

Testing applied nucleation as a strategy to facilitate tropical forest recovery

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Summary

1. Active forest restoration typically involves planting trees over large areas; this practice is costly, however, and establishing homogeneous plantations may favour the recruitment of a particular suite of species and strongly influence the successional trajectory. An alternative approach is to plant nuclei (islands) of trees to simulate the nucleation model of succession and accelerate natural recovery.

2. We evaluated natural tree recruitment over 4 years in a restoration study replicated at eight former pasture sites in the tropical premontane forest zone of southern Costa Rica. At each site, two active restoration strategies were established in 50 × 50 m plots: planting trees throughout, and planting different-sized tree islands (4 × 4, 8 × 8, 12 × 12 m) within the plot. Restoration plots were compared to similar-sized controls undergoing passive restoration. Sites were spread across *c.* 100 km² and distributed along a gradient of surrounding forest, allowing us to compare the relative importance of adjacent forest to that of within-site treatment on tree recruitment.

3. Recruitment of animal-dispersed tree species was more than twofold higher in active ($\mu = 0.45$ recruits m⁻²) as compared to passive restoration; recruitment was equivalent in plantation and island treatments, even though only 20% of the area in island plots was planted originally. The majority of recruits (>90%) represented early successional species (*n* = 54 species total).

4. Density of animal-dispersed recruits was greater in large (0.80 ± 0.66 m⁻²) than small (0.28 ± 0.36 m⁻²) islands and intermediate in medium-sized islands. Seedling recruitment (<1 m tall) was greater in the interior of islands as compared to plantations, whereas sapling recruitment was similar, suggesting that island interiors may develop greater density of woody recruits as succession proceeds.

5. Surrounding forest cover did not influence density or species richness of recruits among sites, although this factor may become more important over time.

6. *Synthesis and applications.* Applied nucleation is a promising restoration strategy that can accelerate forest recovery to a similar degree as plantation-style restoration but is more economical. Appropriate island size is on the order of *c.* 100 m². Practitioners should consider the methodology as an alternative to large-scale plantings.

Key-words: active restoration, Costa Rica, forest succession, passive restoration, seedling establishment, seedling recruitment, tree islands, tree patches, tree plantations

Introduction

There is a critical need to develop tropical forest restoration strategies that are both economically and ecologically viable, as large areas of forest have been converted to agriculture resulting in the loss of biodiversity, altered

hydrological cycling and extensive carbon emissions (Laurance & Useche 2009; Sheil & Murdiyarso 2009; van der Werf *et al.* 2009). Forest recovery is highly variable when agricultural uses cease; the rate of recovery depends on the intensity and duration of past land use, the availability of propagule sources in the surrounding landscape and the resilience of the particular forest type (Holl 2007; Chazdon 2008a).

The most common strategy to accelerate forest recovery is to plant trees that encourage animal seed dispersal,

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reduce cover of light-demanding pasture grasses, ameliorate microclimatic conditions and enhance nutrient availability (Lamb, Erskine & Parrotta 2005; Chazdon 2008b). Planting large areas of land with trees, however, can become costly (Lamb, Erskine & Parrotta 2005; Holl *et al.* 2011). Moreover, planting few selected species, which is widely practiced, may have a strong influence on nutrient cycling and the species that subsequently establish (Cusack & Montagnini 2004; Celentano *et al.* 2011).

Several authors have proposed planting trees in patches or islands, an alternative forest restoration strategy that is less homogeneous and resource intensive (Zahawi & Augspurger 2006; Rey-Benayas, Bullock & Newton 2008; Reis, Bechara & Tres 2010). This applied approach is based on nucleation theory (Yarranton & Morrison 1974), a natural recovery process where pioneer shrubs and trees establish patchily and facilitate the recruitment of other species via enhanced seed dispersal and improved establishment conditions. However, applied nucleation has received relatively little study (Robinson & Handel 2000; Zahawi & Augspurger 2006; Corbin & Holl 2012) and has not been directly compared with more common restoration practices.

An important goal in applied nucleation is to determine a minimum island size that results in enhanced seedling establishment, but is not so large that it becomes too costly to carry out on a large scale. Past research indicates that smaller islands (<25 m²) do not facilitate seed dispersal and seedling recruitment as much as larger islands (>50 m²), because they do not attract seed dispersers to the same extent nor do they reduce grass cover (Holl 2002; Zahawi & Augspurger 2006; Fink *et al.* 2009; Cole, Holl & Zahawi 2010). Additionally, microclimatic conditions may be more favourable for seedling recruitment towards the centre of larger tree islands (Zahawi & Augspurger 2006). Over time, islands are predicted to expand and coalesce into contiguous forest.

Most restoration studies have focused on local-scale barriers to forest recovery (Brudvig 2011), and the relative importance of site-specific vs. landscape scale (e.g. surrounding forest cover) factors on restoration success has rarely been evaluated experimentally (Holl, Crone & Schultz 2003). Many past correlative studies in tropical secondary forest demonstrate the importance of proximity to and quantity of surrounding forest for seed rain and seedling establishment (Thomlinson *et al.* 1996; Zanne & Chapman 2001; Ferguson *et al.* 2003; Luck & Daily 2003). Other studies show no effect of distance to forest edge on seedling recruitment early in succession, probably because pioneers dominate and are ubiquitous in forest fragments and hedgerows in the landscape (Aide *et al.* 1996; Zahawi & Augspurger 2006). Local microsite conditions, particularly canopy and understorey cover, which affect resource competition, have been shown to strongly affect seedling recruitment (Holl & Crone 2004; Hooper, Legendre & Condit 2005; Zahawi & Augspurger 2006).

We quantified natural tree recruitment annually for 4 years at eight sites with three contrasting restoration

treatments: plantation plots, applied nucleation and control plots undergoing passive recovery. Sites were distributed across a gradient of adjacent remnant forest. We addressed the following questions: (i) Does applied nucleation result in greater abundance or more diverse tree recruitment as compared to control or plantation treatments? (ii) Does island size affect the density and/or composition of tree recruits? and (iii) What is the relative importance of forest cover in the surrounding landscape vs. localized restoration strategy on tree recruitment? Based on other studies (Holl & Crone 2004; Zahawi & Augspurger 2006), we anticipated that recruitment, particularly of animal-dispersed species, would be lowest in control treatments and lower in smaller than larger islands. We predicted stronger within-site effects compared to landscape-level factors based on patterns of seed rain at our sites (Cole, Holl & Zahawi 2010). This is the first study to directly compare tree recruitment beneath plantation-style restoration and applied nucleation and highlights the role that the latter strategy may play in accelerating tropical forest recovery.

Materials and methods

STUDY REGION

This study was carried out at eight *c.* 1-ha sites spread across a *c.* 100 km² 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 (appendix C in Cole, Holl & Zahawi 2010). Sites are in the tropical premontane rain forest zone (Holdridge *et al.* 1971), range in elevation from 1060 to 1430 m a.s.l. and receive a mean annual rainfall of 3500–4000 mm with a dry season from December to March. Mean annual temperature is *c.* 21 °C. All sites are separated by a minimum of 500 m, and the surrounding landscape is a highly fragmented mosaic of mixed-use agricultural fields, pasture and forest patches.

All sites had been used for ≥ 18 years for agriculture, 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 (>80% cover) or a combination of three exotic forage grasses, *Axonopus scoparius* (Flüggé) Kuhl., *Pennisetum purpureum* Schumacher., and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R.D. Webster, or hosted a mixture of forage and nonforage grasses, forbs and the fern *Pteridium arachnoideum* (Kaulf.) Maxon (see Holl *et al.* 2011 for a detailed site use history). Most sites are steeply sloped (15–35 °C). Soils are volcanic in origin, mildly acidic (pH 5.5 ± 0.04; mean ± SE), low in P (Mehlich III: 4.5 ± 0.5 mg kg⁻¹) and high in organic matter (15.7 ± 1.0%; Holl *et al.* 2011). Soil nutrients and bulk density were similar across treatments (Celentano *et al.* 2011; Holl *et al.* 2011).

EXPERIMENTAL DESIGN

At each site, we established three 0.25-ha (50 × 50 m) plots, each separated by a *c.* 5-m buffer. Each plot received one of three randomized treatments: plantation, island or control (Fig. 1). Plantations were uniformly planted with tree seedlings, whereas the

island treatment was planted with six islands of tree seedlings (hereafter islands) of three sizes: two each of 4×4 , 8×8 and 12×12 m. Islands sizes were randomly arranged within each row and were separated by ≥ 8 m (Fig. 1). Planting density was kept constant (c. 2.8 m); 313 individuals were planted in plantations, 86 in islands and none in control plots (for a more detailed description, see Holl *et al.* 2011). Although close plot spacing may create a neighbourhood effect with active treatments and impact recovery outside of their planted areas, numerous other spatial factors (e.g. adjacent forest, riparian strips, land-use history, soil type) can also impact recovery. We controlled for the latter by grouping treatments at each site and treating site as a statistical block.

Following clearing of above-ground vegetation in each plot, we planted seedlings of four tree species that have high regional survival, rapid growth and extensive canopy development (Nichols *et al.* 2001; Calvo-Alvarado, Arias & Richter 2007). These included two natives, *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae), that produce valuable timber and facilitate seedling recruitment (Cusack & Montagnini 2004), and two naturalized softwoods, *Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. (Fabaceae). Both legumes are fast-growing N fixers, and *I. edulis* has extensive branching architecture and fruit that attracts birds (Pennington & Fernandes 1998; Nichols *et al.* 2001; Jones *et al.* 2004). They are native to South America and Panama and are used widely in intercropping systems in Costa Rica to provide shade and increase soil nutrients. Seedlings were acquired from a local nursery and were c. 20–30 cm tall when planted.

Five sites were established in 2004 and three in 2005; establishment was spread over two planting seasons due to the logistics of setting up a large-scale project. Because of high variability in tree growth rates, mean tree height and cover development overlapped substantially between planting years (Holl *et al.* 2011). All plots (including control) were cleared to ground level by machete at c. 3-month intervals for the first 2.5 years to allow planted tree seedlings to grow above existing grasses and forbs. Seedlings that died in the first 2 years of the study were replaced.

DATA COLLECTION

Vegetation sampling

Vegetation was sampled using a stratified sampling procedure with sampling area scaled to the size and distribution of cohorts to ensure adequate sample sizes for analyses. Tree seedlings (≥ 0.2 and < 1 m tall) were measured in 1×1 m quadrats ($n = 32$ Plantation/Control, $n = 60$ Islands); saplings (≥ 1 m tall and < 5 cm d.b.h.) in 2×4 m quadrats ($n = 16$ Plantation/Control, $n = 30$ Islands); and small trees (≥ 5 and < 10 cm d.b.h.) in 8×8 m quadrats ($n = 4$ Plantation/Control, $n = 8$ Islands; Fig. 1). Large trees (≥ 10 cm d.b.h.) were surveyed in the interior 40×40 m plot area (5-m edge perimeter not included in any sampling). The island treatment was sampled more intensively to quantify potential differences in recruitment between island interior and exterior, and among island sizes (Fig. 1).

We censused tree seedling recruitment annually from May to July once maintenance clearing ceased; accordingly, sampling began in 2007 for 2004 sites, and in 2008 for 2005 sites. All tree recruits were tagged, and we recorded whether they established from seeds or were resprouts. In subsequent years, we tagged new seedlings and recorded survival of prior recruits. A few planted *I. edulis* trees set seed during the study, and some seedlings established in plots; however, the vast majority of seedlings recruits were from outside sources ($> 97\%$). For half of the seedling quadrats, we estimated percentage cover of grasses, forbs and bare ground using a modified Braun–Blanquet cover-abundance scale: 0%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95% and 95–100% (Müller-Dombois & Ellenberg 1974). We recorded canopy cover over the same seedling quadrats by taking densiometer measurements in four directions and averaging values.

Island mapping

As canopy cover of tree islands grew differentially, we mapped the actual cover of each in July–August 2010. For islands where

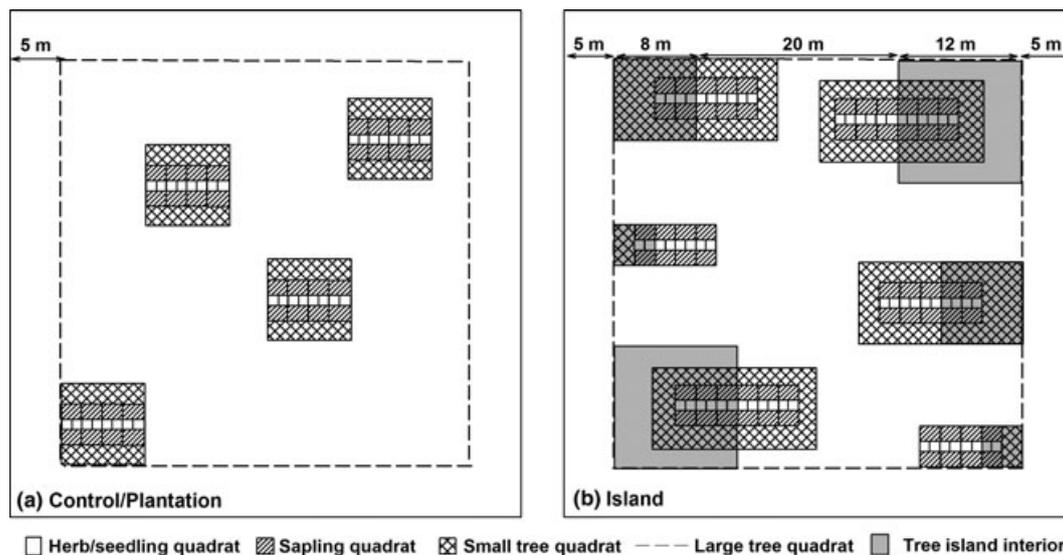


Fig. 1. Sampling layout in control/plantation (a) and island (b) 50×50 m plots. In control and plantation treatments, the location of each sampling quadrat was random with respect to each of the four quadrants of the plot.

canopy cover was contiguous, we mapped their boundary using a compass and laser range finder (± 0.1 m). In islands with >0.5 -m separation between tree canopies, we measured canopy diameter using two perpendicular axes (± 0.1 m) and calculated the canopy area as an ellipse.

Landscape survey

Forest cover within 100- and 500-m radii from the centre of each plot was hand-digitized from orthorectified 2005 aerial photographs and then ground truthed. Forest cover spans a range from $<1\%$ to 66% within a 100-m radius surrounding plots and from 9% to 89% in a 500-m radius (Cole, Holl & Zahawi 2010). There was no overlap among forest cover plots for each site.

DATA ANALYSIS

Seedlings and saplings were analysed separately whenever possible; however, in some cases, data were analysed for all recruits combined due to small numbers. Small and large trees were poorly represented and were only included in comparisons of all recruits. Resprouts (*c.* 3.2%) were excluded from all analyses given that our focus was on the effect of treatments on recruitment. We analysed animal- and wind-dispersed species separately as we anticipated they would show different distribution patterns, but for many analyses we had an insufficient sample size for wind-dispersed species. We analysed data on individuals present in the 2010 survey only as mortality was low, and of primary interest was the number of surviving recruits. For all analyses, data were $\ln(x + 1)$ transformed when necessary to meet assumptions of normality. Post hoc Tukey HSD tests were used to compare treatments when appropriate ($P < 0.05$). All analyses were performed with JMP 9.0 (SAS Institute 2010).

Restoration strategy

One-way randomized complete block ANOVAs were used to compare recruitment of animal- and wind-dispersed species, as well as canopy and herbaceous cover, among treatments (replicate) with site as the blocking factor ($n = 8$ sites). We used the same model to compare mortality of recruits among treatments (wind- and animal-dispersed species were combined for this analysis as we assumed that factors driving mortality were not dispersal specific).

Due to differences in sampling intensity and seedling density among treatments, we used EstimateS (Colwell 2006) to generate species accumulation curves to compare species richness across treatments; analyses were carried out separately for seedlings and saplings. Rarefaction curves and confidence intervals were generated after 50 random iterations of the sample order.

Island size and expansion

We used data from the island interior to compare recruitment among island sizes in two ways. First, we used ANOVA with the planted island size categories and site as a blocking factor to determine whether recruitment varied as a function of island size ($n = 6$ islands/site; 48 total). Second, we regressed density of recruits using actual island sizes measured in 2010. Species accumulation curves for seedlings and saplings were generated for each island size as described above using EstimateS (Colwell

2006). We compared recruitment within the original planted island area (interior) to its exterior using a paired *t*-test. As recruitment was much higher in the island interior, we also ran a randomized complete block ANOVA to compare interior island recruitment to that in plantation.

Local versus landscape

Surrounding forest cover at both 100- and 500-m radii was included as covariates in separate initial models comparing recruitment across treatments. In all cases, they were not significant ($P > 0.2$) and were excluded from the final model.

Results

A total of 983 individuals belonging to 54 species recruited into the eight sites over the 4 years of surveys (Appendix S1, Supporting information). The vast majority ($>90\%$) were early successional species. Mid- to late-successional species represented only 8% of recruits (18 species), and these individuals recruited in plantation or island treatments only. As of 2010, the majority of individuals were categorized as saplings (61.5%), followed by seedlings (32.9%) and small or large trees (5.7%).

Overall mortality in 2010 was *c.* 10% of all recruited seedlings or saplings (103 individuals). Of the surviving individuals (880), most were animal-dispersed (85.3%), with wind-dispersed species second (13.4%) and explosively dispersed species a distant third (1.3%). There were an additional 27 tree resprouts, primarily of agricultural species. The most frequently recruited species were *Conostegia xalapensis* (39.1%), *Heliocarpus appendiculatus* (8.9%), *Miconia trinervia* (7.9%), *Miconia schlimii* (7.7%) and *Cecropia obtusifolia* (4.2% ; Appendix S1, Supporting information).

Of the 146 tree species surveyed in forests adjacent to six of the research sites (R.A. Zahawi *et al.* unpublished data), only 21 were recorded in our study plots. Overlap with the seed rain at the same sites (28 species; Cole, Holl & Zahawi 2010) was higher, with 11 of the more abundant and generally early successional tree species represented in both surveys (*c.* 40% overlap; Appendix S1, Supporting information). Many seeds in the seed rain study, however, were only identified to family or genus level. Accordingly, the observed overlap between seed rain and recruitment at this coarse comparative scale is likely an underestimate.

Canopy cover was highest in plantations ($95.4 \pm 6.1\%$), intermediate in island plots ($73.0 \pm 17.1\%$) and lowest in controls ($36.3 \pm 31.9\%$; $F_{2,14} = 28.2$, $P < 0.0001$; Table S1, Supporting information). Correspondingly, grass cover was highest in controls ($56.6 \pm 38.7\%$), intermediate in islands ($31.5 \pm 20.2\%$) and lowest in plantations ($8.0 \pm 9.9\%$; $F_{2,14} = 13.2$, $P = 0.0006$); forb cover showed a similar but much weaker trend ($F_{2,14} = 6.1$, $P = 0.0123$). Grass cover was negatively correlated with canopy cover, whereas bare ground was positively correlated (Grass: $r = -0.69$, $P < 0.0001$; Bare Ground:

$r = 0.66$, $P < 0.0001$). Although most (>80%) seedlings recruited into quadrats with $\geq 85\%$ overstorey cover and $\leq 25\%$ grass cover, a large proportion (>80%) of quadrats had no seedlings and those spanned a range of grass and forb cover.

RESTORATION STRATEGY

The number of animal-dispersed seedlings and overall recruits was higher in island treatments than controls and did not differ from plantations ($F_{2,14} = 7.0$, $P = 0.0080$ seedlings; $F_{2,14} = 4.3$, $P = 0.0346$ overall; Fig. 2). In contrast, sapling density did not differ across treatments ($F_{2,14} = 0.9$, $P = 0.4165$). The number of wind-dispersed recruits was similar across treatments ($F_{2,14} = 0.4$, $P = 0.6784$; $\mu = 0.04$ recruits m^{-2} overall); analysis was not possible by size class due to the low number of recruits. There was no significant difference in the overall mortality of recruits among treatments ($F_{2,14} < 1$, $P > 0.4$ for seedlings, saplings or all recruits combined).

The 95% confidence interval (CI) for seedling species accumulation curves of island and plantation treatments overlapped indicating no difference in species richness, whereas the number of species in the control was lower. The 95% CI of saplings overlapped substantially for all treatments (Fig. 3a,b).

ISLAND SIZE AND EXPANSION

Large islands had greater overall density of animal-dispersed recruits than small islands ($F_{2,38} = 4.3$, $P = 0.0206$; Fig. 4). Medium islands were intermediate and not different from either. The effect of planted island size on animal-dispersed

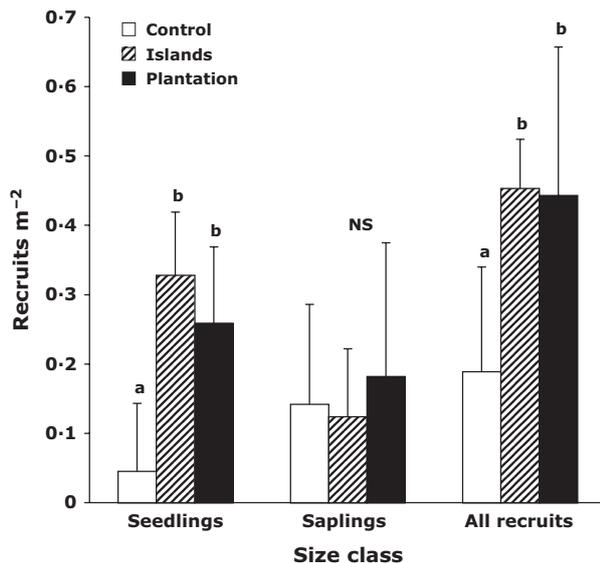


Fig. 2. Density (± 1 SD) of seedling and sapling animal-dispersed recruits, and all recruit size classes combined, grouped by restoration treatment ($n = 8$ sites). Means with the same letter are not significantly different ($P < 0.05$) using Tukey's LSD; NS, not significant.

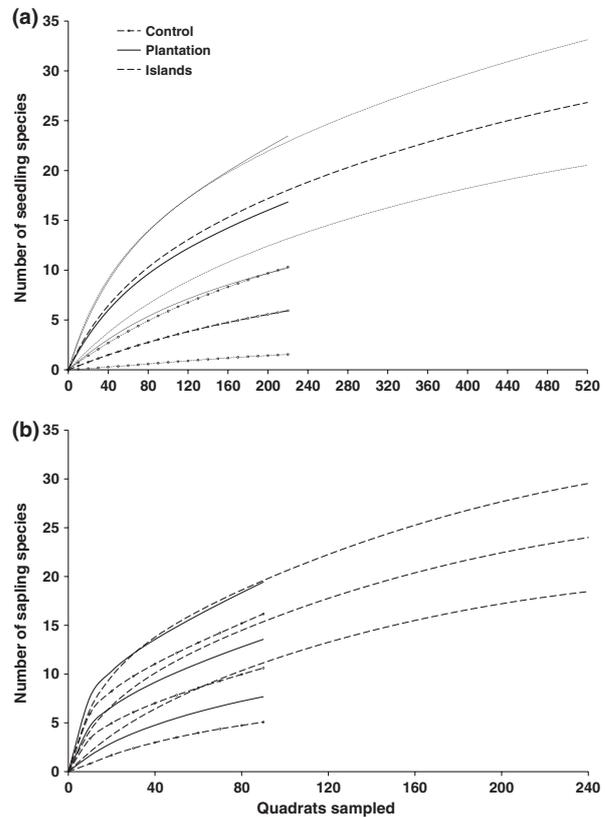


Fig. 3. Species accumulation curves per quadrat (and 95% confidence intervals) for seedlings and saplings grouped by restoration treatment.

seedling ($F_{2,38} = 3.1$, $P = 0.0585$) or sapling ($F_{2,38} = 2.8$, $P = 0.0709$) density was marginally significant (Fig. 4). Not surprisingly, actual island size was highly variable by 2010 and ranged from 26.3 to 52.1% [$\mu = 37.8\%$ (2004 sites); $\mu = 35.5\%$ (2005 sites)]. Mean ± 1 SD for the three island sizes was large: 276.1 ± 75.8 m^2 ; medium: 138.7 ± 44 m^2 ; and small: 45.3 ± 38.3 m^2 , and density of animal-dispersed recruits was positively related to actual island area (seedlings $R^2 = 0.20$, $P = 0.0015$; saplings $R^2 = 0.16$, $P = 0.0056$; overall recruits $R^2 = 0.23$, $P = 0.0006$).

Species accumulation curves were similar among island sizes for seedlings and saplings. Although a trend of lower species richness is notable for smaller islands, CI of all island sizes overlap substantially for both cohort size classes (Fig. S1, Supporting information).

Density of animal-dispersed recruits was three times higher in the interior vs. exterior of planted islands ($t = 3.5$, d.f. = 7, $P = 0.0095$; Fig. 5). In fact, mean seedling recruitment in the interior of islands (0.53 ± 0.37 m^{-2}) was significantly greater than in plantation (0.26 ± 0.21 m^{-2}) or control (0.04 ± 0.05 m^{-2} ; $F_{2,14} = 13.1$, $P = 0.0006$); a weaker trend was found for all recruits combined with interior island recruitment greater than controls but not plantations ($F_{2,14} = 9.8$, $P = 0.0022$; islands 0.76 ± 0.56 m^{-2} ; plantation 0.44 ± 0.33 m^{-2} ; control 0.19 ± 0.30 m^{-2}). Recruitment

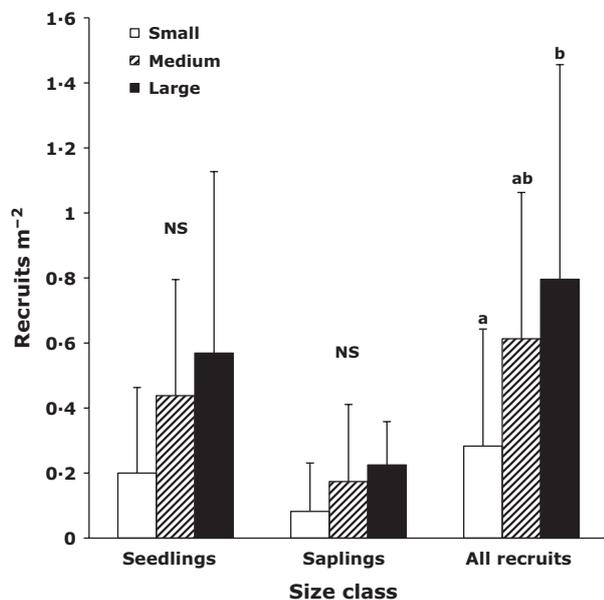


Fig. 4. Density (± 1 SD) of seedling and sapling animal-dispersed recruits, and all recruit size classes combined, grouped by island size ($n = 8$ sites). Means with the same letter are not significantly different ($P < 0.05$) using Tukey's LSD; NS, not significant.

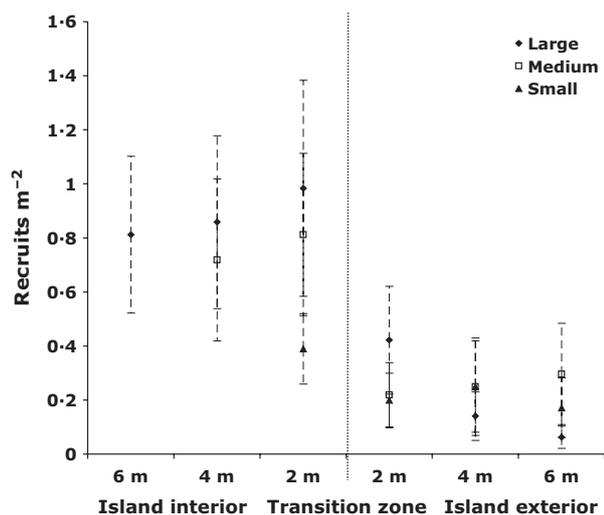


Fig. 5. Density (± 1 SE) of seedling and sapling animal-dispersed recruits for large, medium and small islands as a function of distance from the island edge. Note that medium islands have two interior quadrats and small islands only have one. The smaller island sizes cannot accommodate the full suite of quadrats.

dropped off abruptly at the edge of large and medium islands (Fig. 5).

LOCAL VERSUS LANDSCAPE

Recruitment across sites was variable (range 51–311), resulting in a strong block effect in almost all analyses. However, surrounding forest cover at either 100- or 500-m radius did not explain a significant amount of variation in

the number of animal- or wind-dispersed recruits that established in all treatments across sites ($P \gg 0.05$ in all cases).

Discussion

RESTORATION STRATEGY

Applied nucleation and plantations strongly enhanced tree recruitment compared to passive restoration after 4 years of recovery. Greater recruitment is likely due to increased seed dispersal of zoochorous species by birds (bat dispersal was not affected by restoration practice at our sites; Cole, Holl & Zahawi 2010), and more favourable establishment conditions resulting from decreased competition with shade-intolerant grasses and reduced microclimatic extremes (Nepstad *et al.* 1996; Holl 1999; Hooper, Condit & Legendre 2002). Recruitment differences across treatments were much greater for seedlings than saplings, which is not surprising as most seedlings recruited after planting treatments had well-established canopy cover. This suggests that the effects of planting treatments on recruitment will become stronger over time.

Most recruiting species are small-seeded and early successional animal-dispersed species (>90%, Appendix S1, Supporting information), which is consistent with seed rain at these sites (Cole, Holl & Zahawi 2010). Several other studies have reported the predominance of early successional tree recruits a few years into tropical forest restoration, with dispersal limitation of later-successional and typically larger-seeded species considered a major impediment (Holl 1999; Toh, Gillespie & Lamb 1999; Parrotta & Knowles 2001; del Castillo & Rios 2008). The lack of dispersal of mid-late-successional species suggests that alternate restoration strategies, such as direct-seeding (Hooper, Condit & Legendre 2002; García-Orth & Martínez-Ramos 2008; Cole *et al.* 2011), may be necessary once conditions for establishment become more favourable. That said, we recorded greater seedling species richness in active restoration sites, and all 18 mid- to late-successional species that recruited were censused in island and plantation plots, indicating that both planting treatments enhanced recruitment of later-successional species.

Despite the fact that only 20% of the area in island plots was planted with trees, recruitment abundance was similar to plantations. A few studies have shown that applied nucleation can be a successful restoration strategy in both tropical (Zahawi & Augspurger 2006) and temperate (Robinson & Handel 2000; Rey-Benayas, Bullock & Newton 2008) systems, but these studies did not directly compare results to conventional plantation-style restoration. Although our results indicate that the two strategies have an equivalent influence on recruitment, the cost of implementation for islands is considerably lower (Holl *et al.* 2011). In turn, the potential legacy that plantations may have on succession in the long term is likely far greater due to the entire area being planted often with a

few species, as abundance and composition of recruits can differ widely depending on the species planted (Parrotta & Knowles 2001; Carnevale & Montagnini 2002; Jones *et al.* 2004). There was also a twofold difference in seedling recruitment in island interiors as compared to plantations, suggesting that islands may concentrate recruitment within their core areas relative to areas with similar but more widespread overstorey cover. Although greater density of individuals within a confined area may not seem advantageous, overall densities are low ($<1 \text{ m}^{-2}$), such that a doubling in seedling number is likely to ensure the survival of some individuals, although many factors can preclude these seedlings from reaching a larger-sized cohort.

ISLAND SIZE AND EXPANSION

Large islands had greater density of recruits compared to small islands, which is consistent with higher density of animal-dispersed seeds (Cole, Holl & Zahawi 2010) and greater bird activity in larger islands at our study sites (Fink *et al.* 2009). Other studies show a similar pattern of increased dispersal (Zahawi & Augspurger 2006) and recruitment (Cook *et al.* 2005) in larger islands. There was also a nonsignificant trend towards fewer recruit species for both seedlings and saplings in small islands. Combined, these results suggest that an ideal island size is reached in the medium–large-size range, consistent with the planting size of *c.* 100 m² suggested by Rey-Benayas, Bullock & Newton (2008).

Recruitment in island interiors was threefold that of exterior (unplanted) areas, suggesting a strong nucleation effect similar to recruitment beneath remnant trees and shrubs in pastures (Guevara *et al.* 1992; Vieira, Uhl & Nepstad 1994; Slocum 2001). Two other studies show that such nucleation persists even after the establishment of surrounding secondary forest, both beneath remnant trees 25 years after pasture abandonment (Schlawin & Zahawi 2008) and in a 2010 follow-up survey (J. Corbin *et al.* unpublished data) in the temperate study of Robinson & Handel (2000).

Key to the nucleation model of restoration, however, is whether islands expand and coalesce over time. In this study, island expansion thus far has been driven largely by the crown growth of planted trees, as recruitment drops sharply immediately outside islands. The latter factor is likely to change with time, however, as studies have reported higher recruitment adjacent to islands (Robinson & Handel 2000; Zahawi & Augspurger 2006; Cole, Holl & Zahawi 2010). Although nuclei continue to impact recruitment many years after abandonment, it is not readily apparent whether a surrounding forest forms due to the expansion and coalescence of islands or if recruitment of individuals in open areas becomes more prevalent. It is likely to be a combination of both and will vary depending on the spatial scale of planting. Here, islands were closely spaced (*c.* 8 m; 20% plot planted), whereas Robinson

& Handel (2000) distributed their islands across 6-ha, with *c.* 0.12% area planted. Rey-Benayas, Bullock & Newton (2008) suggest a targeted planting area of $<1\%$. The ideal spatial distribution will be site specific but should be driven by landscape-level considerations (*i.e.* connectivity, remnant vegetation), as well as the size of the degraded area and economic considerations.

LOCAL VERSUS LANDSCAPE

The abundance of remnant forest near a restoration site is considered an important potential resource for propagules (Holl 2007; Brudvig 2011), and many past studies support this assertion (Parrotta & Knowles 2001; Zanne & Chapman 2001; Ferguson *et al.* 2003; Bertoncini & Rodrigues 2008). However, surrounding forest cover had no influence on tree recruitment at this stage in our study, which is consistent with our seed rain data (Cole, Holl & Zahawi 2010) and the movement patterns of migrant birds (Lindell *et al.* 2012), which can be important dispersers in early succession (Lindell, Reid & Cole 2012). Similarly, other tropical studies (Guevara, Purata & Van der Maarel 1986; Zahawi & Augspurger 2006; Howe *et al.* 2010) report no effect of proximity to forest on seed rain and seedling recruitment in earlier successional habitats. The apparent disparity may lie in the timing of when remnant forests become important propagule sources, rather than whether they do, as proximity to forest is important at later stages in recovery (Thomlinson *et al.* 1996; Cook *et al.* 2005). As architectural complexity in our sites increases, they should attract a broader suite of dispersers (Hughes, Kauffman & Jaramillo 1999; Toh, Gillespie & Lamb 1999), and accordingly, we anticipate that the role of adjacent forests will become more important.

Lack of a surrounding forest cover effect on tree recruitment also reflects the availability of nonforest seed sources in the surrounding agricultural landscape. Narrow riparian corridors, live fences and isolated trees are common in mixed-use landscapes such as our study area, creating connectivity for many disperser groups (Estrada, Coates-Estrada & Meritt 1993; Harvey *et al.* 2006; Sekercioglu *et al.* 2007; Mendenhall *et al.* 2011), and providing seed sources for several species commonly recorded in our plots. In contrast, efforts to restore forest in lands devoid of a connective matrix (Parrotta & Knowles 2001; Rodrigues *et al.* 2009) depend entirely on seeds that disperse from forest remnants or are actively introduced in restoration efforts.

We found high variability in tree recruitment among sites, which is a common result (Peterson & Haines 2000; Zahawi & Augspurger 2006) and is likely attributable to local-scale factors, such as the presence of nearby fruiting trees and hedgerows. Site-specific factors, such as past land-use history, likely also are important, as duration and intensity of land use prior to abandonment can be inversely related to the rate of forest recovery (Hughes, Kauffman & Jaramillo 1999; Holl 2007). Predominance

of grasses at some sites (due to slow canopy development) certainly impacted tree recruitment (Hooper, Legendre & Condit 2005; García-Orth & Martínez-Ramos 2011), as few seedlings recruited in plots with >25% grass cover. Regardless of the driver, the high variability in recruitment among sites underscores the importance of designing well-replicated restoration studies across the landscape to avoid reaching erroneous conclusions based on a few sites.

CONCLUSIONS

Results provide clear recommendations for land managers. First, the applied nucleation strategy represents an effective and cheaper alternative to typical plantation-style plantings to accelerate forest recovery. Second, there is a minimum critical island size below which islands do not enhance seed rain (Cole, Holl & Zahawi 2010) and tree recruitment, and for which planting and maintenance are logistically challenging (Holl *et al.* 2011). In our system and in Honduras (Zahawi & Augspurger 2006), this island size was *c.* 100 m², but ideal size depends on various factors. Third, results show that even sites with minimal surrounding forest cover can be rapidly colonized by early successional tree species, when agricultural land uses retain some level of connectivity. Both active restoration strategies accelerated early forest recovery, but applied nucleation represents a viable alternative that should be considered by practitioners under certain circumstances.

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Supporting Information

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

Appendix S1. Tree seedlings and saplings censused in eight sites arranged by species, dispersal mode, successional stage, treatment and number of individuals.

Fig. S1. Species accumulation curves per quadrat for seedlings and saplings grouped by island size.

Table S1. Mean percentage overstorey, bare ground, forb and grass cover grouped by treatment.