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Testing heterogeneity–diversity relationships in tropical forest restoration

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Abstract Restoring small-scale habitat heterogeneity in highly diverse systems, like tropical forests, is a conservation challenge and offers an excellent opportunity to test factors affecting community assembly. We investigated whether (1) the applied nucleation restoration strategy (planting tree islands) resulted in higher habitat heterogeneity than more homogeneous forest restoration approaches, (2) increased heterogeneity resulted in more diverse tree recruitment, and (3) the mean or coefficient of variation of habitat variables best explained tree recruitment. We measured soil nutrients, overstory and understory vegetation structure, and tree recruitment at six sites with three 5- to 7-year-old restoration treatments: control (no planting), planted tree islands, and conventional, mixed-species tree plantations. Canopy openness and soil base saturation were more variable in island treatments than in controls and plantations, whereas most soil nutrients had similar coefficients of variation across treatments, and bare ground was more variable in control plots. Seedling and sapling species density were equivalent in plantations and islands, and were substantially higher than in controls. Species spatial turnover, diversity, and richness were similar in island and plantation treatments. Mean canopy openness, rather than heterogeneity, explained the largest proportion of variance in species density. Our results show that, whereas canopy openness and soil base saturation are more heterogeneous with the applied nucleation restoration strategy, this pattern does not translate into greater tree diversity. The lack of a heterogeneity–diversity relationship is likely due to the fact that recruits respond more strongly to mean resource gradients than variability at this early stage in succession, and that seed dispersal limitation likely reduces the available species pool. Results show that planting tree islands facilitates tree recruitment to a similar degree as intensive plantation-style restoration strategies.

Keywords Canopy structure · Costa Rica · Plantations · Soil nutrients · Tree islands

Introduction

Heterogeneity in abiotic resources, such as light and soil nutrients, can strongly affect forest species composition and diversity. Intact tropical forests, in particular, show high levels of habitat heterogeneity. For instance, light environments in tropical forests vary over small spatial scales, which can influence plant distribution (Clark et al. 1993; Nicotra et al. 1999; Dalling and Hubbell 2002; Balderrama and Chazdon 2005). Likewise, topographic variability and the local influence of individual tree species on nutrient cycling often cause small-scale heterogeneity in nutrient availability (Webb and Peart 2000; Vitousek et al. 2003; Kubota et al. 2004; Townsend et al. 2008). Species often differentially exploit patchily distributed resources, which can lead to higher species spatial turnover and diversity (reviewed in Tilman and Pacala 1993; Chase and Liebold 2003; Questad and Foster 2008).

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Studies across a range of ecosystems, however, show mixed support for the heterogeneity–diversity relationship, and that the relationship commonly varies across spatial scales (Lundholm 2009; Douda et al. 2012). Heterogeneity and diversity are often positively correlated, but some studies show no relationship or occasionally negative correlations between resource heterogeneity and species diversity (reviewed in Lundholm 2009). Likewise, past tropical studies show that heterogeneity in light and nutrient conditions may or may not explain patterns of species density and abundance in tree seedlings (Nicotra et al. 1999; Denslow and Guzman 2000; Webb and Peart 2000; Kubota et al. 2004; Dupuy and Chazdon 2006). Lack of support for the heterogeneity–diversity relationship in some studies has been explained in a number of ways, including dispersal limitation (Questad and Foster 2008), predominance of stochastic processes (Hubbell 2001), and overriding resource limitation (i.e. diversity is more strongly related to mean resource availability than variation in resources; Lundholm 2009).

Most past studies of the heterogeneity–diversity relationship have been conducted in minimally disturbed ecosystems, and the few studies undertaken in a restoration context have all been conducted in temperate habitats (e.g., Baer et al. 2004; Gundale et al. 2006). Intensive anthropogenic disturbances, such as agriculture, often strongly reduce resource heterogeneity and β-diversity of plants and animals (Robertson et al. 1993; Flinn and Marks 2007; Karp et al. 2012). In turn, studies documenting natural forest recovery show that heterogeneity of habitat structure and species distributions increase over time (Denslow and Guzman 2000; Guariguata and Ostertag 2001; Cook et al. 2005), but still are often lower in older secondary forests than in primary forests (Nicotra et al. 1999; Flinn and Marks 2007). Restoration efforts across a range of systems have often failed to restore heterogeneity of abiotic conditions and community composition approaching that of more intact systems (Holl 2002b; Polley et al. 2005). These shortcomings highlight the need for new approaches that create more heterogeneous habitats, particularly in highly diverse systems, such as tropical forests.

The most common strategy for restoring large deforested areas in the tropics is to plant the entire area with a mix of native tree species (reviewed in Holl 2012). Such efforts are often successful in facilitating establishment of native seedlings, but if planted tree survival is high, the tree canopy can result in relatively homogeneous abiotic conditions and understory plant communities (Halpern and Spies 1995; Corbin and Holl 2012). Moreover, there may be a strong legacy of the planted species on resource availability (Celentano et al. 2011) and seedling recruitment (Cusack and Montagnini 2004).

The applied nucleation strategy (i.e. planting tree islands rather than the entire area) has been explored as a low cost restoration alternative to conventional tree plantations (Zahawi and Augspurger 2006; Rey Benayas et al. 2008; Corbin and Holl 2012). These tree islands facilitate natural recovery processes in degraded landscapes, as they slowly expand, through growth of planted seedlings and increased dispersal and establishment of new seedlings, and may ultimately coalesce (Rey Benayas et al. 2008). The method attempts to simulate nucleation processes that naturally occur in successional forest and may leave less of a legacy of planted trees (Yarranton and Morrison 1974; Reis et al. 2010). Indeed, our past research in the neotropics indicates that planted tree islands serve to attract and provide habitat for animals, which encourages zoochorous seed dispersal and seedling establishment (Zahawi and Augspurger 2006; Cole et al. 2010; Zahawi et al. 2013).

Several authors have suggested that planting tree islands should result in higher small-scale habitat heterogeneity and in turn more diverse species composition compared to conventional plantation-style restoration (Rey Benayas et al. 2008; Reis et al. 2010; Corbin and Holl 2012), but this has never been tested experimentally. We compared three restoration strategies (control—no planting, planting tree islands, conventional mixed-species tree plantations) to test three hypotheses: (1) planting tree islands results in greater heterogeneity of vegetation structure (canopy and understory) and soil nutrients than control or plantation treatments; (2) greater habitat heterogeneity results in more tree species recruiting; and (3) tree diversity is more strongly correlated with resource heterogeneity than mean resource availability.

Materials and methods

Site description and experimental design

This study was conducted at six sites in southern Costa Rica, in the vicinity of the Las Cruces Biological Station (8°47′7″N, 82°57′32″W; Holl et al. 2011). The six sites range from 1,110 to 1,290 m in elevation and receive a mean annual rainfall of ca 3,500–4,000 mm with a dry season from December to March. Mean annual temperature is ∼21 °C. All sites were used for >18 years for a mix of pasture, coffee plantation, and vegetable farming (Holl et al. 2011). Soils are volcanic in origin, and mildly acidic. Soil nutrients and bulk density did not vary across treatments at the beginning of the study (Holl et al. 2011).

Each of the six sites were cleared of vegetation and divided into three 50 × 50 m plots which were assigned to one of three treatments: no tree planting (control), planting tree islands (island), and planting the entire area (plantation) (Holl et al. 2011). Four tree species were planted, including two timber species [*Terminalia amazonia* (J.F.

Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae)], and two fast-growing species that form N-fixing mutualisms and are commonly planted in coffee plantations in the region [*Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. (Fabaceae)]. In the plantation treatment, seedlings were planted in alternating rows of *Terminalia/Vochysia* and *Erythrina/Inga* at 2.8-m intervals throughout the entire plot. In the island treatment, two small (16 m^2), two medium (64 m^2), and two large (144 m^2) islands were each planted with a mixture of the four tree species at the same planting density as in the plantations. Islands were arranged in two rows with the order of island size randomized in each row and islands separated by $\geq$8 m (see Cole et al. 2010 for additional details).

Grass and other ruderal vegetation were cleared in all treatments for 2.5 years to allow seedlings to overtop grasses, after which sites were no longer managed. Sites were set up over 3 years (2004–2006), due to the large scale of the study, but by 3 years after planting there was no significant effect of planting year on tree growth given the variability in growth rates across sites (Holl et al. 2011). At the time of data collection, plantation treatments had a nearly continuous canopy cover with a height of 9–11 m. In the island treatment, tree canopy height was similar to plantations, but tree cover ranged from 25 to 63 % of the plot area with the variation largely due to differential growth of planted trees across sites (Zahawi et al. 2013). Control plots and unplanted areas of island plots were mostly covered with dense pasture grasses and ruderal vegetation (<3 m tall) with few to no isolated small trees.

Data collection

In each of the 18 50 × 50 m plots, we measured soil nutrients, canopy and understory structure, and tree recruitment in six 4 × 16 m transects that were subdivided into four consecutive 4 × 4 m quadrats. We took one measurement of canopy height, canopy cover (hemispheric photos), and soil nutrients per 4 × 4 m quadrat ($n = 24$ quadrats per plot). All measurements were taken in June–July 2011, 5–7 years after planting.

We took hemispheric photographs at 1 m height in the center of each 4 × 4 m quadrat using a Nikon Coolpix 950 camera and a fisheye lens. The camera faced north and was leveled. Photos were used to estimate woody species canopy cover, so we prevented nearby grasses from entering into the frame of the picture. Images were analyzed using Gap Light Analyzer (v.2) software. We report percent canopy openness, which was strongly correlated ($r \geq 0.98$) with leaf area index, and both direct and diffuse transmitted solar radiation. At the location of each hemispheric photo,

we measured woody canopy height using a laser range-finder. If there was no woody canopy, we used a canopy height of 1.5 m for analyses, which was the average height of grasses and herbaceous vegetation in these quadrats.

We took six to eight systematically distributed 2.5-cm diameter × 15-cm deep soil cores in each 4 × 4 m quadrat. Cores within each quadrat were composited and air-dried, and then crushed and passed through a 2-mm sieve. The samples were analyzed for pH, organic matter, cation exchange capacity (CEC), Mehlich III extractable phosphorus, potassium, calcium, magnesium, sodium, and other bases at Brookside Labs in Knoxville, Ohio (see www.blinc.com/worksheet_pdf/SoilMethodologies.pdf and Gavlak et al. 2003 for details on protocols). Base saturation was calculated as the concentration of exchangeable base cations divided by CEC.

We used a stratified sampling procedure to reflect the comparative sizes of the vegetation being measured. We sampled tree seedlings ($\geq$0.2 and <1 m tall) in 1 × 4 m quadrats centered within the larger 4 × 4 m quadrat. Saplings ($\geq$1 m tall) were sampled throughout each 4 × 4 m quadrat. In two alternating 1 × 1 m sub-quadrats within each 1 × 4 m seedling quadrat, we estimated percent 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 and Ellenberg 1974). We used the mid-points of these ranges and averaged the two measurements. We estimated shrub cover (1–5 m tall) in the same cover class intervals in two adjacent 2 × 4 m sub-quadrats within the 4 × 4 m sapling quadrat and averaged the values.

Data analysis

We calculated the means and coefficient of variation (CV) of habitat variables across all 24 quadrats for each plot. We used the CV as a measure of heterogeneity (Baer et al. 2005). We compared the means and CVs using ANOVA with site as a random blocking factor and treatment as a fixed effect. Values were log-transformed when necessary to meet assumptions of normality and homogeneity of variance. When the treatment effect was significant, individual treatments were compared using Tukey's multiple comparison tests.

We calculated the species density (number of species per a fixed unit sampling area), abundance, and frequency of quadrats with at least one individual over the entire seedling (1 × 4 m) or sapling (4 × 4 m) quadrat, as well as the species density and abundance at the 50 × 50 m plot level. We analyzed patterns of seedling and sapling abundance separately because (1) they were sampled in different-sized quadrats and (2) we hypothesized that seedlings would more strongly reflect treatment effects as they likely

recruited more recently than saplings. We analyzed species density of seedlings and saplings using a mixed-model ANOVA with site as a random blocking factor and treatment as a fixed effect. For seedling and sapling abundance, we used generalized linear mixed-effects models with a log-link function given the Poisson distribution of these count data (PROC GLIMMIX in SAS 9.3). As in most tropical studies, abundance and species density were strongly correlated for both seedlings and saplings at both the plot and quadrat level, so results for recruitment abundance and species density in each size class were similar. For brevity, we report only species density results since our primary aim was to test the heterogeneity–diversity relationship.

Calculating diversity and dominance measures for seedlings and saplings in control plots was problematic due to the low number of individuals and species in most control treatments. Therefore, we focus these comparisons between island and plantation treatments. Plot level diversity was calculated using Shannon's diversity index, $H' = -\Sigma p_i \ln p_i$, where p_i represent the proportion of individuals in each plot contributed by each species. Dominance was calculated using Simpson's index, $SI = [\Sigma n_i(n_i-1)]/[N(N-1)]$, where n_i and N are the number of individuals and total individuals in each plot. As a measure of community heterogeneity, we calculated species spatial turnover using the additive partitioning approach (Lande 1996), where species spatial turnover (SST) represents the sum of community richness (S_T: i.e., plot level richness) minus patch richness (S_j: i.e., quadrat level richness) and $SST = \Sigma q_j(S_T-S_j)$ where q is the number of species in each of j quadrats. We calculated individual-based rarefaction curves for seedlings and samplings in islands and plantations in R 2.15.0 (R Development Core Team 2012). For each class of recruits, we estimated species richness for the minimum number of individuals observed in one treatment. We used a bootstrap estimation with 1,000 randomizations and a tolerance of 0.05 (i.e., each randomization simulated a community that had within 5 % of the number of individuals observed in the least-abundant treatment). Rarefactions were created using the rich package (Rossi 2011) in R 2.15.0.

If higher resource heterogeneity is driving species diversity then the prediction would be for a positive relationship between species density and the coefficient of variation of habitat variables. We used stepwise regression to identify variables that best explained species density with forward addition of parameters, which included the means and coefficient of variation of all habitat variables (Tables 1, 2). We used a more restrictive significance value ($P < 0.01$) for entry into model to reduce type II error, given the large number of variables being tested.

Results

Vegetation structure and soil nutrients

Mean canopy openness and grass cover were highest in the control plots, intermediate in the island treatment, and lowest in plantations, whereas mean canopy height and bare ground showed the opposite trend (Fig. 1a, b; Table 1). Shrub and herb cover were lowest in plantations, and similar in island and control treatments (Table 1).

The coefficient of variation (CV) for percent canopy openness was higher in islands plots than either plantations or controls, whereas CV of canopy height was higher in both control and islands treatments (Fig. 1c, d). The CV of shrub and herb cover did not vary across treatments (Table 1). In contrast, the CV of grass cover was highest in plantations, intermediate in islands and lowest in controls, whereas the CV of bare ground showed the opposite trend (Table 1).

Means and CVs for organic matter, CEC, Mehlich P, Mg, and Ca were similar across treatments, whereas soil pH, K, and base saturation were lower in plantations than in the island and control treatments (Table 2). Although soil nutrients were highly heterogeneous across sites, in most cases CVs did not differ across treatments. Only the CV of base saturation was higher in the islands, lower in plantations, and intermediate in controls (Table 2).

Seedling and sapling recruitment

In total, we censused 479 seedlings of 49 species, and 1,374 saplings of 40 species (Supplementary Table 1). The vast majority of recruits were animal-dispersed species (>80 %). The total number of seedlings observed, percentage of quadrats with at least one individual, and the total number of species observed were all lowest in controls (Table 3).

Species density of seedlings was higher in islands and plantation treatments than in controls (Fig. 2; $F_{2,10} = 8.4$, $P = 0.0074$); saplings showed a similar but weaker trend ($F_{2,10} = 5.4$, $P = 0.0260$). The total number of seedling species observed in controls was a third of that found in islands and plantations. The Shannon–Weiner diversity (H'), Simpson's dominance index (DI), species spatial turnover, and species richness (from rarefaction curves) were similar in island and plantation treatments for both seedlings and saplings (Table 3).

Recruitment relationships to abiotic conditions

Mean canopy openness explained a significant amount of variation in species density of both seedlings and saplings at the plot level (Fig. 3). No other variables (means or CV)

Table 1 Understory variables in control, island and plantation treatments

Understory	Mean				Coefficient of variation			
	Control	Island	Plantation	F (P)	Control	Island	Plantation	F (P)
Shrub cover	31.8 ± 6.3 a	31.7 ± 6.3 a	10.6 ± 2.7 b	5.6 (0.02)	101.0 ± 23.3 a	93.8 ± 1.6 a	129.2 ± 13.5 b	1.2 (0.34)
Herb cover	40.7 ± 6.9 a	31.3 ± 4.8 a	10.1 ± 1.7 b	13.1 (0.002)	80.4 ± 7.6 a	86.2 ± 0.5 a	98.4 ± 10.3 a	0.5 (0.62)
Grass cover	46.8 ± 12.2 a	19.0 ± 5.1 b	4.9 ± 2.1 b	11.6 (0.003)	71.6 ± 14.6 a	116.2 ± 9.8 a,b	154.9 ± 22.0 b	6.7 (0.02)
Bare ground	13.4 ± 4.9 a	49.0 ± 1.0 b	83.8 ± 3.5 c	89.2 (<0.0001)	136.9 ± 17.9 a	68.2 ± 4.0 b	15.6 ± 3.0 c	35.9 (<0.0001)

Values are mean ± SE ($n = 6$ per treatment) of the within-plot means and coefficients of variation ($n = 24$ quadrats per plot). Values with the same letter are not significantly different among treatments using Tukey's multiple comparison test ($P < 0.05$). ANOVA F and P values for means and coefficient of variation (CV) are given for each variable

Table 2 Soil variables in control, island and plantation treatments

Soil variable	Mean				Coefficient of variation			
	Control	Island	Plantation	F (P)	Control	Island	Plantation	F (P)
pH	5.48 ± 0.14 a	5.42 ± 0.14 a	5.03 ± 0.13 b	24.7 (0.0001)	3.4 ± 0.3 a	4.9 ± 1.3 a	3.1 ± 0.4 a	1.6 (0.26)
OM	17.12 ± 1.89 b	17.30 ± 2.21 a	18.75 ± 2.08 a	1.1 (0.38)	13.7 ± 4.0 a	11.5 ± 2.5 a	10.6 ± 3.1 a	0.4 (0.70)
Mehlich III P (mg kg^{-1})	4.9 ± 0.6 a	4.3 ± 0.8 a	4.2 ± 0.3 a	0.5 (0.65)	29.9 ± 4.5 a	33.0 ± 3.8 a	26.3 ± 2.5 a	0.8 (0.48)
CEC (me 100 g^{-1})	10.55 ± 1.04 a	11.65 ± 1.51 a	12.63 ± 0.84 a	0.9 (0.46)	26.2 ± 2.9 a	30.2 ± 2.5 a	24.8 ± 3.4 a	1.5 (0.27)
Ca (mg kg^{-1})	953.0 ± 120.2 a	1,079.4 ± 165.5 a	965.0 ± 93.1 a	0.3 (0.76)	32.6 ± 3.6 a	39.5 ± 5.5 a	31.5 ± 4.4 a	1.4 (0.30)
Mg (mg kg^{-1})	152.1 ± 15.5 a	151.5 ± 26.8 a	132.1 ± 13.8 a	0.9 (0.51)	31.4 ± 3.5 a	30.7 ± 1.9 a	28.3 ± 2.7 a	0.4 (0.67)
K (mg kg^{-1})	152.7 ± 20.1 a	122.1 ± 23.6 a,b	70.5 ± 3.8 b	9.3 (0.005)	34.1 ± 4.5 a	37.4 ± 5.6 a	24.7 ± 3.3 a	3.1 (0.09)
Base saturation (%)	68.8 ± 4.0 a	66.4 ± 4.3 a	57.1 ± 3.1 b	15.4 (0.0009)	10.1 ± 2.7 a,b	17.2 ± 3.6 a	6.9 ± 0.7 b	4.9 (0.03)

Values are mean ± SE ($n = 6$ per treatment) of the within-plot means and coefficients of variation ($n = 24$ quadrats per plot). Values with the same letter are not significantly different among treatments using Tukey's multiple comparison test ($P < 0.05$). ANOVA F and P values for means and coefficient of variation (CV) are given for each variable

CEC Cation exchange capacity

explained a significant amount of the remaining variation. Mean canopy openness was strongly positively correlated with a number of variables (Table 4), grass cover and organic matter in particular; it was negatively correlated with bare ground and canopy height. Mean canopy openness was not significantly correlated with the CV of canopy openness ($r = 0.12$, $P = 0.6273$).

Discussion

Resource heterogeneity

We hypothesized that resource heterogeneity would be higher in the applied nucleation (tree island) restoration plots given the patchy planting design, and we found mixed support for this hypothesis. Not surprisingly, canopy openness was more variable in plots planted with tree islands than the other treatments. Interestingly, base saturation, which was correlated with canopy cover, showed the same pattern. 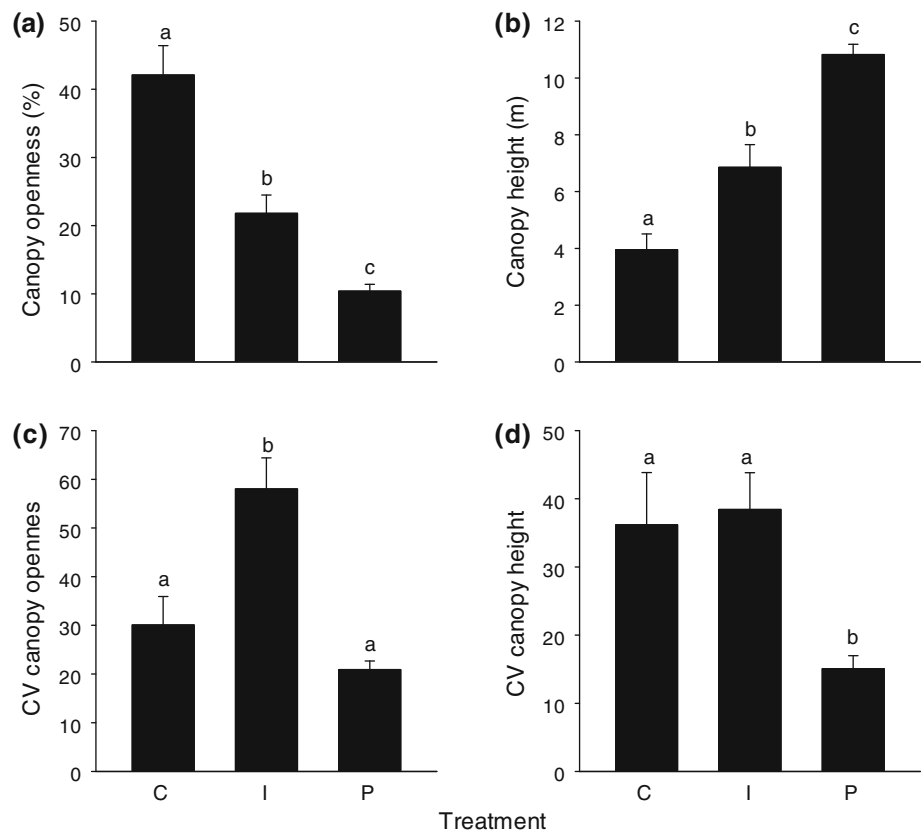Other habitat variables, however, showed different trends (Tables 1, 2); most soil nutrients had similar variability across treatments and bare ground was more variable in control plots.

Whereas a number of authors have suggested that habitat heterogeneity should be higher with a tree island planting approach (Rey Benayas et al. 2008; Reis et al. 2010; Corbin and Holl 2012), we know of no other studies that have directly compared this approach to more homogeneous restoration strategies. Past studies, however, have shown that other restoration strategies that are applied in a patchy manner (e.g., Baer et al. 2004—fertilization and soil depth; Gundale et al. 2006—forest thinning) can successfully restore small-scale nutrient heterogeneity.

Heterogeneity–diversity relationship

Although canopy openness, which best explained patterns of species density, was more heterogeneous in the island treatment, this did not result in higher diversity of tree recruits in island plots, as we predicted. All indices of species diversity and spatial turnover were similar in

Fig. 1 Treatment effects on mean percent **a** canopy openness, and **b** canopy height, and coefficient of variation (CV) of **c** canopy openness and **d** canopy height in control (*C*), island (*I*) and plantation (*P*) treatments. *Bars* mean ± SE (*n* = 6 plots per treatment). Means with the same *letter* are not significantly different across treatments using Tukey's multiple comparison test ($P < 0.05$)

Table 3 Seedling and sapling communities in control, island, and plantation treatments

	No. of individuals	Animal-dispersed individuals (%)	Quadrats with ≥1 individual (%)	Total observed species	H′[a]	DI[a]	Species turnover[a]	Species richness[b]
Seedling								
Control	47	87	16	12	–	–	–	–
Island	249	89	47	34	1.71 ± 0.25	0.71 ± 0.06	5.49 ± 1.41	25.2 ± 3.2
Plantation	183	91	55	31	1.49 ± 0.17	0.65 ± 0.06	4.77 ± 0.66	24.0 ± 2.5
Sapling								
Control	370	79	40	20	–	–	–	–
Island	436	82	61	27	1.59 ± 0.17	0.69 ± 0.06	5.03 ± 0.97	23.0 ± 2.1
Plantation	568	80	85	31	1.40 ± 0.20	0.62 ± 0.08	6.12 ± 0.94	24.1 ± 2.7

Shannon-Weiner Diversity (*H′*), Simpson's Dominance Index (*DI*), species spatial turnover (Lande index of turnover), and species richness from individual-based rarefaction curves are also presented for plantation and island treatments, but could not be calculated for the control treatment due to the low number of individuals recorded. H′, DI, and species turnover were not significantly different ($P > 0.05$) between island and plantation treatments for seedlings or saplings
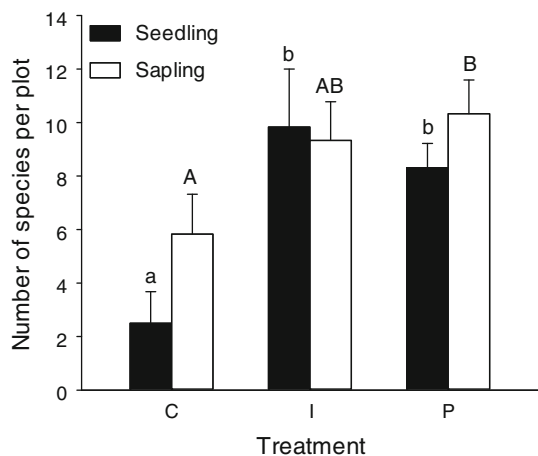
[a] Values are mean ± SE (*n* = 6 plots per treatment)

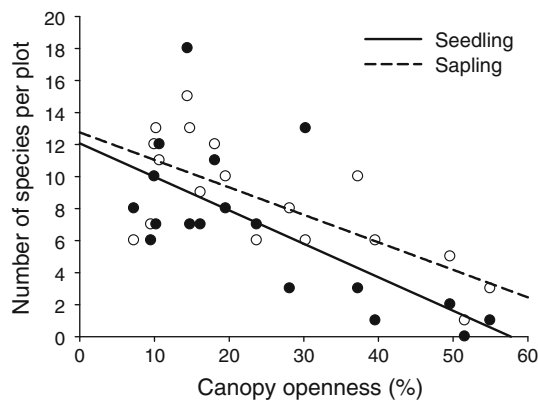[b] Values are mean ± SD (*n* = 1,000 simulations per treatment)

islands and plantations, and species density was better explained by mean resource availability than variation. Past research in relatively intact systems shows highly variable support for the heterogeneity–diversity relationship (reviewed in Lundholm 2009) and results from the few restoration studies, all conducted in temperate systems, are similarly mixed. For example, Richardson et al. (2012) found evidence that both fine-scale habitat heterogeneity and increased seed rain diversity enhance the diversity of herbaceous species on limestone quarries in Ontario, Canada. In contrast, Baer et al. (2004, 2005) report that more heterogeneous soil nutrients did not result in higher

Fig. 2 Seedling and sapling species density in control (*C*), island (*I*) and plantation (*P*) treatments. *Bars* mean ± SE (*n* = 6 plots per treatment). Means with the same *letter* are not significantly different across treatments using a Tukey's multiple comparison test; *lowercase letters* seedling and *uppercase letters* sapling ($P < 0.05$)

Table 4 Pearson correlation coefficients between percent canopy openness and vegetation structure and soil variables at the plot level ($n = 18$)

Site	R	P
Canopy height (m)	−0.85	<0.0001
Shrub cover (%)	0.36	0.1399
Herb cover (%)	0.49	0.0371
Grass cover (%)	0.77	0.0002
Bare ground (%)	−0.89	<0.0001
pH	−0.36	0.1415
Organic matter (%)	0.60	0.0090
Mehlich III P (mg kg^{-1})	0.23	0.2333
CEC (me 100 g^{-1})	0.16	0.1637
Ca (mg kg^{-1})	0.01	0.5162
Mg (mg kg^{-1})	0.12	0.9816
K (mg kg^{-1})	0.59	0.6307
Base saturation (%)	0.58	0.0108

CEC Cation exchange capacity

Fig. 3 Relationship between canopy openness and seedling (*solid circles*) and sapling (*open circles*) species density in all plots (*n* = 18). Regression statistics for Seedling: $y = 12.07 - 0.21x$, $r^2 = 0.50$, $P = 0.0010$; Sapling: $y = 12.76 - 0.17x$, $r^2 = 0.47$, $P = 0.0016$

plant community diversity in prairie restoration, which they attribute to the strong effects of a single dominant species. In turn, Gundale et al. (2006) found that higher N heterogeneity in restored pine/fir forests corresponded with higher plant diversity, but many species were ruderal, nonnatives. Several possible explanations for the lack of consistent support for a heterogeneity–diversity relationship have been suggested (Questad and Foster 2008; Lundholm 2009), and we discuss three that we consider to be the most likely drivers in this system.

First, plants may respond more strongly to mean resource availability than to localized variation (Lundholm 2009). This is the case in our study where mean canopy openness better explained species density than did variability in canopy openness or the other habitat factors that

we measured. Moreover, treatment differences in mean habitat variables were stronger and more consistent than differences in the coefficient of variation. Tree recruitment in recently abandoned pastures is strongly limited by a lack of seed dispersal, competition with pasture grasses, and stressful microclimatic conditions, all of which are ameliorated by establishing tree canopy cover (reviewed in Holl 2012; discussed in more detail below). Significant correlations between species density and mean, but not CV, of canopy openness suggests that at this early stage in succession providing appropriate establishment conditions for early colonizers is more important than a range of habitat niches.

Second, dispersal limitation may reduce the available species pool and in turn community composition to a greater degree than niche availability (Tilman 1997; Questad and Foster 2008; Douda et al. 2012). There is strong evidence of dispersal limitation at our study site (Cole et al. 2010) and other abandoned pastures in the tropics (e.g., Holl 1999; Harvey 2000b; Martinez-Garza and Gonzalez-Montagut 2002; Zahawi and Augspurger 2006), with very few large-seeded, mid-to-late successional species arriving; this limits the trait variation within the available species pool and, therefore, the potential for species to exploit all available niches (Questad and Foster 2008). Moreover, seed predation may be high in former pastures (Uhl et al. 1988; Jones et al. 2003; Cole 2009), which further decreases seed availability.

Third, it simply may be too early in the successional process, and the heterogeneity–diversity relationship could become stronger over time. Heterogeneity in habitat variables and species composition may increase over time

(Guariguata and Ostertag 2001; Cook et al. 2005), and the abundance and diversity of seed rain in successional tropical forest usually increases with stand age (Tabarelli and Peres 2002; del Castillo and Rios 2008). We found weaker effects of the island planting treatment on sapling than seedling diversity patterns. The majority of, but certainly not all, saplings established earlier than seedlings, when canopy cover was less well established, and, therefore, do not reflect recruitment in relation to current levels of resource heterogeneity. Together, these suggest that as treatments become more established and seed dispersal increases, tree species composition is likely to diversify and may more strongly reflect habitat heterogeneity, but longer-term data are need to test these hypotheses.

Habitat conditions that facilitate tree recruitment

Of the various vegetation structure and soil resource variables we measured, mean canopy openness explained the most variation in plot level species richness, strongly supporting the importance of establishing a tree canopy to facilitate woody seedling recruitment and growth in tropical pastures (Harvey 2000a; Cusack and Montagnini 2004; Wydhayagarn et al. 2009). Canopy cover influences woody recruitment through a number of mechanisms including: enhancing bird activity and thereby dispersal of zoochorous seeds (Howe 1990; Jones et al. 2004; Fink et al. 2009); reducing cover of light-demanding pasture grasses (Holl 2002a; Hooper et al. 2002); providing intermediate light conditions favorable for tree growth (Loik and Holl 2001); and enhancing nutrient availability (Siddique et al. 2008; Celentano et al. 2011). These mechanisms are all likely operating at our sites, but it is impossible to evaluate their relative importance without manipulating them independently.

Our results show that vegetation structure variables, both overstory and understory, were more strongly affected by restoration treatment than were soil nutrients and better explained patterns of woody recruitment overall. This finding coincides with Luzuriaga and Escudero (2008), who argue that abiotic factors such as soil nutrients do not sufficiently explain species recruitment and composition in successional forests. Soil nutrients likely affect plant growth much more than recruitment or seedling survival (Jin et al. 2000; Holste et al. 2011).

Although the focus of our study was on resource heterogeneity, one interesting difference between treatment means was that plantations soils were significantly more acidic and had lower levels of base saturation than in control or island treatments. Ewel et al. (1991) found that soil nutrients declined and soil acidity typically increased over 5 years as plant communities became more diverse and as plants uptake more nutrients with growth. Other studies have shown similar decreases in pH and base

cations in conventional tree plantations (Rhoades and Binkley 1996; Gomes and Luizão 2012), which can in turn affect the activity of soil biota (Hinsinger et al. 2003). These nutrient differences are likely to have a stronger effect on soil resource heterogeneity and species composition as succession proceeds.

Conclusions

Our data showed mixed support for the prediction that a tree island planting strategy creates more heterogeneous resource conditions, and no support for the hypothesis that the more variable canopy cover of island plantings results in more diverse tree recruitment than a homogeneous planting strategy at this early stage in the successional process. Our results clearly show that both plantation and island planting approaches substantially increase both the abundance and diversity of tree recruitment in abandoned tropical pasture, as compared to simply abandoning land. The applied nucleation approach, however, is substantially cheaper given the smaller area planted with seedlings (Holl et al. 2011). Therefore, applied nucleation is a promising tropical forest restoration strategy that should be more widely considered by land managers, but longer-term data are needed before making robust recommendations.

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