

## TOWARD PREDICTION IN THE RESTORATION OF BIODIVERSITY

**Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover****Karen D. Holl<sup>1\*</sup>, John Leighton Reid<sup>2</sup>, José Miguel Chaves-Fallas<sup>3†</sup>, Federico Oviedo-Brenes<sup>3</sup> and Rakan A. Zahawi<sup>3</sup>**<sup>1</sup>*Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA;* <sup>2</sup>*Center for Conservation and Sustainable Development, Missouri Botanical Garden, PO Box 299, St. Louis, MO 63166-0299, USA;* and<sup>3</sup>*Las Cruces Biological Station, Organization for Tropical Studies, Apdo. 73-8257, San Vito, Costa Rica***Summary**

1. Developing restoration strategies that accelerate natural successional processes and are resource-efficient is critical to facilitating tropical forest recovery across millions of hectares of deforested lands in the tropics.

2. We compared tree recruitment after a decade in three restoration treatments (natural regeneration, applied nucleation/island tree planting and plantation) and nearby reference forest in the premontane rain forest zone in southern Costa Rica. The study was replicated at 13 sites with a range of surrounding forest cover, enabling us to evaluate the relative influence of local restoration treatments and landscape forest cover on tree recruitment.

3. Density of small-seeded (<5 mm), animal-dispersed recruits was lower in natural regeneration than in applied nucleation, plantation or reference forest plots. Species richness, species density and density of medium (5–10 mm)- and large (>10 mm)-seeded, animal-dispersed recruits were greatest in reference forest, intermediate in applied nucleation and plantation and lowest in natural regeneration plots.

4. Recruit composition differed substantially between reference forest and all restoration treatments. In general, plantation recruit composition was more similar to reference forests and natural regeneration least similar; however, there was high within-treatment variation.

5. Models suggested weak support for the effect of surrounding forest cover on tropical tree recruit density and composition, as compared to restoration treatment and site conditions (e.g. elevation), in this intermediate forest cover landscape.

6. *Synthesis and applications.* Applied nucleation appears to be a cost-effective strategy as compared to plantation-style planting to accelerate tropical forest recovery regardless of the amount of forest cover immediately adjacent to the site. However, even with active restoration interventions, forest recovery is a multidecade process that proceeds at highly variable rates.

**Key-words:** animal-dispersed seeds, applied nucleation, forest recovery, island tree planting, landscape forest cover, natural regeneration, seedling recruitment, succession, tree plantation, tropical reforestation

**Introduction**

Secondary forests comprise >60% of forest area worldwide and a growing portion of tropical landscapes

(Chazdon 2014). Human interventions to direct successional trajectories of these recovering habitats provide an ideal opportunity to experimentally test the effect of initial conditions on community assembly processes (Suding, Gross & Houseman 2004; Chazdon 2008) and provide guidance on how to allocate limited resources to manage and restore forest ecosystems.

Some tropical forests recover with little intervention when the impeding disturbance (e.g. grazing, fire) is

\*Correspondence author. E-mail: kholl@ucsc.edu

†Present address: Department of Biology, Whitney R. Harris World Ecology Center, University of Missouri-St. Louis, St. Louis, MO 63121, USA

removed and succession can proceed (Aide *et al.* 1996; Guariguata *et al.* 1997; Letcher & Chazdon 2009). In areas with extensive deforestation, however, a combination of low seed dispersal, aggressive exotic vegetation, microclimatic extremes and/or soil degradation can slow or arrest forest succession (Ashton *et al.* 2001; Holl 2012). The most widespread strategy to overcome these barriers is to plant trees (Lamb 2011; Holl 2012), but expansive tree planting can create homogeneous habitat conditions (Holl *et al.* 2013) that lead to legacy effects on nutrient cycling and vegetation composition (Cusack & Montagnini 2004; Boley, Drew & Andrus 2009; Sansevero *et al.* 2011).

Less homogeneous planting strategies may overcome barriers to recovery without redirecting the successional trajectory (Zahawi & Augspurger 2006; Rey Benayas, Bullock & Newton 2008). One such approach is applied nucleation, where trees are planted in patches rather than as a contiguous plantation (Corbin & Holl 2012). This approach is based on nucleation theory (Yarranton & Morrison 1974), a natural recovery process where pioneer shrubs and trees establish patchily and facilitate recruitment via enhanced seed dispersal and improved establishment conditions; patches spread outward clonally and/or by facilitating the colonization of later-successional species. Applied nucleation has shown a great deal of promise as a restoration approach (Rey Benayas, Bullock & Newton 2008; Corbin & Holl 2012), given that it simulates a natural recovery pattern and reduces tree planting costs, but it remains unclear how this strategy influences successional trajectories. Whereas several studies show that applied nucleation catalyses seed dispersal and seedling recruitment over short time periods (e.g. Robinson & Handel 2000; Zahawi & Augspurger 2006; Zahawi *et al.* 2013), its efficacy diminished over time in two longer-term, temperate forest studies. Both Corbin *et al.* (2016) and Rey Benayas *et al.* (2015) found less spread of planted tree nuclei than anticipated due to strong limitation of animal-dispersed seeds and, in the latter study, intensive seed predation and seedling herbivory. However, it is not known whether restored plant communities will be more or less similar to reference forests under applied nucleation relative to alternative restoration strategies.

Successional trajectories are affected not only by restoration strategy and local site conditions, but also by proximity to propagule sources, such as old-growth forests. Many past studies demonstrate the importance of proximity or functional connectivity to remnant forest for increased seed rain and tree recruitment in tropical forest succession (Zanne & Chapman 2001; Kauano *et al.* 2014; Crouzeilles & Curran 2016; de la Peña-Domene, Minor & Howe 2016), but some show no such trend (e.g. Aide *et al.* 1996; Zahawi *et al.* 2013; Rocha, Vieira & Simon 2016). At the same time, local factors, such as canopy cover and understorey vegetation, strongly affect seed dispersal and seedling establishment and survival (Hooper, Legendre & Condit 2005; Omeja *et al.* 2011; Holl 2012). What rarely has been tested is how the relative influence

of local site interventions vs. surrounding landscape changes over time during forest recovery, as most studies have been conducted at one or a few sites and for a short time period (reviewed in Chazdon 2008).

We use a decade-long tropical forest restoration experiment to evaluate the relative importance of local restoration treatment and surrounding forest cover on tree recruit abundance, diversity and community composition in restored sites relative to nearby reference forests. The study specifically compares three restoration treatments (natural regeneration, applied nucleation and tree plantations) replicated at 13 sites with a range of surrounding forest cover. Based on tree recruitment data from the first few years (Zahawi *et al.* 2013), seed rain data collected 3 years prior to this study (Reid, Holl & Zahawi 2015) and extensive past literature on tropical forest recovery, we predicted that tree recruit communities in applied nucleation and plantation treatments would be more similar to reference forest than in natural regeneration plots, largely due to greater recruitment of species with large, animal-dispersed seeds. We also hypothesized that recruitment composition would be more similar to reference forest in sites with higher surrounding forest cover, due to a more similar suite of seed dispersers (Reid *et al.* 2014). This is the first study comparing multiple tropical forest restoration strategies replicated at several sites from the time of inception through the first decade. We compare the relative effects of different restoration approaches on forest recovery and their interactions with landscape processes, which is critical to most efficiently allocate the limited funds available to restore the immense areas of degraded tropical lands (Chazdon *et al.* 2009; Aide *et al.* 2013).

## Materials and methods

### STUDY REGION

This study was conducted at thirteen ~1-ha sites spread across an ~100-km<sup>2</sup> 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 (see Fig. S1 and Table S1, Supporting Information). Sites are in the tropical premontane rain forest zone (Holdridge *et al.* 1971), range in elevation from 1100 to 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 a minimum of 700 m, and the surrounding landscape is a mosaic of agricultural fields and pasture interspersed with remnant forest patches. Tree cover surrounding the plots ranged from 0 to 85% and 11 to 89% at 100- and 500-m buffers, respectively (see Fig. S1 and Table S1).

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) Kuhl., *Pennisetum purpureum* Schumacher and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R.D. Webster, or hosted a mixture of

grasses, forbs and the fern *Pteridium arachnoideum* (Kaulf.) Maxon. Most sites are steeply sloped (15–35°). Soils are volcanic in origin, mildly acidic (pH = 5.3 ± 0.04; mean ± SE), low in P (Mehlich III: 3.9 ± 0.4 mg kg<sup>-1</sup>) and high in organic matter (16.7 ± 0.8%) (Holl & Zahawi 2014).

#### EXPERIMENTAL DESIGN

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, applied nucleation or plantation (see Fig. S2). Plantations were uniformly planted with tree seedlings, whereas the applied nucleation treatment was planted with six tree islands of three sizes: two each of 4 × 4, 8 × 8 and 12 × 12 m. Tree island sizes were randomly arranged within each row and were separated by ≥8 m. Planting density was kept constant (~2.8 m); 313 trees were planted in plantation, 86 in applied nucleation and none in natural regeneration plots (Holl *et al.* 2011). All plots (including natural regeneration) were cleared to ground level by machete at ~3-month intervals for the first 2.5 years to allow planted tree seedlings to grow above existing vegetation.

We planted seedlings (20–30 cm tall) of four tree species that have high survival, rapid growth and extensive canopy development (Nichols & Carpenter 2006; Calvo-Alvarado, Arias & Richter 2007). 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.

Five sites were established in 2004, five in 2005 and three in 2006. Because of high variability in tree growth rates, mean tree height and cover development overlapped substantially among planting years (see Table S1; Holl *et al.* 2011; Holl & Zahawi 2014), so no temporal planting consideration was included in analyses. At the time of this study (2015), most natural regeneration plots had sparse canopy cover and dense grass cover (Table S2 and Fig. S3), but a couple had more extensive cover of trees and shrubs. In applied nucleation plots, canopy cover (mean 45.5% canopy >5 m tall based on overflights in 2013) was much greater than the initial planted area (18%), but varied depending on the amount of expansion of the planted tree nuclei. Most plantations and all reference forests had dense canopy cover with substantial bare ground.

#### DATA COLLECTION

In June–July 2015 (9–11 years after plot establishment), we sampled tree seedlings (≥0.2 and <1 m tall) and saplings (≥1 m tall and <5 cm d.b.h.) in all restoration treatment and reference forest plots at the six sites with a sufficient area of remnant forest nearby that had not been logged or used for agriculture. We focused on smaller recruit size classes, as they typically show the strongest habitat filtering, change rapidly and can foreshadow shifts in forest community composition. We identified saplings in forty 2 × 4 m quadrats in each plot (320 m<sup>2</sup> per plot) and recorded seedlings in 1 × 2 m quadrats nested within the sapling quadrats (80 m<sup>2</sup> total). Quadrats were distributed in four belt transects of 10 m each in natural regeneration, plantation and reference forest treatments with one randomly located in each of the four quadrants of the plot (see Fig. S2). In the applied nucleation treatment, quadrats were distributed along six belt transects

aligned from the interior to outside the initial planted areas of the three nuclei sizes, with six adjacent quadrats in small and medium nuclei and seven in large nuclei. The 5-m edge at the perimeter of the plot was not sampled.

#### DATA ANALYSIS

We initially conducted analyses on seedlings and saplings separately, but results were similar so we present analyses of all recruits combined, hereafter referred to as 'recruits'. All analyses were carried out using R v. 3.2.4. ([www.r-project.org](http://www.r-project.org)). Means ± 1 standard error are reported, unless otherwise specified.

We tested the relative influences of restoration treatments and landscape forest cover on tree recruitment using linear mixed-effects regression (lme4; [cran.r-project.org/web/packages/lme4](http://cran.r-project.org/web/packages/lme4)). Response variables included recruit density (individuals per m<sup>2</sup>), species density (number of species per plot) and compositional similarity to recruitment in the six reference forests. Recruit density was analysed separately for wind- and animal-dispersed species in three seed size classes (≤5, 5–10, ≥10 mm). We conducted recruit density analyses with and without recruits of planted tree species. As recommended by Anderson *et al.* (2011), compositional similarity was quantified using three indices with different characteristics: Morisita–Horn (abundance-based), Chao (abundance-based and corrects for unseen species in diverse systems) and Sørensen (presence/absence). Results of all three were similar; we present the Morisita–Horn results in the main text since it is the most robust to uneven sampling (Chao *et al.* 2006) and the others in supplementary information. We removed one natural regeneration plot from community similarity comparisons, as it only had one recruit. Recruit and species densities were log-transformed, and compositional similarities were arcsine-square-root-transformed to meet model assumptions.

Lacking *a priori* knowledge about the scale of landscape effects, we compared models using forest cover calculated within 13 concentric buffers around each plot (50–650 m; Fahrig 2013). We calculated forest cover using a hand-digitized map (2-m resolution) based on aerial photography from 2003 and 2005 (Mendenhall *et al.* 2011), the time period when our experiment was initiated. Forest cover included old-growth and regrowth forest fragments, and trees growing in fence rows, gardens and tree plantations. For each response variable, we chose the forest cover buffer that minimized model deviance and then used AIC<sub>c</sub> scores to compare a fully specified model to all nested models. In cases where AIC<sub>c</sub> support was nearly equivalent (ΔAIC<sub>c</sub> < 2), we selected the simplest model.

All models used Gaussian error distribution and included a random, intercept-varying site factor to account for our randomized block design. Model fit was assessed by plotting residuals, and by calculating the proportion null model deviance explained by the fitted model. Pairwise tests for treatment effects were performed using simultaneous linear hypothesis testing (function `glht` in R package `multcomp`), which uses a single-step method to account for familywise error.

To visualize compositional differences between restoration plots and reference forests, we used non-metric multidimensional scaling (NMDS) with Morisita–Horn, Chao and Sørensen distances to account for patterns based on abundance and presence/absence (vegan v. 2.3-4; [cran.r-project.org/web/packages/vegan](http://cran.r-project.org/web/packages/vegan)). We evaluated differences between the centroid and variances of restoration treatments and reference forests using permutational

analysis of variance (PERMANOVA) and dispersion (PERMDISP) tests (Anderson & Walsh 2013). We tested for correlations between geographic distances and dissimilarities in recruit composition among sites with a Mantel test (vegan v. 2.3-4).

## Results

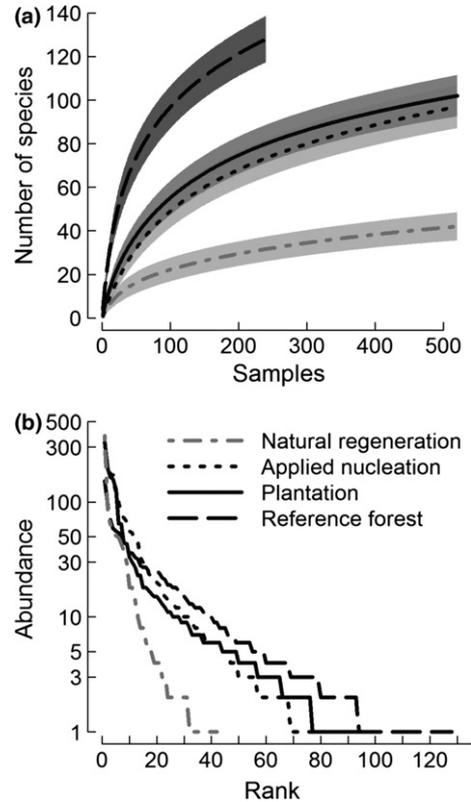
### OVERVIEW OF TREE RECRUITMENT

We recorded 6215 recruits belonging to 181 species and 56 families, 43% of which were seedlings and 57% were saplings. In the restored sites, 0.8% of saplings and 8.9% of seedlings were from planted species, primarily *E. poeppigiana* recruits (75%) that largely die within the first year after establishment (K. D. Holl & R. A. Zahawi, unpublished data), and 24% were of *I. edulis*; only two recruits of *T. amazonia* and none of *V. guatemalensis* were recorded. Across all restored plots, 87.9% of recruits had seed adapted for animal dispersal, 10.2% for wind dispersal and 1.8% for explosive dispersal (all *Croton tenuicaudatus*). In contrast, 96.9% of recruits in reference forests were animal-dispersed, 2.0% gravity-dispersed, 0.4% wind-dispersed and 0.4% explosively dispersed.

### RESTORATION TREATMENT

We recorded 42 species in natural regeneration plots, 97 species in applied nucleation and 102 in plantations across all 13 restoration sites, as well as 129 species in the six reference forest plots (Fig. 1a; see Table S3). Average species density per plot was greatest in reference forests ( $51.5 \pm 7.6$ ), intermediate in applied nucleation ( $20.8 \pm 2.8$ ) and plantation ( $22.3 \pm 3.2$ ) and lowest in natural regeneration ( $8.5 \pm 1.4$ ) (see Table S4). Recruits in natural regeneration plots were composed of a small set of common species, whereas some species in applied nucleation and plantation plots and many species in the reference forest were represented by a few individuals (Fig. 1b).

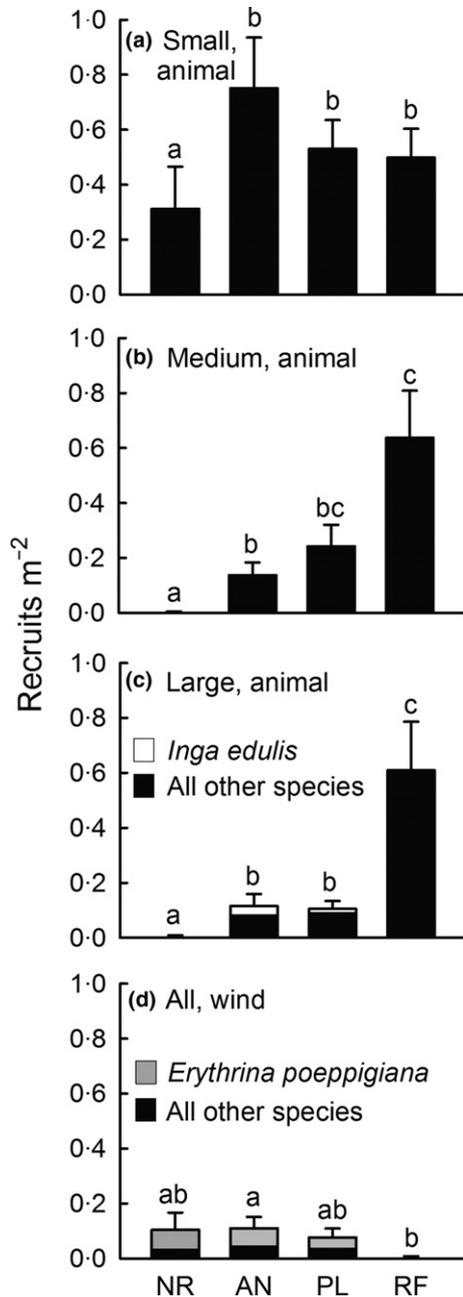
The density of small-seeded, animal-dispersed recruits was lower in natural regeneration plots than in applied nucleation, plantation or reference forest (Fig. 2a), and this difference was much stronger when we removed one natural regeneration plot with particularly high recruitment (50% of small-seeded, animal-dispersed recruits recorded in all natural regeneration plots). Density of small-seeded, animal-dispersed recruits did not differ among the other treatments, although there was a trend towards higher density in the applied nucleation treatment (Fig. 2a). Density of medium- and large-seeded animal-dispersed recruits was significantly greater in applied nucleation and plantation than in natural regeneration plots, but the values were much lower than in reference forests, particularly for large-seeded species (Fig. 2b,c); the planted species *I. edulis* comprised 30% of large-seeded, animal-dispersed recruits in applied nucleation plots and 15% in plantations. Wind-dispersed recruit densities were low in all treatments, and over half of wind-dispersed seedlings in all restoration treatments were from



**Fig. 1.** (a) Species accumulation and (b) rank abundance curves for tree recruits in four treatments. In (a), lines denote means and shading denotes 95% confidence intervals. Samples are recruit quadrats ( $n = 520$  for natural regeneration, applied nucleation and plantation treatments;  $n = 240$  for reference forests).

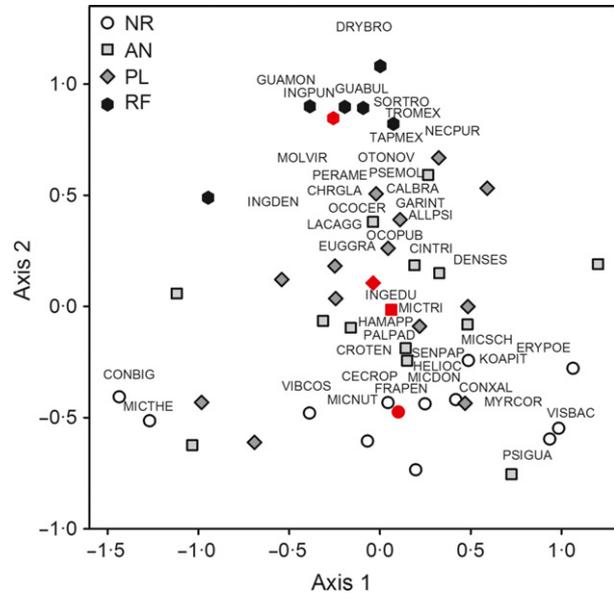
*E. poeppigiana*, a planted species (Fig. 2d). Total density of recruits was lowest in natural regeneration ( $0.4 \pm 0.1 \text{ m}^{-2}$ ), intermediate in applied nucleation ( $1.2 \pm 0.2$ ) and plantations ( $1.0 \pm 0.2$ ) and highest in reference forest ( $1.8 \pm 0.3$ ), although differences between reference forests, plantations and applied nucleation were not significant given high within-treatment variation (see Table S4).

Non-metric multidimensional scaling for three similarity indices (Morisita–Horn, Chao and Sørensen) resulted in similar two-dimensional solutions (Fig. 3; see Fig. S4). The two higher-elevation sites (AC and SP; see Table S1) were separated from the rest of the sites on axis 1 due to the presence of a few higher-elevation species rarely found at the rest of the sites (e.g. *Conostegia bigibbosa*, *Miconia theizans*). Axis 2 was driven by a gradient from wide-spread, small-seeded species in the restored plots (e.g. various Melastomataceae, *Psidium guajava*, *Viburnum costaricanum*) to large, animal-dispersed species (e.g. *Drypetes brownii*, *Guarea* spp., *Inga punctata*) in the reference plots. The most common species in restoration plots, and natural regeneration plots in particular (40% of all recruits), was *Conostegia xalapensis*. A few >5-mm animal-dispersed species (e.g. *Allophylus psilospermus*, *Ocotea puberula*) were well represented in applied nucleation and plantation plots, as well as reference forest, and hence were located more centrally in the NMDS.



**Fig. 2.** Density of (a) small ( $\leq 5$  mm), (b) medium (5–10 mm) and (c) large ( $\geq 10$  mm) animal-dispersed tree recruits and (d) all wind-dispersed recruits in natural regeneration (NR), applied nucleation (AN), plantation (PL) and reference forest (RF). Values are means  $\pm$  1 SE ( $n = 13$  plots for NR, AN and PL;  $n = 6$  for RF). Letters indicate significant ( $\alpha = 0.05$ ) differences in recruit density for specified guild using *post hoc* contrasts.

Permutational analysis of variance supported a distinctive composition of seedlings and saplings in reference forest compared to restoration plots (see Table S5). In general, recruit composition similarity to reference forest was higher in plantation and applied nucleation than in natural regeneration plots; there was high within-treatment variability, however, so of the restoration treatments, only plantation and natural regeneration



**Fig. 3.** Morisita–Horn non-metric multidimensional scaling scores for natural regeneration (NR), applied nucleation (AN) plantation (PL) and reference forest (RF) plots (symbols) and species (first three letters of generic and specific epithets) for two-dimensional solution. Permutational analysis of variance supported a distinctive composition of recruits in reference forest compared to all restoration treatments (see Table S5). Centroids for each treatment are indicated with red symbols (electronic version)/grey symbols (print version). Species with  $\geq 30$  individuals are shown. For full species names, see Table S3. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

composition differed significantly for two of the three similarity indices (see Table S5). The four treatments showed similar levels of multivariate dispersion (PERMDISP) among sites (see Table S5). Geographic distances among sites were not correlated with any of the three dissimilarity indices (Mantel test,  $R < 0.10$ ,  $P > 0.35$  in all cases).

#### LANDSCAPE ANALYSES

We found weak support for landscape forest cover effects on tree recruitment. For species density and recruit density of all three seed sizes of animal-dispersed species, the model with only restoration treatment had more support ( $\Delta AIC_c > 2$ ) than models with landscape forest cover (see Table S6a–d). The null model was the most parsimonious for wind-dispersed species (see Table S6e). For the three measures of similarity to reference forest, models including forest cover at 50 or 200 m and restoration treatment had equal support to models with treatment only, and the forest cover effect was generally driven by one or two sites (see Table S6f–h).

## Discussion

#### EFFICACY OF RESTORATION STRATEGIES

Tree recruit composition varied considerably across restoration treatments after a decade of recovery.

Community composition in the plantation treatment was more similar to reference forest than in the natural regeneration treatment with intermediate values in applied nucleation plots. Applied nucleation was as effective as plantations in enhancing species richness, species density and density of animal-dispersed tree recruits, despite the much smaller number of trees planted. Whereas active tree planting enhanced animal-dispersed seedling recruitment, consistent with numerous studies (e.g. de la Peña-Domene, Martínez-Garza & Howe 2013; Kauano *et al.* 2014; Shoo *et al.* 2016), tree recruit community composition in all restoration treatments was distinct from reference forest a decade into the recovery process. This result is not surprising given that recent meta-analyses indicate that full recovery of a range of measures in tropical forests requires several decades to a century (Jones & Schmitz 2009; Curran, Hellweg & Beck 2014; Crouzeilles *et al.* 2016).

Differences in recruit composition among treatments were driven by contrasting patterns in densities across the three seed size classes of animal-dispersed recruits. Small-seeded recruit density was significantly lower in natural regeneration plots, but did not differ among applied nucleation, plantations and reference forests. This finding contrasts with seed rain data, which showed that small, animal-dispersed tree seeds arrived at similar densities across all treatments (Reid, Holl & Zahawi 2015). The seed rain data suggest that these common, primarily pioneer, species are not strongly dispersal-limited after the first few years of succession, as many are present as isolated trees or along fence rows in this landscape and are dispersed by common birds and bats (Lindell, Reid & Cole 2013). Instead, the lower density of small-seeded recruits in natural regeneration plots suggests recruitment limitation, which is consistent with extensive literature showing that small-seeded species are often light-demanding (Dalling, Hubbell & Silvera 1998; Pearson *et al.* 2002) and have lower germination and survival rates in areas with dense grass and other ruderal vegetation (Holl 1999; Hooper, Legendre & Condit 2005).

Both plantation and applied nucleation treatments enhanced abundance and richness of medium- and large-seeded recruits, which is consistent with seed rain patterns (Reid, Holl & Zahawi 2015). There was a trend towards greater density of medium-seeded recruits in plantation than in applied nucleation plots; this pattern was likely driven by differential recruitment limitation, resulting from lower competition with grass and herbaceous species in plantations, as well as possibly more tolerance to dense shade (Dalling, Hubbell & Silvera 1998; Pearson *et al.* 2002). Nonetheless, recruit density of medium- and particularly large-seeded species was much lower in restored plots than in reference forest. Many past studies highlight the paucity of recruitment in restored sites of the diverse suite of larger-seeded, typically later-successional, species that dominate old-growth forest (e.g. de la Peña-Domene, Martínez-Garza & Howe 2013; Shoo *et al.* 2016).

Planted trees can influence ecosystem trajectories by altering nutrient cycling, which in turn affects the survival and growth of recruiting species (Lawrence 2003; Nichols & Carpenter 2006; Siddique *et al.* 2008) and can result in planted trees self-recruiting (Sansevero *et al.* 2011). Accordingly, we had anticipated a stronger recruitment legacy effect in plantations compared to the other restoration treatments, which was not the case. Recruit density of planted species was similar in all restoration treatments, likely due to the fact that the commonly recruiting planted species (*E. poeppigiana* and *I. edulis*) are widespread in the agricultural landscape, providing ample seed sources near all our sites. We have recorded higher litter-fall N inputs, but lower soil pH and K, in plantation plots compared to other restoration treatments (Celentano *et al.* 2011; Holl *et al.* 2013), which may affect tree recruit survival and growth; it is impossible, however, to tease out nutrient effects without manipulative experiments isolating different factors.

#### SURROUNDING FOREST COVER

We anticipated that recruit density, particularly of medium- and large-seeded species, and similarity of recruit composition to reference forest would be positively correlated with higher surrounding forest cover, as most studies show that tree recruitment in secondary tropical forests is strongly dispersal-limited, and hence, the rate of forest regeneration is positively correlated with the amount of surrounding forest cover (e.g. Crk *et al.* 2009; de Souza Leite *et al.* 2013; Kauano *et al.* 2014; Crouzeilles & Curran 2016). However, the lack of a strong forest cover effect is consistent with seed rain patterns in these sites (Reid, Holl & Zahawi 2015) and some other studies of tropical forest recovery (e.g. Aide *et al.* 1996; Letcher & Chazdon 2009; Rocha, Vieira & Simon 2016).

There are a few plausible explanations for the weak surrounding forest cover effect we observed at the 50–650 m range. First, our study landscape features numerous isolated trees, live fences and riparian corridors that facilitate movement of dispersers between forest remnants that are sources of tree seeds (Mendenhall *et al.* 2011; Sekercioglu *et al.* 2015; Zahawi, Duran & Kormann 2015). A second possible explanation is that we, like many field and remote sensing studies, evaluated the effect of overall forest cover, rather than presence of individual species around each plot. We would be more likely to detect a landscape effect if we mapped individual tree species (de la Peña-Domene, Minor & Howe 2016), but this is impractical at the community level given the large scale of the study. Thirdly, we quantified the abundance and composition of small tree recruits, which, as discussed previously, may be more strongly establishment-limited by site conditions than by sources of seeds in the surrounding landscape. Fourthly, a decade may not be a sufficient time interval to observe a surrounding forest cover effect, as many remote sensing studies look at forest transitions

over multiple decades. We anticipate a stronger forest cover effect over time, as the density of medium- and large-seeded recruits increases.

Finally, it may be a question of scale. Whereas we did not detect forest cover effects at radii of 50–650 m around individual sites, our results are consistent with work in fragmented forests in Brazil suggesting that active restoration efforts should be most effective in facilitating forest recovery in landscapes (hundreds to thousands of hectares) with intermediate (~30%) levels of forest cover (Tambosi *et al.* 2014). Forest cover across our entire study area is 28% (Zahawi, Duran & Kormann 2015) consistent with this prediction. Likewise, studies in others regions support the prediction that natural regeneration occurs more rapidly in landscapes with higher forest cover (Letcher & Chazdon 2009; Crouzeilles & Curran 2016; Rocha, Vieira & Simon 2016) than in large areas nearly devoid of trees (Blackham, Webb & Corlett 2014).

#### VARIATION IN RECOVERY ACROSS SITES

Our results underscore the importance of replicating restoration studies and collecting long-term data at multiple sites from the outset of succession to capture the full range of recovery outcomes and enable robust ecological conclusions and management recommendations. We observed high variability in recruitment rates within the same treatment at different sites. This variability is consistent with previous studies highlighting the stochastic nature of tropical forest recovery (Norden *et al.* 2015). Many studies on tropical forest community assembly have fewer than five replicates (e.g. Holl 1999; Zahawi & Augspurger 2006; Dent, DeWalt & Denslow 2013), yet results from one or two sites can be strongly affected by differences in prior land-use (Holl & Zahawi 2014) or site conditions (e.g. elevation, soil type). Moreover, many studies rely on chronosequences, which have limited utility in predicting successional trajectories within individual sites (Chazdon *et al.* 2007; Feldpausch *et al.* 2007). Chronosequence studies often equate a certain degree of canopy cover with site age, thereby biasing towards sites where recovery is more rapid. Moreover, in our experience, sites where tree recruitment is limited, and hence appear as failures, are more likely to be recleared (Zahawi, Reid & Holl 2014), which further favours the selection of 'successful' recovery sites for inclusion in chronosequence studies.

#### MANAGEMENT IMPLICATIONS

Our results suggest that applied nucleation is a promising strategy for facilitating forest recovery, particularly in former agricultural lands in the tropics, where planted trees enhance dispersal of many animal-dispersed species and reduce competition with pasture grasses. In our case, we planted 27% of the trees in applied nucleation plots as in plantations, which resulted in a corresponding reduction in planting and maintenance costs over the first few years.

Although there are slightly more medium-seeded, animal-dispersed tree species recruiting in plantation plots, the overall effect in enhancing recruitment was similar using applied nucleation and the more costly plantation restoration approach.

Local site conditions and restoration strategy had a much stronger effect on recovery than did surrounding forest cover. This is promising, as it suggests that in landscapes with sources of seed dispersing fauna and vegetative propagules, active restoration efforts can help facilitate the establishment of a diversity of species regardless of amount of forest cover immediately surrounding a site (Tambosi *et al.* 2014).

Finally, our results demonstrate the slow and highly unpredictable nature of tropical forest recovery in former agricultural lands. Although tree planting served to accelerate recovery, many large-seeded species have yet to colonize. More will likely colonize over time, but including large-seeded tree species in the mix of trees planted at the outset or later as part of enrichment planting would facilitate their establishment (Martínez-Garza & Howe 2003). Given the slow recovery time for a full complement of species, these results reiterate the importance of protecting old-growth forest to conserve a region's full complement of biodiversity.

#### Acknowledgements

We thank Y. Ilama, A. Kulikowski, J. A. Rosales, H. Sandi, J. Sylvester and many field assistants for dedicated field research and data entry help; C. Mendenhall for sharing the GIS layers for landscape analyses; staff at Las Cruces Biological Station for their support; and J.M. Rey Benayas and an anonymous reviewer for helpful comments on the manuscript. Financial support for this project was provided by NSF (DEB 05-15577; DEB 09-18112; DEB 14-56520) to K.D.H. and R.A.Z. J.M.C.F. was supported by the Whitney R. Harris World Ecology Center.

#### Data accessibility

The data are available at <http://n2t.net/ark:/13030/m5dk03kt>.

#### References

- Aide, T.M., Zimmerman, J.D., Rosario, M. & Marcano, H. (1996) Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica*, **28**, 537–548.
- Aide, T.M., Clark, M.L., Grau, H.R., López-Carr, D., Levy, M.A., Redo, D. *et al.* (2013) Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica*, **45**, 262–271.
- Anderson, M.J. & Walsh, D.C.I. (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecological Monographs*, **83**, 557–574.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Free-stone, A.L. *et al.* (2011) Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.
- Ashton, M.S., Gunatilleke, C.V.S., Singhakumara, B.M.P. & Gunatilleke, I. (2001) Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *Forest Ecology and Management*, **154**, 409–430.
- Blackham, G.V., Webb, E.L. & Corlett, R.T. (2014) Natural regeneration in a degraded tropical peatland, Central Kalimantan, Indonesia: implications for forest restoration. *Forest Ecology and Management*, **324**, 8–15.
- Boley, J.D., Drew, A.P. & Andrus, R.E. (2009) Effects of active pasture, teak (*Tectona grandis*) and mixed native plantations on soil chemistry in Costa Rica. *Forest Ecology and Management*, **257**, 2254–2261.

- Calvo-Alvarado, J.C., Arias, D. & Richter, D.D. (2007) Early growth performance of native and introduced fast growing tree species in wet to sub-humid climates of the southern region of Costa Rica. *Forest Ecology and Management*, **242**, 227–235.
- Celentano, D., Zahawi, R.A., Finegan, B., Ostertag, R., Cole, R.J. & Holl, K.D. (2011) Litterfall dynamics under different tropical forest restoration strategies. *Biotropica*, **43**, 279–287.
- Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.J. (2006) Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, **62**, 361–371.
- Chazdon, R. (2008) Chance and determinism in tropical forest succession. *Tropical Forest Community Ecology* (eds W.P. Carson & S.A. Schnitzer), pp. 384–408. Wiley-Blackwell, Oxford, UK.
- Chazdon, R.L. (2014) *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. University of Chicago Press, Chicago, IL, USA.
- Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F. & Finegan, B. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 273–289.
- Chazdon, R., Harvey, C.A., Komar, O., Van Breugel, M., Ferguson, B.G., Griffith, D.M. *et al.* (2009) Beyond reserves: a research agenda for conserving biodiversity in tropical cultural landscapes. *Biotropica*, **41**, 141–153.
- Corbin, J.D. & Holl, K.D. (2012) Applied nucleation as a forest restoration strategy. *Forest Ecology and Management*, **265**, 37–46.
- Corbin, J.D., Robinson, G.R., Hafkemeyer, L.M. & Handel, S.N. (2016) A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. *Ecological Applications*, **26**, 104–114.
- Crk, T., Uriarte, M., Corsi, F. & Flynn, D. (2009) Forest recovery in a tropical landscape: what is the relative importance of biophysical, socioeconomic, and landscape variables? *Landscape Ecology*, **24**, 629–642.
- Crouzeilles, R. & Curran, M. (2016) Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *Journal of Applied Ecology*, **53**, 440–448.
- Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E.V. & Rey Benayas, J.M. (2016) A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications*, **7**, 11666.
- Curran, M., Hellweg, S. & Beck, J. (2014) Is there any empirical support for biodiversity offset policy? *Ecological Applications*, **24**, 617–632.
- Cusack, D. & Montagnini, F. (2004) The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. *Forest Ecology and Management*, **188**, 1–15.
- Dalling, J.W., Hubbell, S.P. & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, **86**, 674–689.
- Dent, D.H., DeWalt, S.J. & Denslow, J.S. (2013) Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. *Journal of Vegetation Science*, **24**, 530–542.
- Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.
- Feldpausch, T.R., Prates-Clark, C.D., Fernandes, E.C.M. & Riha, S.J. (2007) Secondary forest growth deviation from chronosequence predictions in central Amazonia. *Global Change Biology*, **13**, 967–979.
- Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M. & Anderson, L. (1997) Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecology*, **132**, 107–120.
- Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. Jr (1971) *Forest Environments in Tropical Life Zones*. Pergamon Press, Oxford, UK.
- Holl, K.D. (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica*, **31**, 229–241.
- Holl, K.D. (2012) Tropical forest restoration. *Restoration Ecology* (eds J. Van Andel & J. Aronson), pp. 103–114. Blackwell Publishing, Malden, MA, USA.
- Holl, K.D. & Zahawi, R.A. (2014) Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. *Forest Ecology and Management*, **319**, 36–43.
- 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. *Restoration Ecology*, **19**, 470–479.
- 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.
- Hooper, E., Legendre, P. & Condit, R. (2005) Barriers to forest regeneration of deforested and abandoned land in Panama. *Journal of Applied Ecology*, **42**, 1165–1174.
- Jones, H.P. & Schmitz, O.J. (2009) Rapid recovery of damaged ecosystems. *PLoS One*, **4**, e5653.
- Kauano, E.E., Cardoso, F.C.G., Torezan, J.M.D. & Marques, M.C.M. (2014) Micro- and meso-scale factors affect the restoration of Atlantic forest. *Natureza & Conservação*, **11**, 145–151.
- Lamb, D. (2011) *Regreening the Bare Hills: Tropical Forest Restoration in the Asia-Pacific Region*. Springer, Dordrecht, the Netherlands.
- Lawrence, D. (2003) The response of tropical tree seedlings to nutrient supply: meta-analysis for understanding a changing tropical landscape. *Journal of Tropical Ecology*, **19**, 239–250.
- Letcher, S.G. & Chazdon, R.L. (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in north-eastern Costa Rica. *Biotropica*, **41**, 608–617.
- Lindell, C.A., Reid, J.L. & Cole, R.J. (2013) Planting design effects on avian seed dispersers in a tropical forest restoration experiment. *Restoration Ecology*, **21**, 515–522.
- Martínez-Garza, C. & Howe, H.F. (2003) Restoring tropical diversity: beating the time tax on species loss. *Journal of Applied Ecology*, **40**, 423–429.
- Mendenhall, C.D., Sekercioglu, C.H., Brenes, F.O., Ehrlich, P.R. & Daily, G.C. (2011) Predictive model for sustaining biodiversity in tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 16313–16316.
- Nichols, J.D. & Carpenter, F.L. (2006) Interplanting *Inga edulis* yields nitrogen benefits to *Terminalia amazonia*. *Forest Ecology and Management*, **233**, 344–351.
- Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., Breugel, M. *et al.* (2015) Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 8013–8018.
- Omeja, P.A., Chapman, C.A., Obua, J., Lwanga, J.S., Jacob, A.L., Wanyama, F. & Mugenyi, R. (2011) Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda. *Forest Ecology and Management*, **261**, 703–709.
- Pearson, T.R.H., Burslem, D., Mullins, C.E. & Dalling, J.W. (2002) Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology*, **83**, 2798–2807.
- de la Peña-Domene, M., Martínez-Garza, C. & Howe, H.F. (2013) Early recruitment dynamics in tropical restoration. *Ecological Applications*, **23**, 1124–1134.
- de la Peña-Domene, M., Minor, E.S. & Howe, H.F. (2016) Restored connectivity facilitates recruitment by an endemic large-seeded tree in a fragmented tropical landscape. *Ecology*, 2511–2517.
- Reid, J.L., Holl, K.D. & Zahawi, R.A. (2015) Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications*, **25**, 1072–1082.
- Reid, J.L., Mendenhall, C.D., Rosales, J.A., Zahawi, R.A. & Holl, K.D. (2014) Landscape context mediates avian habitat choice in tropical forest restoration. *PLoS One*, **9**, e90573.
- Rey Benayas, J.M., Bullock, J.M. & Newton, A.C. (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment*, **6**, 329–336.
- Rey Benayas, J.M., Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P. & Holl, K.D. (2015) Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. *New Forests*, **46**, 841–853.
- Robinson, G.R. & Handel, S.N. (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecological Applications*, **10**, 174–188.
- Rocha, G.P.E., Vieira, D.L.M. & Simon, M.F. (2016) Fast natural regeneration in abandoned pastures in southern Amazonia. *Forest Ecology and Management*, **370**, 93–101.
- Sansevero, J.B.B., Prieto, P.V., de Moraes, L.F.D. & Rodrigues, P.J.P. (2011) Natural regeneration in plantations of native trees in lowland Brazilian Atlantic forest: community structure, diversity, and dispersal syndromes. *Restoration Ecology*, **19**, 379–389.
- Sekercioglu, C.H., Loarie, S.R., Oviedo-Brenes, F., Mendenhall, C.D., Daily, G.C. & Ehrlich, P.R. (2015) Tropical countryside riparian

corridors provide critical habitat and connectivity for seed-dispersing forest birds in a fragmented landscape. *Journal of Ornithology*, **156**, S343–S353.

Shoo, L.P., Freebody, K., Kanowski, J. & Catterall, C.P. (2016) Slow recovery of tropical old-field rainforest regrowth and the value and limitations of active restoration. *Conservation Biology*, **30**, 121–132.

Siddique, I., Engel, V.L., Parrotta, J.A., Lamb, D., Nardoto, G.B., Ometto, J., Martinelli, L.A. & Schmidt, S. (2008) Dominance of legume trees alters nutrient relations in mixed species forest restoration plantings within seven years. *Biogeochemistry*, **88**, 89–101.

de Souza Leite, M., Tambosi, L.R., Romitelli, I. & Metzger, J.P. (2013) Landscape ecology perspective in restoration projects for biodiversity conservation: a review. *Natureza & Conservação*, **11**, 108–118.

Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46–53.

Tambosi, L.R., Martensen, A.C., Ribeiro, M.C. & Metzger, J.P. (2014) A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. *Restoration Ecology*, **22**, 169–177.

Yarranton, G.A. & Morrison, R.G. (1974) Spatial dynamics of a primary succession: nucleation. *Journal of Ecology*, **62**, 417–428.

Zahawi, R.A. & Augspurger, C.K. (2006) Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. *Ecological Applications*, **16**, 464–478.

Zahawi, R.A., Duran, G. & Kormann, U. (2015) Sixty-seven years of land-use change in southern Costa Rica. *PLoS One*, **10**, e0143554.

Zahawi, R.A., Reid, J.L. & Holl, K.D. (2014) Hidden costs of passive restoration. *Restoration Ecology*, **22**, 284–287.

Zahawi, R.A., Holl, K.D., Cole, R.J. & Reid, J.L. (2013) Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology*, **50**, 88–96.

Zanne, A.E. & Chapman, C.A. (2001) Expediting reforestation in tropical grasslands: distance and isolation from seed sources in plantations. *Ecological Applications*, **11**, 1610–1621.

Received 7 June 2016; accepted 7 October 2016

Handling Editor: Lars Brudvig

## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Site characteristics.

**Table S2.** Canopy and understorey vegetation cover.

**Table S3.** Species list.

**Table S4.** Recruit density and species density by treatment.

**Table S5.** Tests of homogeneity of centroids among (PERMANOVA) and dispersion within (PERMDISP) treatments.

**Table S6.** Recruit density, richness, and composition model comparisons.

**Fig. S1.** Map of study and tree cover surrounding plots.

**Fig. S2.** Experimental and sampling design.

**Fig. S3.** Photographs of restoration treatments.

**Fig. S4.** NMDS scores for Chao and Sørensen similarity indices.