g., birds, bats, primates [Corlett 2009]). Forest cover was based on classification of aerial photographs (Cole et al. 2010). We did not quantify other landscape features, such as live fences, hedgerows, and remnant trees (Harvey et al. 2006), which are common in the study area.

Five mature forest plots formed the basis for our reference community comparisons. Two of these plots were situated in the largest remnant in the region (Las Cruces Biological Reserve; 320 ha) and three were located in smaller remnants (~2–20 ha). Forest plots were paired with restoration plots and separated from them by 5–15 m. Reference forests in this study were not "pristine"; such forests are not present in our study area (Clement and Horn 2001). Rather, they were selected as representative of regional forest communities. The completeness of these forests' frugivore communities was variable, however, all reference forests had large fruit-eating birds (e.g., toucans, chachalacas) and bats (e.g., *Artibeus* spp.). We observed arboreal frugivores (e.g., kinkajous, olingos, capuchin monkeys) at three of the five sites.

Seed rain monitoring

Seed rain was collected twice per month from 15 February 2012 to 14 February 2013 in 420 0.25-m² traps. In each restoration and reference plot, we established four trapping stations along permanent vegetation transects (Fig. A1). Each station had three traps. In island plots, we placed two of the 12 traps (16%) in the planted patches and the remainder in unplanted areas to match the proportion of the area that was initially planted (18%). All traps were located >5 m from the plot edge. Seed traps in reference forests were situated 5–50 m from the forest edge to be comparable to restoration plots.

Seeds were collected in paper envelopes and heated in a drying oven prior to identification. We identified seeds using a local reference collection (Cole et al. 2010). Voucher specimens were stored in the Luis Diego Gómez Herbarium (HLDG) at Las Cruces Biological Station. Through consultation with regional botanists, we assigned species to broad dispersal groups (animal, wind, gravity) and growth forms (tree, shrub, terrestrial herb, epiphyte, vine, woody liana, palm), and we measured seed length. Because we collected only one or two seeds of some species, we could not evaluate important variation in seed length (Brewer 2001), so we grouped seeds into length categories (≤2, 2–5, 5–10, >10 mm). We did not identify grass seeds (Poaceae) or seeds in the genus *Aster* (Asteraceae), which are highly abundant in recently abandoned agricultural lands, but form a very small component of the forest flora. We also omitted some externally dispersed seeds of herbaceous species common in agricultural lands but not forests, i.e., *Bidens* (Asteraceae) and *Desmodium* (Fabaceae) spp., which stuck to our clothing and to the seed trap material, potentially biasing measurements.

Seed traps were inverted pentahedrons of fiberglass window screening (0.69-mm mesh) affixed to a square, metal frame with three legs (Fig. A2). The opening was 50 × 50 cm, trap rim was 55 cm above the ground, and the pocket depth was 30 cm. We field tested our seed trap design for several potential biases. First, to test whether seeds were removed from traps by animals, we placed 16 marked seeds of four species in 48 seed traps over a two-week sampling period. We recovered >95% of marked seeds, indicating that seed removal was minimal. Second, we observed seed traps in several habitats and found no evidence that birds or other animals biased seed rain measurements through seed addition (Reid et al. 2012). Third, we dropped large seeds into trap prototypes from 15 m height to determine the minimum seed trap pocket depth for which no seeds bounced out. One unavoidable limitation to our elevated traps, common to seed rain studies, is that secondary seed dispersal (e.g., by terrestrial mammals, ants) was not recorded.

Data analysis

We compared five community attributes of seed rain in restoration plots and reference forests: (1) species diversity, (2) species evenness, (3) species richness, (4) seed abundance, and (5) compositional similarity to seed rain in reference forest. Community analyses were performed in R version 3.0.2 (R Development Core Team 2013) with packages vegan (Oksanen et al. 2012) and BiodiversityR (Kindt and Coe 2005). Means ± SE is reported, except where noted. See *Data Availability* for archive location.

To calculate species diversity and evenness we used Jost's (2006) true diversity and Pielou's (1966) *J*, respectively. For species richness, we rarified to the smallest number of individuals observed in any plot. We

TABLE 1. Restoration treatment effects on seed rain structure and composition.

Variable	Control	Island	Plantation	Reference	$F_{3,22}$	P
All species						
Rarified species richness, S ($N = 304$)	**10.8[a] ± 0.9**	**13.8[ab] ± 0.7**	**16.1[b] ± 1.2**	**18.4[b] ± 3.5**	**5.3**	**0.021**
True diversity, $\exp(H')$†	4.0 ± 0.7	4.9 ± 0.8	6.6 ± 0.9	7.7 ± 2.5	1.9	0.501
Evenness, J	0.4 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	1.4	0.840
Similarity to reference, Chao-Jaccard‡	**0.66[a] ± 0.05**	**0.67[a] ± 0.07**	**0.76[ab] ± 0.02**	**0.84[b] ± 0.03**	**4.9**	**0.028**
Similarity to reference, Sørensen	**0.56[a] ± 0.02**	**0.59[a] ± 0.02**	**0.60[a] ± 0.01**	**0.68[b] ± 0.01**	**7.4**	**0.004**
Trees						
Rarified species richness, S ($N = 18$)	**2.4[a] ± 0.2**	**3.5[ab] ± 0.4**	**4.1[b] ± 0.5**	**4.3[b] ± 1.0**	**5.4**	**0.019**
True diversity, $\exp(H')$†	**1.9[a] ± 0.2**	**2.9[ab] ± 0.4**	**3.6[b] ± 0.5**	**3.8[b] ± 1.0**	**4.8**	**0.030**
Evenness, J	0.4 ± 0.1	0.5 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	2.0	0.442
Similarity to reference, Chao-Jaccard‡	0.76 ± 0.06	0.80 ± 0.04	0.75 ± 0.05	0.85 ± 0.03	1.7	0.609
Similarity to reference, Sørensen	0.55 ± 0.03	0.59 ± 0.03	0.59 ± 0.03	0.67 ± 0.02	2.8	0.192
Shrubs						
Rarified species richness, S ($N = 25$)	4.6 ± 0.3	4.5 ± 0.4	4.9 ± 0.4	5.7 ± 0.2	1.5	0.714
True diversity, $\exp(H')$	3.4 ± 0.4	3.5 ± 0.5	3.8 ± 0.3	4.8 ± 0.4	1.9	0.498
Evenness, J	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	2.4	0.290
Similarity to reference, Chao-Jaccard‡	0.66 ± 0.06	0.65 ± 0.08	0.81 ± 0.05	0.72 ± 0.03	1.8	0.555
Similarity to reference, Sørensen	0.75 ± 0.03	0.75 ± 0.02	0.80 ± 0.02	0.79 ± 0.03	1.3	0.933

Notes: Means and standard errors are reported. Superscript letters denote significant differences in post hoc tests (Tukey's HSD, $\alpha = 0.05$). P values are Bonferroni adjusted for family-wise error. Significant results are highlighted in boldface type. N denotes the number of individuals to which richness was rarified (i.e., the minimum number of individuals observed in any plot).

† Variable was log-transformed to meet model assumptions.

‡ Variable was rank-transformed to meet model assumptions.

visualized these community attributes by plotting species accumulation and rank abundance curves. Species accumulation curves used the exact method with unconditional standard deviations (Ugland et al. 2003).

Seed abundance was analyzed as the total number of seeds collected from a plot. We report seed abundances as a rate (seeds·m^{-2}·yr^{-1}) to facilitate comparison across studies. Abundance was analyzed across the entire seed community, as well as for particular growth forms with >50 detections. For the two most common growth forms, trees and shrubs (both >40 000 detections), we also analyzed abundance within subsets ($\geq$52 detections) based on seed length ($\leq$5 mm, >5 mm) and dispersal type (animal, wind).

We used two measures of compositional similarity to compare restoration plots to reference forests. For an abundance-based measure, we used Chao-Jaccard dissimilarity, which accounts for rare species and undersampling (Chao et al. 2005). For a presence-only measure, we used Sørensen dissimilarity. Both indices were converted to similarity (1 − dissimilarity) prior to analysis. For each index we calculated pairwise similarity between restoration plots and reference forest plots. For this analysis only, we removed pairs of restoration and reference plots located at the same site to get a general measure of similarity between restoration and reference plots not biased by proximity.

We evaluated restoration treatment effects on seed community attributes using two-way analysis of variance (ANOVA) with treatment (control, island, plantation, reference forest) as the main effect and site ($N = 10$ sites) as a blocking factor. Several variables were log- or rank-transformed to meet model assumptions (Tables 1, A2). P values were corrected for multiple comparisons using

Bonferroni adjustments. We used a post-hoc test (Tukey's HSD) for pairwise comparisons. For all comparisons, we used a significance cut-off of 0.05.

We visualized seed community composition using nonmetric multidimensional scaling (NMDS). We created NMDS plots using both Chao-Jaccard and Sørensen distance matrices. For both analyses, we report a three-dimensional fit because the stress of a two-dimensional fit was >20, i.e., too high for reliable interpretation (Clarke 1993). We used permutational multivariate analysis of variance (PERMANOVA) to evaluate differences in treatment centroids (Anderson and Walsh 2013).

Restoration treatment effects were compared with landscape forest cover using generalized linear mixed-effects models (GLMM). Eight candidate models included (1) a null (intercept) model, (2–3) forested area within 100 or 500 m (%), (4) restoration treatment (control, island, plantation), and (5–8) restoration treatment combined with forest cover, with and without interaction (Table A3). Site was included as a random term (variable intercept) to account for our randomized block design. Error distribution was modeled as negative binomial for seed abundances and Gaussian for other community measurements. We compared models using Akaike information criterion scores corrected for small sample sizes (AIC$_c$; Burnham and Anderson 1998). We interpreted candidate models with ΔAIC$_c$ < 2 as having approximately equal support. GLMM analysis was performed with packages glmmADMB (Skaug et al. 2013) and lme4 (Bates et al. 2014).

RESULTS

We collected 107 845 seeds from 70 species in 37 families (Appendix B). Trees and shrubs comprised
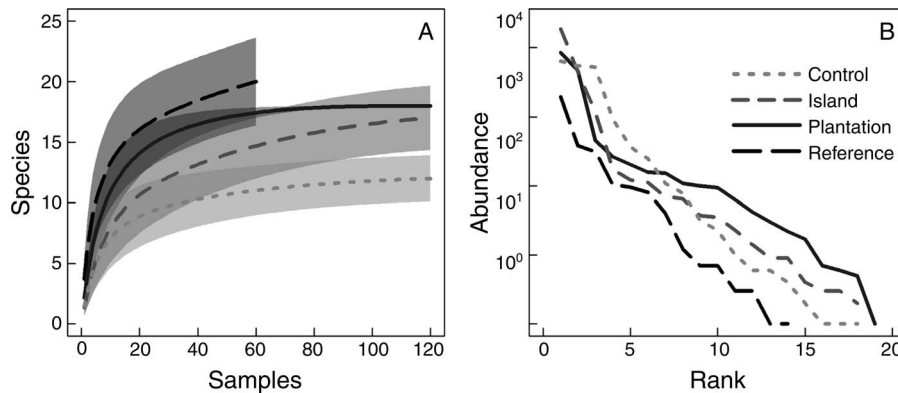
Fig. 1. (A) Species accumulation and (B) rank abundance curves for tree seeds. Plot types are denoted by shading and line type. Lines denote means, and shading in (A) denotes 95% confidence intervals, which converged for plantations. Samples are seed traps ($N = 120$ traps for controls, islands, and plantations; $N = 60$ traps for reference forests).

97% of seeds, and 94% of these came from six families: Solanaceae (23%), Melastomataceae (23%), Malvaceae (19%), Urticaceae (12%), Asteraceae (9%), and Piperaceae (6%). Approximately two-thirds of seeds had an animal-dispersal syndrome (69%), and one-third had a wind-dispersal syndrome (30%). The vast majority (97%) was ≤5 mm long (Fig. A3).

Restoration treatment effects

Seed community structure and composition varied among restoration treatments and reference forests (Fig. 1). Overall species richness, tree species richness, and tree diversity were greatest in plantations and reference

forests and lowest in controls (all $P < 0.03$, Table 1); islands were intermediate to controls and plantations but lower than reference forests in each case. Variance in community similarity to reference forests was primarily driven by the contrast between restoration plots and reference forests, although plantations were not significantly different from reference forests using an abundance-based index (Table 1).

Restoration treatment effects on seed abundance varied by seed size, growth form, and dispersal type (Fig. 2). Total seed abundance was equivalent among restoration treatments and reference forests (1017.3 ± 200.7 seeds·m^{-2}·yr^{-1}), as were abundances of tree (585.1
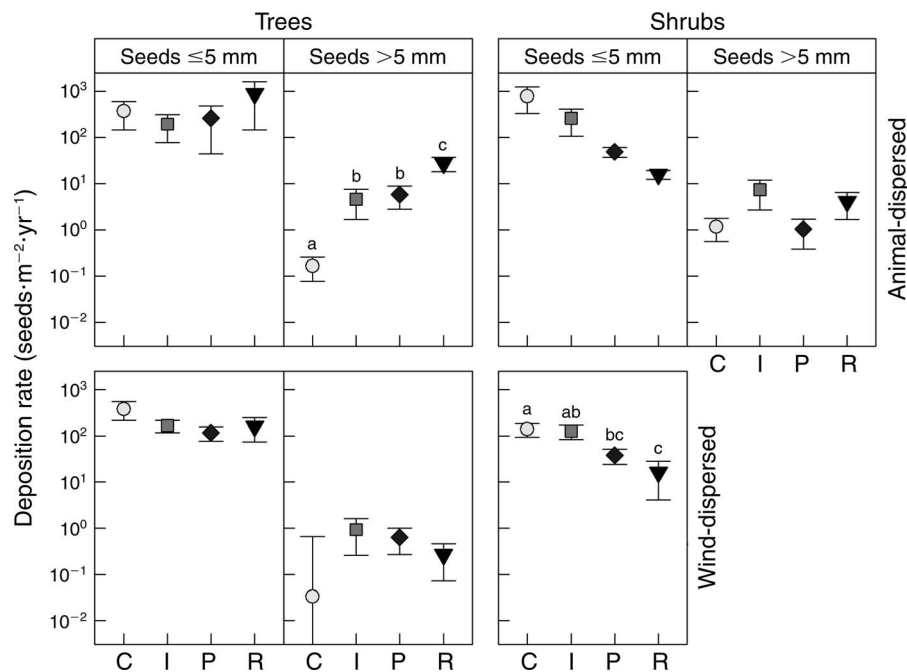

Fig. 2. Tree and shrub seed deposition rates by seed length (mm) and dispersal syndrome. Treatments are C, control; I, island; P, plantation; and R, reference forest. Means and standard errors are shown. Different lowercase letters denote significant differences from post hoc pairwise comparisons (Tukey's HSD, $\alpha = 0.05$).
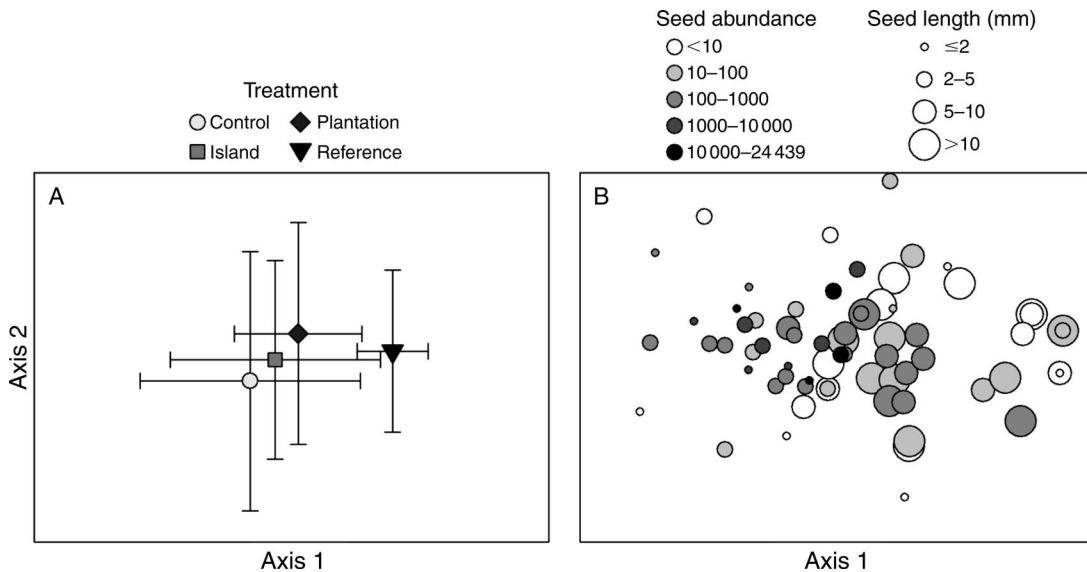
Fig. 3. First two axes of a three-dimensional nonmetric multidimensional scaling fit based on Chao-Jaccard distances (stress = 0.19). (A) Restoration plots and reference forests. Means and 95% confidence intervals shown. Plot type is denoted by shading and shape. (B) Seed species depicted by length (mm) and abundance (individuals recorded). Point size denotes seed length. Shading denotes abundance. Figures showing individual experimental plots and species names can be found in Appendix A.

± 142.0) and vine seeds (14.8 ± 3.0; Table A2). In contrast, large, animal-dispersed tree seeds were more abundant in island (4.6 ± 2.9) and plantation (5.8 ± 3.0) treatments than controls (0.2 ± 0.1), although well below the number falling in reference forests (27.7 ± 9.7; $F_{3,22}$ = 19.1, P = <0.001). Shrub seeds were most abundant in controls (924.6 ± 497.8) and least abundant in reference forests (36.3 ± 11.7; Table A2). We recorded lower numbers of liana and epiphyte seeds in general and nearly all were in reference forests (Table A2). Seeds of planted tree species comprised <1% of seed rain. Planted tree seeds (92% *Terminalia amazonia*) were more abundant in plantations (17.1 ± 10.5) than in controls, islands, and reference forests (9.9 ± 4.5; $F_{3,22}$ = 5.4, P = 0.006).

NMDS analysis showed that seed rain in reference forests was compositionally distinct from restoration plots (Fig. 3). A three-dimensional non-metric scaling solution was the most parsimonious fit using Chao-Jaccard distances (Fig. A4). Reference forest plots grouped separately from restoration plots on axis 1, which was characterized by a gradient from small, common seeds to large, rare seeds. Differences among treatments were supported by PERMANOVA (R^2 = 0.29, P = 0.009). Nonmetric scaling based on Sørensen distances was similar (stress = 0.17, R^2 = 17.7, P = 0.002; Fig. A5). Seven species were found only in reference forests, including large-seeded trees in the Lauraceae and Sapindaceae, and an epiphyte in the genus *Struthanthus* (Loranthaceae). Eighteen species were unique to restoration plots, including a shrub, *Piper friedrichsthalii* (Piperaceae), an ornamental tree, *Acnistus arborescens* (Solanaceae), and a planted tree species (*I. edulis*).

Landscape forest cover effects

We found sparse support for landscape forest cover effects on seed rain composition or abundance (Table A4). Several community attributes increased with greater landscape forest cover at 100- or 500-m scales including seed abundance for lianas, small wind-dispersed trees, and large animal-dispersed shrubs (ΔAIC_c < 2); however, these patterns were each driven by one or two outliers, and null models outperformed models that included landscape forest cover for all variables except liana abundance. Null models likewise outperformed landscape forest cover models for richness, diversity, evenness, and compositional similarity to reference forest.

DISCUSSION

We observed abundant seed rain in actively restored and naturally regenerating tropical farmlands within the first decade of recovery. Seed rain was dominated by a few pioneer trees and shrubs, but community differences between restored sites and reference forests were driven by large seeds, particularly of animal-dispersed trees. Tree plantations and applied nucleation (island) treatments had more large, animal-dispersed tree seeds than naturally regenerating controls; however, the scarcity of large seeds in regenerating forests indicates that seed rain limitation did not completely abate, but shifted to a specific limitation on later successional species.

Shifting seed rain limitation

Many previous studies demonstrate that a lack of seed rain limits forest regeneration in early, post-agricultural succession (Aide and Cavelier 1994, Duncan and

Chapman 1999, Wijdeven and Kuzee 2000, Cubiña and Aide 2001). Lack of seed rain is commonly considered a primary barrier to forest recovery because seed absence precludes other potentially limiting processes, such as seed germination and seedling survival, from coming into play (Nepstad et al. 1990, Holl 2012). Whereas most studies have documented depauperate seed rain during the first few years of forest recovery, we observed abundant, ubiquitous seed rain after 6–9 years of recovery. Compared to data from our experiment after 1.5–4 years of recovery (Cole et al. 2010), naturally regenerating controls had 217% more animal-dispersed tree seeds. Likewise, the mean difference in animal-dispersed tree seed abundance between plantations and controls decreased by 130% over the same time period. These observations indicate that the complete lack of seed rain observed in previous years abated within the first decade of regeneration.

The greatest increases came from a small set of pioneer species. Many of these trees (e.g., *Cecropia* spp., *Heliocarpus* spp.) and shrubs (e.g., *Piper* spp., *Solanum* spp.), were also among the most common seed species during the first few years of recovery (Cole et al. 2010). Small seeds dispersed by birds, bats, and wind are typically the first to recolonize disturbed sites (Muñiz-Castro et al. 2012, de la Peña-Domene et al. 2014). However, some authors have questioned whether small, isolated, regenerating forests will ultimately facilitate recolonization by large-seeded, shade-tolerant species or whether succession will be arrested in an early-successional, alternative stable state (Martínez-Garza and Howe 2003, Costa et al. 2012). Indeed, even some remnant forest fragments may be undergoing retrogressive succession, or secondarization, as pioneer species displace other species (Tabarelli et al. 2008). Our observations are consistent with pioneer dominance in seed rain and seedling recruitment during the first decade of recovery (Zahawi et al. 2013), but it is too early to say whether sites will continue to change or remain in an alternative stable state (Hobbs and Suding 2009).

Whereas small-seeded, pioneer species drove abundance patterns, compositional differences between regenerating plots and reference forests stemmed from large, uncommon seeds. Greater abundances of large-seeded species in reference forests compared to restoration sites signify that dispersal limitation shifted from a complete lack of seed rain to a specific lack of large-seeded species. The largest internally dispersed tree seeds in this study were 1.5 cm long (*Pseudolmedia glabrata* (Liebm.) C.C. Berg [Moraceae]), more than one-half the length of the largest bird-dispersed seeds in the Monteverde cloud forest (Wheelwright 1985) and larger than the palm seeds that Galetti et al. (2013) found were shrinking due to defaunation in the Brazilian Atlantic Forest. Large seeds typically recruit at greater rates than small seeds (Muscarella et al. 2013, but see Brewer 2001), and their rarity may also improve per-capita

survival (Harms et al. 2000). Thus, even at low abundances, large tree seeds are likely to contribute meaningfully to seedling recruitment provided they can reach regenerating forests (Hooper et al. 2005).

Limited large, animal-dispersed, tree seed deposition could have resulted from distance, disperser, or seed availability effects. We attribute the patterns we recorded primarily to lack of large, avian dispersers in restoration sites and secondarily to the other factors. First, reference forests received large seeds, and these sites were adjacent to some restoration sites, suggesting that there were seeds available in the landscape. Large seeds also may have been sourced from remnant trees scattered throughout the agricultural matrix. Second, sites adjacent to reference forests were well within estimated the seed shadows produced by large, avian frugivores (Holbrook 2010, Kays et al. 2011), so it is unlikely that the distance between restoration sites and seed sources was always too far. A more likely explanation is that large frugivores may have selected areas outside of restoration sites with more fruit-bearing trees.

In addition to large, animal-dispersed tree seeds, liana and epiphyte seeds were also more abundant in reference forests than restoration plots. Secondary forest studies elsewhere in Latin America suggest that lianas are likely to recolonize (Schnitzer and Bongers 2011, Letcher and Chazdon 2012), however epiphyte communities may not recover for many decades (Martin et al. 2013, Woods and DeWalt 2013). Epiphytes in this study were dominated by a single species of secondary hemiepiphyte (*Monstera* sp.), i.e., one whose seeds germinate on the ground and then climb to the canopy. To demonstrate dispersal limitation for primary epiphytes (i.e., those whose seeds must germinate in the canopy), it would be better to measure seed rain in the canopy of restored forests (Sheldon and Nadkarni 2013).

Restoration treatment effects on seed rain

Treatment effects on total seed abundance were non-significant after 6–9 years due primarily to increased seed rain in natural regeneration plots. This increase was likely due to a combination of increasingly complex vegetation structure combined with increasing seed inputs from within the plots. Increasing structural complexity in our plots stemmed from newly established shrubs and isolated tree coppices consistent with a nucleation hypothesis (Yarranton and Morrison 1974) as well as encroachment from surrounding fencerows and forest fragments. While planted tree species' contributions to overall seed rain were small, many of the most abundant seed species recorded during this time period had fruiting individuals in some of the control plots. We cannot rule out the possibility that some seeds also came from pioneers that established in adjacent islands or plantations.

Whereas total seed rain abundance was equivalent in planted and unplanted plots, tree planting continued to

influence seed rain composition six to nine years after land abandonment. Compared to naturally regenerating controls, tree plantations and applied nucleation treatments had greater abundances of large, animal-dispersed tree seeds, a group that characterized seed rain in reference communities. This trend contributed to greater overall tree seed richness and diversity in plantations as compared to controls with intermediate values in the applied nucleation treatment.

Restoration effects on large, animal-dispersed, tree seed abundance are attributable to the habitat preferences of large, fruit-eating birds. The four most common tree species in this category were *Alchornea latifolia* Sw. (Euphorbiaceae), *Senna papillosa* (Britton and Rose) H.S. Irwin and Barneby (Fabaceae), *Virola* sp. (Myristicaceae), and *Viburnum costaricanum* (Oerst.) Hemsl. (Adoxaceae), all of which produce fleshy fruits consumed by birds but not necessarily by bats (Lobova et al. 2009). Cole et al. (2010) found that plantations increased tree seed dispersal by birds, but not bats. Patterns of large, animal-dispersed, tree seed abundances are also more consistent with our observations of large, fruit-eating birds (Reid et al. 2014) than bats (J. L. Reid, C. D. Mendenhall, R. A. Zahawi, and K. D. Holl, *unpublished data*) in these sites. Additional support for this interpretation comes from southern Mexico, where de la Peña-Domene et al. (2014) showed that later-successional seedling species establishing in restoration sites were predominantly dispersed by birds rather than bats. Large, bat-dispersed, tree seed species (e.g., *Calophyllum brasiliense* Cambess. [Calophyllaceae]) have been recorded as seedlings in our plots (Zahawi et al. 2013), yet we did not capture them in seed traps. This could be because large, bat-dispersed seeds were spatially clumped below feeding roosts (Melo et al. 2009) and thus difficult to detect with passive seed rain monitoring.

A purported advantage of applied nucleation is that it is a light-handed intervention compared to tree plantations (Corbin and Holl 2012), and it promotes more heterogeneous habitat conditions (Reis et al. 2010, Holl et al. 2013). Because only one-third as many trees were initially planted in applied nucleation treatments, these plots may have fewer unintended consequences as a result of species selection. For example, Celentano et al. (2011) showed that the planted tree species *Inga edulis* contributed 70% of leaf litter in tree plantations but only 47% in islands, a difference reflected in nitrogen inputs. Likewise, we found that planted tree species contributed a larger proportion of seed rain in plantations than islands, potentially conferring planted trees a reproductive advantage. This conclusion should be tempered by the fact that planted tree species comprised <1% of all seeds captured in this study.

Landscape effects on seed rain

Proximity to mature forest is thought to confer resilience to regenerating sites because mature forests act as propagule sources (Chazdon et al. 2009, Tambosi et al. 2013), but we found scarce evidence for relationships between seed rain attributes and the amount of forest within 100- or 500-m buffers. The lack of an observed relationship between seed rain and surrounding forest area may stem from the abundance of non-forest seed sources in the landscape, such as scattered trees growing along fencerows and in farms and gardens. A similar study in an intensive, homogeneous, agricultural landscape could produce a different result. Several other seed rain and seedling recruitment studies have also looked for but not found relationships with surrounding forest area or proximity (Duncan and Chapman 1999, Pejchar et al. 2008, Howe et al. 2010). Landscape effects in our experiment have been more apparent for birds, whose similarity to communities in old-growth forests increases when plantations are embedded in high tree cover landscapes (Reid et al. 2014). Like others (del Castillo and Pérez Ríos 2008), we expect that the proximity of restoration sites to mature forests should increase seed arrival for mature forest plant species in the future, but quantifying these events is difficult (Nathan 2006, Caughlin et al. 2013).

Implications for restoration and reforestation

Our seed rain observations have several implications for tropical forest restoration. First, increased seed rain in naturally regenerating plots relative to plantations and applied nucleation plots after 6–9 years of recovery suggests that low seed input ceased to limit forest regeneration on degraded farmlands within a decade. Whereas sites may persist for years in grass- or fern-dominated states (e.g., Douterlungne et al. 2010), our results suggest that lack of seed rain is unlikely to be the primary cause. Second, we found that large, animal-dispersed tree seeds were typical of reference forests and had lower abundances in all restoration treatment plots. These seeds may survive if introduced into regenerating forests, for example, through enrichment plantings (Cole et al. 2011). Third, tree plantations and applied nucleation treatments had greater abundances of large, animal-dispersed tree seeds compared to controls, demonstrating that these restoration treatments continued to enrich seed rain composition after 6–9 years of regeneration, regardless of forest cover in the surrounding landscape. Since we recorded similar abundances of these seeds in plantations and applied nucleation plots, this study adds to a growing body of literature indicating that applied nucleation is a cost-effective strategy for restoring tropical forests.

Key questions for future research include (1) Will seed rain remain dominated by pioneers or will large, interior forest species become more prevalent? (2) If the latter, at what rate will seed enrichment occur, and will it translate to a richer seedling assemblage? (3) How far into the future will initial restoration treatment effects extend? (4) Will surrounding forest cover have an increasing influence on seed rain and seedling commu-

nity composition over time? To address these questions, it will be important to continue monitoring forest regeneration in sites with known histories and starting conditions.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-1399.1.sm

Data Availability

Data associated with this paper have been deposited in Merritt at the University of California Curation Center, California Digital Library: https://merritt.cdlib.org/m/ucsc_lib_hollzahawi