



## Recovery of floristic diversity and basal area in natural forest regeneration and planted plots in a Costa Rican wet forest

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### ABSTRACT

When compared to planted reforestation, natural unassisted regeneration is often reported to result in slow recovery of biomass and biodiversity, especially early in succession. In some cases, naturally regenerating forests are not comparable to the community structure of primary forests after many decades. However, direct comparison of the outcomes of tropical forest restoration and natural regeneration is hindered by differences in metrics of forest recovery, inconsistency in land use histories, and dissimilarities in experimental design. We present the results of a replicated reforestation experiment comparing natural regeneration and polyculture tree planting at multiple diversity levels (3, 6, 9, or 12 native tree species), with uniform land use history and initial edaphic conditions. We compare the recovery of basal area and floristic diversity in these treatments after 5 yr of succession. Total basal area was higher in planted plots than in naturally regenerating plots, but it did not vary among the different planted diversity levels. The basal area of woody recruits did not differ among treatments. The diversity of woody recruits increased substantially over time but did not vary among planting treatments. Species composition trajectories showed directional turnover over time, with no consistent differences among treatments. The convergence of restoration trajectories and similarity of floristic community diversity and composition across all treatments, after only 5 yr, provides evidence of the viability of natural regeneration for rapid restoration of forest biodiversity.

Abstract in Spanish is available with online material.

*Key words:* basal area; forest restoration; natural regeneration; plantation; recovery of biodiversity; tropical wet forest.

ALTHOUGH GLOBAL FOREST COVER IS ESTIMATED AT JUST OVER 4 BILLION HECTARES, annual deforestation for the period 2000–2010 resulted in an estimated loss of 5.2 million hectares each year (FAO, 2011), with an estimated loss of \$4.3 to \$20.2 billion per year in associated ecosystem services (Costanza *et al.* 2014, Suding *et al.* 2015). Restoration of forest habitat through afforestation using timber plantations and natural regeneration has significantly reduced the net loss of forest area at national and global scales (FAO 2011). Many land managers and restoration practitioners faced with the opportunity of restoring degraded lands now understand the critical role that human-impacted forest habitats play in provision of ecosystem services and resources that support biodiversity (Chazdon 2008b, Chazdon *et al.* 2015). The global restoration movement is gaining momentum and over 60 million hectares has been committed to restoration by 20 countries (IUCN 2014, Chazdon *et al.* 2015). Successional forest habitats, including naturally regenerated secondary forests and managed tree plantations, have become the dominant forests in many tropical regions (FAO 2011).

Experimental work is needed in order to identify optimal strategies for restoring biodiversity and ecosystem services in deforested habitats. One of the most debated questions in restoration ecology is the extent to which community-level changes during succession may be predicted, influenced, and accelerated (Van der Putten *et al.* 2000). A long-standing dichotomy in the forestry and ecology literature has separated the evaluation of outcomes of forest regrowth in plantations managed for timber production from the evaluation of forests managed for the restoration of biodiversity and ecosystem services. Studies of biodiversity and ecosystem services in regenerating tropical landscapes have focused predominantly on unmanaged naturally regenerated secondary forests in comparison to nearby primary forest, (Guariguata & Ostertag 2001, Letcher & Chazdon 2009, Martin *et al.* 2013, Norden *et al.* 2015, Rozendaal & Chazdon 2015), while research in forest plantations has focused mainly on silviculture for optimal timber production (Montagnini 2000, Piotto 2008, Bonner *et al.* 2013, Campoe *et al.* 2014). Although some recent publications have addressed the importance of plantation forests as biodiversity reservoirs and providers of ecosystem services (Ruiz-Jaen & Potvin 2011, Thompson *et al.* 2014, Locatelli *et al.* 2015, Sukanuma & Durigan 2015), there is still a

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clear need for integrative, experimental studies that permit the direct comparison of plantation and naturally regenerating secondary forest systems using ecological and silvicultural measures of recovery.

Natural regeneration of secondary forest, also known as passive forest restoration, consists of letting forest grow back without active intervention by excluding grazing animals and eliminating other sources of chronic disturbance. Historically, naturally regenerating secondary forests have been considered by some to have low conservation value, but in recent years the importance of these forests in the tropical landscape has been highlighted (Chazdon 2008b, Jones & Schmitz 2009, FAO 2011, Lamb 2011). Depending on the starting conditions, natural regeneration can be an effective strategy for recovering biomass and species richness (Letcher & Chazdon 2009, Poorter *et al.* 2016), but it is most effective in minimally degraded landscapes (Chazdon 2008b). Limitations to natural regeneration include insufficient seed rain (Cubiña & Aide 2001, Martínez-Garza & Howe 2003, Muniz-Castro *et al.* 2006, Barnes & Chapman 2014), a depleted soil seed bank due to previous land use (Kalesnik *et al.* 2013), seed and seedling predation (Holl & Lulow 1997, Jones *et al.* 2003, Cole 2009), unsuitable microsites for seed establishment (Holl 1999, Holl & Aide 2011), and competition from established species (Duncan & Chapman 1999, but see Elgar *et al.* 2014, Bueno & Llambí 2015). Natural regeneration is often promoted in state-owned or private protected areas, or in regions where landowners have financial limitations that preclude active restoration (Parrotta *et al.* 1997, Holl & Aide 2011, Zahawi *et al.* 2015). However, natural regeneration is generally slower to accumulate biomass and species richness in comparison to active restoration (Bonner *et al.* 2013), and potentially unpredictable in terms of restoration trajectories (Lamb 2011).

Active restoration strategies such as tree planting seek to speed up forest recovery and can jump-start the establishment of a forest ecosystem on an abandoned pasture, as planting bypasses some of the ecological filters that prevent seedling establishment during natural regeneration (Holl & Aide 2011, De la Peña-Domene *et al.* 2013, Zahawi *et al.* 2013). Variation in ecological filters between passive and active regeneration strategies may also result in a difference in recruiting species composition. However, planting trees can be costly and labor-intensive compared to passive regeneration (van Kooten *et al.* 2004). If the established pasture grasses are aggressive competitors, several months to years of maintenance may be required before the trees begin to shade out the grasses (Hooper *et al.* 2005). Many of the forest plantations in the tropics are large-scale industrial monocultures, which provide few resources for wildlife (Gerber 2011) and are inherently unstable, from an ecological perspective. Monocultures are vulnerable to pests and pathogens, and their nutrient use efficiency and productivity are low compared to polycultures (Tilman *et al.* 2014). Mixed-species plantations, particularly of native species, may provide a way forward that combines the rapid biomass increase of plantations and some of the diversity of natural regeneration. Mixed-species plantations accumulate biomass faster and produce higher timber yields than monocultures, as a result of

facilitation and complementary resource use by diverse species with different functional traits (Lugo 1992, Erskine *et al.* 2006, Kely 2006, Thompson *et al.* 2009, Kanowski & Catterall 2010, Richards & Schmidt 2010). These polycultural plantations may also outperform naturally regenerating secondary forests, according to a meta-analysis showing that aboveground biomass is greater in tropical forest plantations up to 39 yr of age than in naturally regenerating forests up to 80 yr of age (Bonner *et al.* 2013). However, individual studies that control for site-specific differences in land use history have shown that long-term aboveground biomass gain in naturally regenerating secondary forests can sometimes be greater than in plantations (Jordan & Farnworth 1982, Han *et al.* 2010). Holl and Zahawi (2014) found that after 6–8 yr, planted trees contributed to higher total aboveground biomass in plantation plots, but the biomass of recruited saplings was comparable between natural regeneration and plantation treatments.

Experimental comparisons of recovery of biomass, diversity, or recruiting species composition between natural regeneration sites and plantations are scarce, and often pair plantation sites with naturally regenerating sites that may differ in prior land use and starting conditions (Tsai & Hamzah 1985, Nicolas *et al.* 2009). Indeed, in a recent meta-analysis of restoration methods (Shoo & Catterall 2013), more than half of the studies evaluated failed to include a natural regeneration (unplanted) control for comparative purposes with active strategies. In addition, most of the experiments on polyculture plantations have used relatively few species (2–4), limiting our ability to extrapolate to higher levels of planted diversity (Piotto 2008, Thompson *et al.* 2009).

We are presenting data from the first 5 yr of a long-term reforestation experiment. The overall objective of this experiment is to contribute key comparative data for evaluating the efficacy of active restoration versus natural regeneration, in light of the need for data-driven approaches to large-scale restoration planning. We compare active restoration and natural regeneration in a replicated set of plots that were identical in land use history, similar in initial edaphic conditions, and similar in distance to surrounding forest at the time of establishment. The planted plots have different levels of diversity, ranging from 3–12 native species per plot, allowing us to further examine how planted diversity within a polyculture affects forest recovery. We assess both ecological and silvicultural measures of recovery after 5 yr of succession. The specific objectives of this study were: (i) to compare natural regeneration and planted plots in terms of diversity of plant woody recruits and basal area, (ii) to evaluate the effect of planted diversity of native trees on basal area and diversity of naturally regenerating woody recruits, and (iii) to investigate whether the trajectory of species composition in naturally recruiting vegetation differs between planted and unplanted plots or among planted plots of different diversity levels. We test the following hypotheses: (i) the total basal area will be greater in planted treatments than in naturally regenerating control plots, as tree planting circumvents some of the ecological filters that slow biomass accumulation during natural regeneration (Holl & Aide 2011, Bonner *et al.* 2013, De la Peña-Domene *et al.* 2013), particularly

when the planted species are selected for their timber value (Butterfield & Mariano 1995); (ii) species richness and basal area of woody recruits will be higher in planted plots than in naturally regenerating plots, as the presence of planted saplings alters the microclimate, provides perches for dispersers, and ameliorates some of the establishment limitations for recruiting plants (Holl 1998, 1999, Zahawi *et al.* 2013); (iii) in the planted plots, basal area and species richness of woody recruits will be higher in plots with greater diversity of planted saplings, due to facilitation and/or complementary resource use (Ersikine *et al.* 2006, Kelty 2006, Potvin & Gotelli 2008, Richards & Schmidt 2010); and (iv) trajectories of species composition will differ between planted and naturally regenerating plots, due to differences in initial conditions that may affect community assembly (Chazdon 2008a). Testing these hypotheses in a robust experimental framework will provide vital data for planning reforestation strategies.

## METHODS

**STUDY SITE AND DESIGN.**—We established 35 long-term experimental plots in October–November of 2009 in abandoned cattle pastures at Finca Los Nacientes, Sarapiquí, Costa Rica, within the San Juan-La Selva Biological Corridor (10°21'30"4 N, 84°08'02" W, 280–300 m asl). Average annual rainfall (2009–2014) is *ca* 4667 mm with no distinct dry season; average annual temperature is 24.3°C. Heavy machinery cleared the forest as recently as 1980, and dairy cattle intensively grazed until 2009; no remnant trees are in the experimental plots. The dominant native pasture grass, *Homolepis aturensis*, was cut by machete prior to planting of saplings and in the initial 4 yr after planting, vegetation was cut back from saplings every 3–4 months. We selected 18 native tree species for planting (Appendix S1). The species selection was based on local availability; we incorporated species with a broad range of ecological strategies, including some timber species that have been overexploited in the region. Plots measure 18 × 18 m, with saplings planted every 3 m for a density of 36 saplings per plot. To control for effects of landscape configuration, all plots are within 120 m of approximately 15-yr-old secondary forest that provides propagules and habitat for dispersers. Plots were established in a replicated ( $N = 7$ ) randomized block design, and each block contains five plots with different levels of planted diversity (0, 3, 6, 9, or 12 mixed species). The 0 species plots are unplanted naturally regenerating controls. In the control plots, we used PVC tubes to mark the grid points where trees are planted in the other plots, facilitating navigation and maintenance and allowing us to locate subplots for vegetation sampling. In each planted plot, 33 percent of the planted saplings are N-fixers, following the approximate frequency of N-fixing trees at the nearby La Selva Biological Station (McDade 1994). Nitrogen-fixing trees also play an important role in forest succession in the Sarapiquí region (Menge & Chazdon 2016). The N-fixing individuals are spaced evenly across each plot in the same configuration to control for local-scale effects on soil nutrients. To separate the influence of planted diversity from that of species-specific characteristics, the species for each plot were randomly chosen from

the larger pool of 18 tree species, such that each replicate of the same planted diversity level contains a unique mix of species. The species for each plot were randomly selected from two pools, one consisting of N-fixing species, and the other consisting of non-N-fixing species. At planting, the saplings ranged from 10 to 40 cm in height. Saplings that died before January 2010 were replanted, but no replanting occurred after this time.

In November 2010, we removed soil cores from 5–15 cm depths at five random locations from the central 12 m<sup>2</sup> of each plot to assess initial edaphic conditions. Samples were air-dried, sieved (2 mm), ground, and sent to the University of California Davis, USA, for analysis of total N and C (combustion method; AOAC International 2005), Bray P (dilute acid-fluoride extractant; Diamond 1995, Olsen & Sommers 1982), nitrate, extractable ammonium (flow injection analyzer method; Knepel 2003), pH (Richards 1954), exchangeable cation content (K, Na, Ca, and Mg), and cation exchange capacity (using ammonium acetate and subsequent determination by atomic absorption/emission spectrometry; Thomas 1982) and organic matter (loss on ignition; Nelson & Sommers 1996).

We used these soil variables to conduct a PCA ordination to examine the initial similarity of soil conditions across planting treatments, except for Bray P, which was at or below the detection limit of 0.5 ppm in every plot. Soil organic matter was highly collinear with total C and was eliminated from the analysis. We used the permutation test *adonis* in Vegan (Oksanen *et al.* 2013) to test whether soil conditions differed significantly among planted diversity treatments.

The dbh (diameter at 1.3 m height) was measured periodically for all planted stems in order to assess the contribution of planted saplings to the recovery of basal area, beginning as soon as each stem had a measurable diameter at 1.3 m height. Therefore, basal area represents a conservative estimate of the total biomass in each plot because it excludes seedlings that have not yet reached 1.3 m in height. For individuals with multiple stems, the basal area of all stems was summed. Measurements were taken every 3–4 months during the first 2 yr of the experiment, twice annually from 2012 to 2014, and annually since then, with surveys conducted every January.

The diversity of naturally recruiting herbs, shrubs, and trees was assessed annually in May from 2011 to 2015, using three 2 × 15 m Gentry-style transects (Gentry & Dodson 1987) per plot, positioned in the interior of each plot to avoid edge effects. Height and species identity was recorded for all woody stems >80 cm in height, and diameter was measured for all individuals with a dbh ≥ 1 cm.

We used dbh measurements to calculate basal area of naturally recruiting stems at each census. We expressed basal area on a per-ha basis, extrapolating from the basal area per m<sup>2</sup> in the actual area sampled (324 m<sup>2</sup> per plot for the planted saplings and 90 m<sup>2</sup> per plot for woody recruits) to estimate the basal area per plot. Because the census dates for planted and recruited saplings were offset, we compared total basal area in the 35 plots by adding the estimated basal area from planted saplings in January 2015 and the estimate for recruited saplings from May 2015.

This result is most likely an underestimate of total basal area, as planted saplings continued to grow between January and May, but it provides a conservative benchmark for comparing basal area across plots. In the initial census (2011), no recruited stems had yet reached 1 cm dbh, so we present species richness data for recruits from 2011 onwards and basal area data from 2012 onwards. We used a one-way ANOVA and Tukey HSD *post-hoc* tests to compare basal area among diversity treatments.

The initial cover in all plots was 100 percent grasses. In January 2015, we sampled the percent cover of ferns, grasses, herbs, and litter/bare ground in 12 subplots of 1 m<sup>2</sup> in the interior of each plot to avoid edge effects. We used linear mixed effects models in the package lme4 (Bates *et al.* 2015) in R (R Core Team 2014) to examine the relationship between total (planted and naturally regenerating woody recruits) basal area and each of these percent cover classes, with planted diversity as a random factor.

In June 2012 and June 2014, we measured the light level in the plots using a red: far red sensor (Skye Instruments, Llan-drindod Wells, UK) and calculated the % transmittance from the ratio with the equation

$$\%T = 0.5458 + \exp(-2.4541 + 5.6594 R : FR)$$

where %*T* is the % diffuse transmittance and R:FR is the red: far red ratio (Capers & Chazdon 2004). We mounted the sensor on a tripod with a bubble level at 1 m height and took all readings on days with an evenly overcast sky, <3 h on either side of local noon.

In order to compare species richness of naturally regenerating woody recruits at an equivalent level of information across all plots, we used a combination of rarefaction (Gotelli & Colwell 2001) and extrapolation (Colwell *et al.* 2012, Chao *et al.* 2014) performed in EstimateS 9.1.0 (Colwell 2013). We compared the species richness of all plots using the number of species calculated for 40 individuals, as the mean number of naturally regenerating individuals per plot across all years was 41.4.

We examined the trajectories of species composition during succession by calculating the pairwise Jaccard similarity between each plot-yr combination in EstimateS 9.1.0 (Chao *et al.* 2005, Colwell 2013) and using the isoMDS function in the package MASS (Venables & Ripley 2013) in R (R Core Team 2014).

## RESULTS

The soils of this region are nutrient-poor oxisols of volcanic origin with extremely low P, low N, low exchangeable cations, and low cation exchange capacity (Table 1). Initial soil conditions did not differ significantly among planted diversity treatments (Fig. 1; *adonis* test,  $P = 0.53$ ).

In both planted and naturally regenerating plots, forest cover is returning. Between 2012 and 2014, the average percent of light transmittance in the 35 plots (mean  $\pm$  standard error) fell from  $20.2 \pm 1.6\%$  to  $12.0 \pm 1.4\%$ . The highest light levels in 2014 were found in control plots ( $22.0 \pm 4.3\%$ ), with lower light levels

TABLE 1. The average soil conditions for plots each of the planted diversity treatments in 2010. Soils of this region are oxisols of low fertility. Phosphorus levels in all plots were at (2 plots) or below (33 plots) the detection limit of 0.5 ppm.

	Planted species richness				
	0 (control)	3 spp.	6 spp.	9 spp.	12 spp.
Nitrates (ppm)	10.6	16.7	13.2	7.1	16.4
Exchangeable K (ppm)	48.3	58.3	57.1	46.0	50.1
Exchangeable Na (ppm)	12.0	11.3	12.1	12.4	11.6
Exchangeable Ca (ppm)	0.9	0.9	0.8	0.7	0.9
Exchangeable Mg (ppm)	0.6	0.6	0.5	0.7	0.6
Total % N	0.4	0.4	0.4	0.4	0.5
Total % C	4.5	4.4	4.1	4.1	4.6
CEC (meq/100 g)	1.7	1.7	1.5	1.5	1.7
pH	4.9	4.8	4.8	4.9	4.8

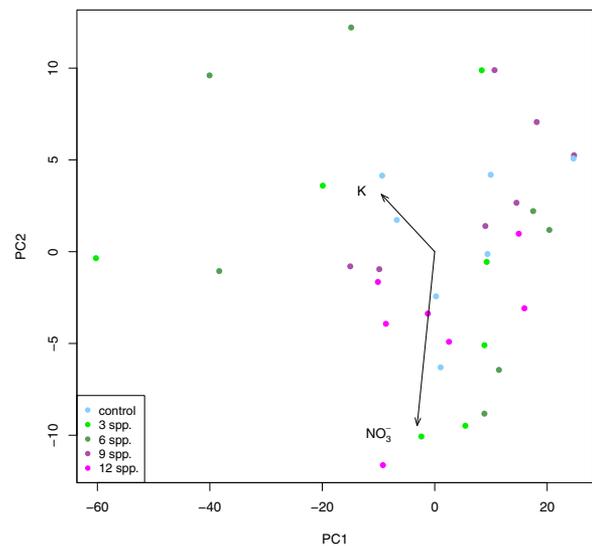


FIGURE 1. PCA of the covariance matrix among eight soil variables: nitrates, K, Na, Ca, and Mg (ppm), total %N, total %C, cation exchange capacity (meq/100 g), and pH. PCA axis 1 explained 89.5% of the variance and axis 2 explained an additional 8.9%. Nitrates and K had the largest axis loadings; loadings for the remaining soil variables were very small, so they are omitted for clarity. Initial edaphic conditions do not vary among planted diversity treatments (*adonis* permutation test,  $P = 0.53$ ).

in the planted plots (3 spp.:  $7.1 \pm 1.8\%$ ; 6 spp.:  $8.7 \pm 3.8\%$ ; 9 spp.:  $13.5 \pm 3.2\%$ ; 12 spp.:  $8.3 \pm 2.0\%$ ). Control plots had significantly higher light levels than all planted plots except the nine spp. plots, and there were no significant differences in light level among planted plots (one-way ANOVA,  $F_{4,6} = 3.64$ ,  $P = 0.015$ ; Tukey HSD *post-hoc* test).

Basal area has accumulated rapidly in most plots (Fig. 2). Forest succession proceeds very rapidly in this region (Letcher & Chazdon 2009), due to the relatively high year-round water availability (Poorter *et al.* 2016). The highest value of basal area for

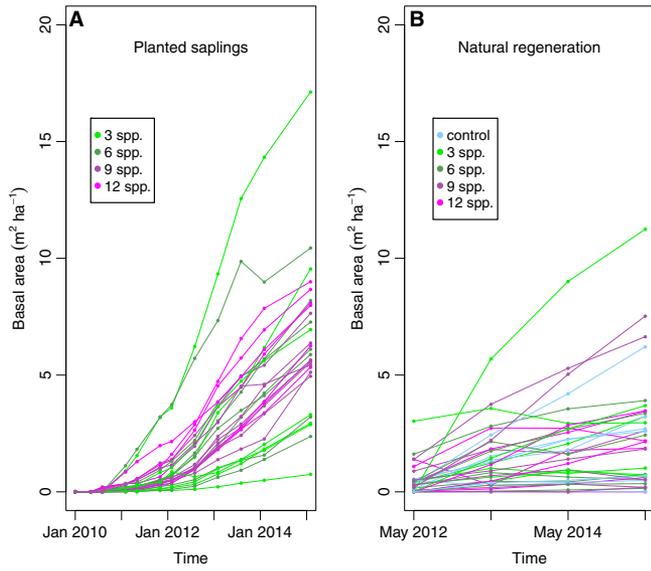


FIGURE 2. Basal area accumulation of (A) planted saplings and (B) naturally recruiting saplings over time in the 35 plots, color-coded by planted diversity level.

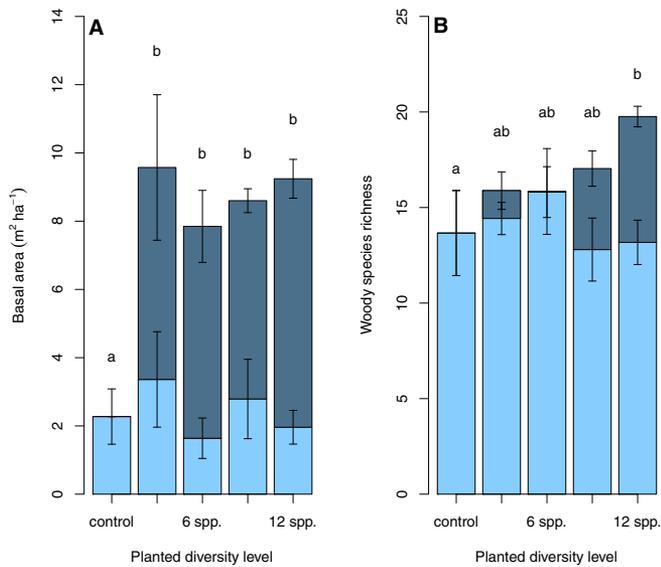


FIGURE 3. (A) Basal area and (B) species richness in the 2015 censuses compared by planted diversity level. The pale blue portion at the bottom of the bar shows the contribution from natural regeneration, and the dark blue part of the bar shows the additional contribution from the planted saplings. There were no significant differences in the basal area or species richness contributed by natural regeneration among any of the planted diversity levels. Letters above the bars in each panel show significant differences (one-way ANOVA and Tukey HSD) among diversity levels in the total basal area and total species richness; error bars show  $\pm 1$  SE.

planted saplings in the most recent census (January 2015) was 17.1 m<sup>2</sup>/ha, with a mean of 5.1 m<sup>2</sup>/ha. Naturally recruited saplings also contributed basal area to the ongoing regeneration,

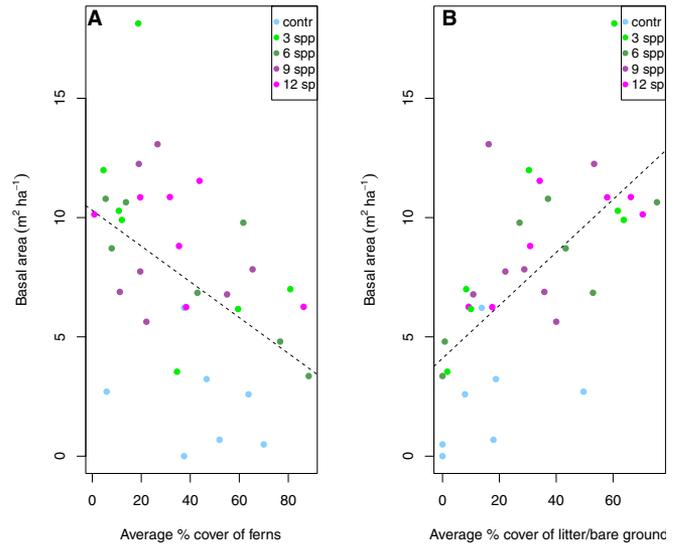


FIGURE 4. (A) Average fern cover and (B) average % cover of litter/bare ground (2014) versus total basal area (planted and naturally regenerating woody recruits, 2015) in the 35 plots, color-coded by planted diversity level.

though in almost every case the contribution of recruits to basal area was lower than that of planted saplings (Fig. 2). In the most recent census of naturally regenerating vegetation (May 2015), woody recruits contributed a mean basal area of 2.4 m<sup>2</sup>/ha, a maximum of 11.2 m<sup>2</sup>/ha, and a minimum of 0 m<sup>2</sup>/ha: in two of the 35 plots, there were no naturally regenerating saplings with a dbh >1 cm in the survey area during this census.

Using the combined basal area from the most recent censuses for planted trees and recruits (Fig. 3A), we found a significant difference among planted diversity levels (one-way ANOVA,  $F_{4,6} = 8.008$ ,  $P = 0.0003$ ). However, the significance was driven entirely by the difference between control and planted plots. Control plots had significantly lower basal area than all planted plots (Tukey HSD, all comparisons  $P < 0.003$ ), and there were no significant differences among planted diversity levels (Tukey HSD, all comparisons  $P > 0.77$ ). In some plots, particularly those planted with six species, the planted saplings do not contribute to measures of woody species richness because they have not reached the minimum height for inclusion in the survey.

There was a significant negative relationship between % fern cover and the total woody basal area (planted + recruiting saplings) (Fig. 4; linear mixed effects model,  $P = 0.0015$ ), and a significant positive relationship between the % cover of litter/bare ground and total basal area (linear mixed effects model,  $P < 0.0001$ ). The other two cover variables had no significant relationship with total basal area (grass cover:  $P = 0.59$ ; herb cover:  $P = 0.30$ ).

Species richness of woody recruits increased over time in nearly all the plots, with some local variation (Fig. 5). The average species richness of recruits across all plots increased from 7.4 species per 40 stems in 2011 to 14.3 species per 40 stems in 2015, a highly significant change (one-way ANOVA,

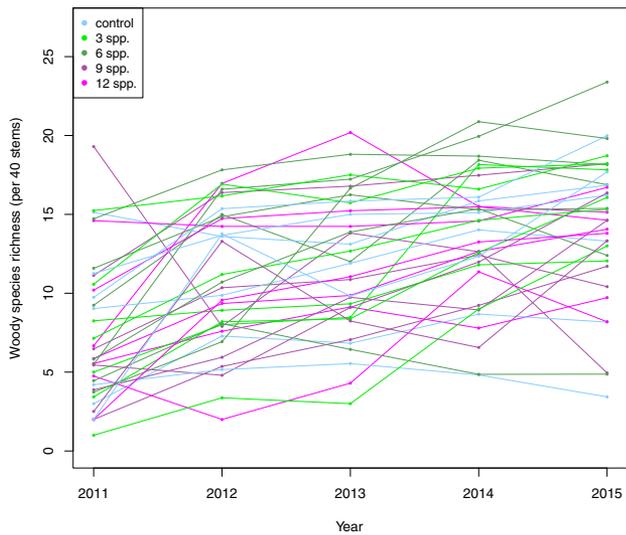


FIGURE 5. Species richness of naturally regenerating woody recruits  $\geq 80$  cm height in the 35 plots.

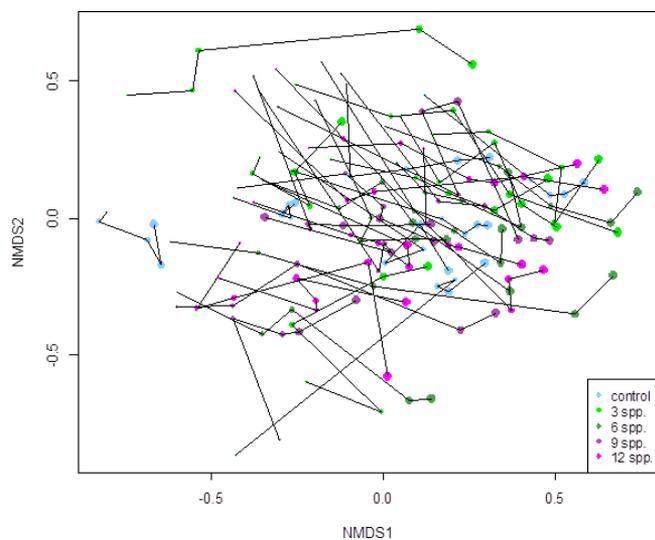


FIGURE 6. Species composition trajectories for the 35 plots, based on a non-metric multidimensional scaling plot of Chao–Jaccard estimated similarity among all plot-year combinations. Point color indicates the planted species richness of each plot; point size indicates the year, with the smallest points representing 2011 and point size increasing over time. Black lines connect the successive sample years for each plot. The 2D stress = 23.9. 6.

$F_{4,170} = 12.96$ ,  $P < 0.00001$ ). Comparing the 2015 species richness of all plots among planted diversity levels (Fig. 3B), we found no significant difference in the diversity of recruited woody vegetation among planting treatments (one-way ANOVA,  $F_{4,30} = 0.732$ ,  $P = 0.577$ ). The plots with higher planted diversity did show higher total species richness (one-way ANOVA,  $F_{4,30} = 3.368$ ,  $P = 0.023$ ), due to the diversity of planted saplings.

Species composition trajectories (Fig. 6) showed highly directional turnover across the 35 plots from 2011 to 2015. Species

composition shifted in the same direction along axis 1 in all of the 35 plots from 2011 to 2015, and 30 out of the 35 plots shifted in the same direction along axis 2 during that time period. There was no indication that the natural regeneration control plots are following a different trajectory from the planted plots, because the control plots fall into the same regions of ordination space as the planted plots. The choice of similarity index had little effect on the patterns of turnover displayed in the ordination plot (Appendix S2).

## DISCUSSION

Our study is the first to explicitly compare natural regeneration and planted forest plots in terms of diversity and composition of plant woody recruits and basal area while controlling for previous land use history and initial edaphic conditions. All the plots were situated on pastures previously used for dairy and beef production at the same intensity by a single landowner. The initial soil conditions show no systematic variation in soil nutrient content, pH, or cation exchange capacity across the study area (Table 1, Fig. 1). Our replicated design, paired with this control of initial conditions, provides a powerful experimental framework for comparing natural regeneration and reforestation and for examining the effect of planted diversity level on forest recovery.

As early succession progressed, total and naturally recruiting basal area increased as predicted (Tsai & Hamzah 1985, Brown & Lugo 1990, Silver *et al.* 2000, Cardinale *et al.* 2011). Total basal area was slower to recover in the first 5 yr in naturally regenerating control plots than in all of the planted plots (Figs 2 and 3), which is comparable to findings of other recent studies (Bonner *et al.* 2013, Holl & Zahawi 2014). Tree planting bypasses barriers to dispersal and establishment in early succession (Holl 1999), increasing overall biomass accumulation (and thus carbon capture) in young regenerating forests. Another factor contributing to the rapid basal area increase in active restoration plots was the use of species with rapid early growth rates used for timber production in this region (Butterfield & Mariano 1995), such as *Hieronyma alchorneoides*, *Terminalia amazona*, and *Vochysia guatemalensis*.

Our highest value of basal area for planted saplings from January 2015 was  $17.1 \text{ m}^2/\text{ha}$ . Data for mature tropical wet forests compiled by Leigh (1999) show average basal area values of  $30 \text{ m}^2/\text{ha}$  (although these data were recorded for stems  $\geq 10$  cm dbh, and not  $\geq 1$  cm as in this study). The rapid basal area increase that we observed, despite the relatively infertile soils of this region, highlights the regenerative capacity of tropical wet forests. A recent analysis of 45 Neotropical secondary forest study sites found that secondary forests in the lowland tropics reach 90 percent of old growth biomass in a median time of 66 yr (Poorter *et al.* 2016). Forests in Sarapiquí have particularly rapid biomass accumulation, reaching old growth levels in as little as 21–30 yr (Letcher & Chazdon 2009).

Although the planted plots had a higher total basal area after 5 yr, we found that the contribution of basal area derived from naturally recruiting woody stems is consistent across all control and planted treatments (Fig. 3A). This finding does not support

our second hypothesis that basal area of new recruits would be higher in planted plots than in natural regenerating plots. Greater recruiting biomass has been reported in plantations than in natural regeneration in other early successional investigations (Holl & Aide 2011, De la Peña-Domene *et al.* 2013, Zahawi *et al.* 2013). Elsewhere in Costa Rica, Holl and Zahawi (2014) also found that naturally recruiting stems contributed a consistent amount of aboveground woody biomass recovery across natural regeneration control plots and plantation treatments, but they found extremely high variability among sites. We demonstrated low levels of variation between treatment replicates, in contrast to Holl and Zahawi (2014), who attribute their large variations between blocks to the diversity of historical land use across their study site. In our site, the proximity of secondary forest for all plots may have reduced the importance of dispersal limitation, and the homogeneity of initial soil conditions and land use history appear to have resulted in similar biotic and abiotic filters across all the plots. Ongoing investigations of seed rain and seedling establishment may permit us to confirm the similarity of ecological filters among all plots.

We predicted that the plots with higher planted diversity would have higher basal area of recruits, due to complementary resource use (Ketyl 2006, Tilman *et al.* 2014). Resource partitioning among competing individuals of different species is widely cited as the driving force behind high productivity in diverse communities (Tilman & Lehman 2001, Tilman *et al.* 2002). In a meta-analysis of forest plantations, Thompson *et al.* (2009) found that forest ecosystems with higher species diversity are more productive than those with low species richness. Plantations with higher diversity show greater light capture efficiency, due to structural diversity, plasticity of crown shape, and temporal niche partitioning (Sapjanskas *et al.* 2014). More diverse plantations also show higher rates of transpiration, due to complementarity in water use (Kunert *et al.* 2012). Surprisingly, in early succession we did not find any effect of planted diversity level on basal area among the planted plots (Fig. 3A), which suggests that competition has not yet started to prevent woody species from recruiting. Our planted and recruiting species are still relatively small, and they may not be facing sufficient resource limitation to evoke the beneficial effect of complementary resource use. One of the other factors often implicated in the biodiversity-productivity relationship is the contribution of beneficial species such as nitrogen fixers (Binkley *et al.* 2003, Forrester *et al.* 2006, Cardinale *et al.* 2011, Tilman *et al.* 2014). The high survival rates of N-fixing trees make them important contributors to biomass accumulation during succession (Menge & Chazdon 2016). In our experimental design, we held the quantity and position of nitrogen fixers constant across all planted treatments, potentially controlling for facilitative effects. Variation in basal area among the planted plots in our experiment is likely due to species-specific differences in growth rates, which have been identified in many plantation productivity experiments (*e.g.*, Potvin & Gotelli 2008, Potvin *et al.* 2011, Salisbury & Potvin 2015), rather than facilitation or diversity *per se*.

Depending on the species composition of plantations and natural regeneration, basal area may be an inexact proxy for

carbon uptake and more variables should be considered, such as belowground biomass allocation and species-specific wood density estimates. Cuevas *et al.* (1991) reported that total carbon uptake between paired plantations and naturally regenerating forests was equal, because regenerating forests allocated a much higher percent of their carbon to belowground biomass as compared to plantations. Lugo (1992) also observed similar trends in paired plantations and naturally regenerating forests in Puerto Rico. Variation in wood density, particularly between fast growing, less dense, sun tolerant early pioneer species and denser, slow growing, shade tolerant timber species, influences biomass estimates (Chave *et al.* 2006, 2009). These studies highlight that common ecological and silvicultural measures of forest recovery may poorly estimate the actual recovery of biomass and carbon uptake in naturally regenerating forests. The land use history and species composition of recovering forests, whether planted or naturally regenerating, strongly impact biomass allocation and rates of recovery (Silver *et al.* 2000). In Costa Rica, most plantations employ a small group of exotic and native species that have been selected for stemwood production (Butterfield & Mariano 1995). In contrast, in natural regeneration, species arrive randomly, constrained by limitations of dispersal and establishment, and likely have more variation across species in allocation of biomass and wood density. These differences may explain differences in basal area recovery between plantation and naturally regenerating forests (Bonner *et al.* 2013). However, few studies have investigated belowground biomass allocation in secondary forests, and thus we have a limited ability to speculate on how the belowground biomass fraction contributes to carbon storage in these systems.

Recruiting species richness was surprisingly high and consistent across all treatments (Fig. 3B). Most previous studies comparing active and passive regeneration strategies across tropical forest sites show greater diversity in plantations than in natural regeneration (De la Peña-Domene *et al.* 2013, Holl and Zahawi, 2014, Shoo and Caterall, 2013). One comparison of a 3-yr-old plantation to naturally regenerated forest in Sarawak did find lower floral diversity in the plantation site, which was attributed to light limitations on establishment under the plantation canopy (Tsai & Hamzah 1985), although their comparison of diversity did not account for the different numbers of individuals in plantation and regeneration treatments (Gotelli & Colwell 2001). The lack of response of recruiting species richness to active strategies or increased planting diversity in our study is a novel finding for early successional forests. Lugo (1992) found equivalent species richness in the understory of plantations and natural regeneration sites in Puerto Rican montane forests after 50 yr of succession. The equivalent levels of recruiting woody species richness across all treatments after only 5 yr of forest succession suggest that community reassembly is proceeding rapidly, in both the active and passive restoration plots. This finding supports the value of natural regeneration strategies for rapid restoration of biodiversity, although this may be dependent on landscape context. In this study, our novel species richness results may be influenced by the proximity of our experimental plots to forests which serve as

seed sources and the relatively low level of soil degradation from previous land use.

One of the noteworthy transitions we witnessed during this period of early forest development was the gradual shift from the dominance of pasture grasses in some of our plots to the dominance of shade-intolerant ferns such as *Hypolepis repens* (Dennstaedtiaceae). This species is known to colonize abandoned pastures in this region (Montgomery 2004), and competes vigorously with tree seedlings and saplings, forming a dense layer of fronds up to 2 m in height. *Nephrolepis* spp. (Lomariopsidaceae), another fern taxon that has been reported to compete with tree seedlings for establishment in open areas (Denslow *et al.* 2006), have also increased rapidly in some plots. Shifts in grass and herb cover showed no relationship with basal area of recruiting woody species in our dataset, but we found a negative relationship between fern cover and woody basal area (Fig. 4). Under these circumstances it is possible that clearing of aggressive ferns in areas of natural regeneration to make way for new recruits would provide a cost-effective management technique compared to planting tree saplings.

As a closed canopy has begun to develop and light transmittance has declined, the abundance of several species of shade-intolerant weedy shrubs commonly found in cattle pasture such as *Solanum jamaicense* (Solanaceae) and *Lantana camara* (Verbenaceae; both native to the region) has dropped precipitously. Woody species more tolerant of intermediate light levels, such as *Warszewiczia coccinea* (Rubiaceae), *Vitex cooperi* (Lamiaceae), and *Vochysia ferruginea* (Vochysiaceae), have begun to recruit in the plots. Floristic turnover is projected to continue as the canopy structure develops. Diffuse transmittance levels of light on the forest floor of old growth forests in the Sarapiquí region are low, with a mean of 1.8 percent and a range of 0.45–14.93 percent (Montgomery & Chazdon 2001). The light level in our plots has declined with canopy closure, but it is still considerably higher than in intact forest. Canopy development is associated with an increase in bare soil and leaf litter and decreased herbaceous ground cover in our study. Shade-tolerant species commonly associated with primary forest and mature secondary forest have not yet become common in any plots. We did find lower light levels in planted plots than in natural regeneration control plots, suggesting that active planting can promote faster canopy formation. However, we did not find a difference in the species composition trajectories of naturally regenerating and planted plots (Fig. 6).

As succession progresses, shifts in edaphic conditions have been documented in other studies, with faster recovery of soil carbon and nitrogen pools in actively restored native species plantation plots than in natural regeneration after 3 yr of establishment (Roa-Fuentes *et al.* 2015). The accelerated recovery of carbon and nitrogen pools as well as soil nutrients under planted canopy as compared to natural regeneration controls can be attributed to increased leaf fall as the canopy matures (Celentano *et al.* 2011). Future examinations of soil carbon and nitrogen in our plots will reveal the extent to which ecosystem function has recovered with tree basal area.

In contrast to our predictions that the composition of planted plots would diverge from that of naturally regenerating plots, floristic composition and community recovery trajectories were consistent across our treatments (Fig. 5), and showed no variation between active and passive restoration strategies. Floristic composition in the first year of data collection (2011) can be identified on the left of the NDMS figure with a low score on axis 1, and as succession progresses and species richness increases, it is possible to see a directionality to these data whereby points from our most recent census (2015) are positioned on the right side of the plot with a higher score on axis 1, and all plots are following a similar directional trend indicating consistent successional trajectories. The general overlap of trajectories and the absence of specific clusters by planted diversity treatment supports the conclusion that species composition is unaffected by planted diversity level. The similar community recovery trajectories of planted and natural regeneration plots (Fig. 5) suggest that seed rain and seedling establishment limitations do not vary strongly among these treatments, once again supporting the conclusion that natural regeneration and active restoration can generate similar outcomes when controlling for the initial edaphic conditions and land use history.

## CONCLUSION

This study fills a key information gap by demonstrating for the first time that floristic diversity and composition of regenerating plant species in naturally regenerated habitat can be comparable to recruitment in plantations, when controlling for soil fertility and initial conditions. Although planted treatments resulted in higher total basal area, we found that recruiting woody plants showed no difference in basal area, species richness, and species composition between passive and active restoration treatments. This suggests that the facilitative effects of active planting may be minimal during the first 5 yr of succession. This finding challenges the widely held view that natural regeneration is of lower conservation value when compared with plantation forests. We highlight the value of natural regeneration for the restoration of biodiversity in early succession. We emphasize, however, that these results are presented for the first 5 yr of secondary succession and call for longer term studies of recovery of diversity and biomass to permit comparisons of active and passive restoration strategies in order to identify optimal planting strategies for future forest restoration projects.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Eighteen species of native trees utilized in experimental design.

APPENDIX S2 Comparison of species composition trajectories using different similarity indices.

FIGURE S1. Jaccard index.

FIGURE S2. Sorenson index.

FIGURE S3 Chao–Jaccard estimated abundance-based index.

FIGURE S4. Chao–Sorenson raw index.

FIGURE S5. Chao–Sorenson estimated index.

FIGURE S6. Morisita–Horn.

FIGURE S7. Bray–Curtis.

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