Research Article

Composition and Diversity of Woody Plants in Tree Plantations Versus Secondary Forests in Costa Rican Lowlands

J. Benjamin Longworth[1] and G. Bruce Williamson[1,2]

Abstract

Efforts to sequester carbon through tree plantations and natural regeneration in the tropics may also provide an opportunity to restore native forest ecosystems. However, the degree to which species composition of native species differs between tree plantations and secondary forests is unknown. In this study, we conducted surveys of woody plants (≥ 2 cm dbh) in 20 secondary forest and tree plantation plots (30×30 m) in a tropical lowland forest landscape. Sites were 8 to 21 years old and were either abandoned cattle pastures (secondary forests) or monoculture tree plantations (*Hieronyma alchorneoides* and *Vochysia guatemalensis*) planted for carbon sequestration. We compared species composition, ecological traits, and diversity of woody plants in secondary forests and tree plantations, while accounting for distance from primary forest. Species composition, but not species richness, of the natural regeneration was significantly different in tree plantations and secondary forests. The abundances of understory species, short-lived pioneers, and bat-dispersed species were all higher in secondary forests than in tree plantations. Abundances of canopy species, long-lived pioneers, shade-tolerant species, and dispersal categories besides bats were not associated with forest type. We conclude that tree plantations can alter species composition of regeneration compared with secondary forests perhaps by altering composition of seed disperser assemblages or inhibiting early successional species.

Keywords

dispersal, fragmentation, landscape, regeneration guild, restoration, tropical forest

Introduction

As tree plantations and secondary forests are increasingly used for carbon sequestration in the tropics, their potential for conserving biodiversity should be examined. Planted forests already comprise 3.3% of all tropical forested area (Keenan et al., 2015) and secondary forests cover approximately 11.8% of tropical land area (Wright, 2010). Both types of forest continue to expand due to several economic and social drivers, including for carbon sequestration (Bonner, Schmidt, & Shoo, 2013; Chazdon et al., 2016). For example, the Costa Rican government, as part of a UN program (REDD+) for mitigating carbon emissions, has proposed reforestation of 124,000 ha with natural regeneration and 72,000 ha with tree plantations—a total which is equivalent to a 7.3% increase in forest cover area (Government of Costa Rica, 2013). These types of projects provide an opportunity to restore native forest ecosystems in addition to carbon

sequestration (Alexander et al., 2011). Governments, land managers, and restoration practitioners need information on the relative biodiversity value of tree plantations and secondary forests to guide these efforts.

Studies that compare biodiversity of tree plantations to secondary forests at the same sites are scarce (Meli et al., 2017); however, recovery rates of plant diversity

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and composition in tropical secondary forests are generally understood (Chazdon et al., 2007). Under ideal conditions, abundance and species diversity in secondary forests reach levels similar to mature forest within a few decades of succession (Brown & Lugo, 1990; Chazdon et al., 2009; Poorter et al., 2016; Saldarriaga, West, Tharp, & Uhl, 1988). Species composition takes longer to recover because pioneer tree species (short- or long-lived) often remain dominant for several decades after establishment (Finegan, 1996; Guariguata & Ostertag, 2001). Shade-tolerant tree species characteristic of mature forest do not dominate the canopy for many decades (Norden, Chazdon, Chao, Jiang, & Vílchez-Alvarado, 2009; Peña-Claros, 2003). However, intense past land-use (Jakovac, Peña-Claros, Kuyper, & Bongers, 2015; Laliberté et al., 2010; Mesquita, Ickes, Ganade, & Williamson, 2001) and lack of forest in the surrounding landscape (Crouzeilles et al., 2016; Goosem et al., 2016; Holl, 1999) can greatly reduce recovery rate of diversity and species composition.

Ability of tree plantations grown for carbon sequestration to support native plant species depends on management practices. Diversity of native flora found in tree plantations is generally larger than in other agricultural uses, but lower than in primary forests (Bremer & Farley, 2010; Felton, Knight, Wood, Zammit, & Lindenmayer, 2010), and depends on intensity of plantation use (Newbold et al., 2015). Industrial tree plantations with exotic species, short-rotation periods, and frequent understory clearing sustain a low diversity of native plants, as diversity tends to be larger in native than exotic plantations (Bremer & Farley, 2010; Proença, Pereira, Guilherme, & Vicente, 2010) and tends to increase as plantations age (Brockerhoff, Ecroyd, Leckie, & Kimberley, 2003). However, tree plantations used for forest restoration, in which natural regeneration is allowed, can support a high diversity of forest species (Lugo, 1992; Powers, Haggar, & Fisher, 1997). In Costa Rica, it has been reported that between 15% and 38% of tree plantations are planted only for restoration purposes (Piotto, Montagnini, Ugalde, & Kanninen, 2003; Redondo-Brenes, 2007). Restoration plantations can even be used to catalyze recovery of plant abundance and diversity on land where succession has been impeded by intense previous land-use or lack of seed sources (Butler, Montagnini, & Arroyo, 2008; Parrotta, 1995).

Most direct comparisons of plant communities in tree plantations and secondary forests have studied purely restoration plantations at sites less than 10 years old and have focused on abundance and diversity (Bone, Lawrence, & Magombo, 1997; Guariguata, Rheingans, & Montagnini, 1995; Parrotta, 1995; Powers et al., 1997; Zahawi, Holl, Cole, & Reid, 2013), although recent studies have also evaluated species composition (Gilman et al., 2016; Holl, Reid, Chaves-Fallas, Oviedo-Brenes, & Zahawi, 2017). It is unknown if tree plantations support different plant assemblages than secondary forests. Rapid development of a dense canopy in tree plantations compared with secondary forests may alter types and abundances of seed dispersers (Zamora & Montagnini, 2007), light availability, and microclimate (Bizuti et al., 2016; Holl, 1999) relative to open pastures in which secondary growth typically originates. Tree plantations may lead to alternative successional pathways or more rapid succession than secondary forests.

We conducted censuses of 20 secondary forest and tree plantation plots in a tropical forest landscape to compare composition and diversity of woody plants. These forests were 8 to 21 years old and shared a similar land-use history (cattle pastures >30 years). Tree plantations were grown for carbon sequestration, were of two different native species (*Hieronyma alchorneoides* [Phyllanthaceae] and *Vochysia guatemalensis* [Vochysiaceae]), and had management practices intermediate between typical timber production and pure restoration. Species found naturally regenerating were categorized by dispersal mode, growth form, and regeneration guild. Distance from primary forest was measured to account for landscape effects on regeneration. Since tree plantations can catalyze succession following intense land-use and in fragmented landscapes (conditions found in this study), we made the following predictions: (a) tree plantations would have fewer early successional species, like short-lived pioneers and wind-dispersed plants, than secondary forest; (b) tree plantations would have more late-successional species, like shade-tolerant species and mammal-dispersed plants, than secondary forest; (c) species richness would be greater in tree plantations than in secondary forests; (d) distance from primary forest would have a greater effect on composition and diversity of secondary forests than tree plantations.

Methods

Study Area

This study was carried out at Universidad Earth, Pocora, Limón Province in north-east Costa Rica (10°13′9″N, 83°35′29″W, 30–100 m asl). The natural vegetation is categorized as tropical moist forest (Holdridge, Grenke, Hatheway, Liang, & Tosi, 1975). Average annual temperature and precipitation are 26°C and 3,500 mm, respectively. Underlying geology of the area is composed of quaternary sedimentary and volcanic rocks (Castillo-Muñoz, 1983) with poorly drained alluvial soils on flat relief (Vásquez-Morera, 1983).

University land contains a 605-ha forest reserve of selectively logged primary forest, tree plantations (400 ha), secondary forest, and various agricultural uses, most predominantly pastures and banana plantations (Figure 1). Study sites were on land used as cattle pasture
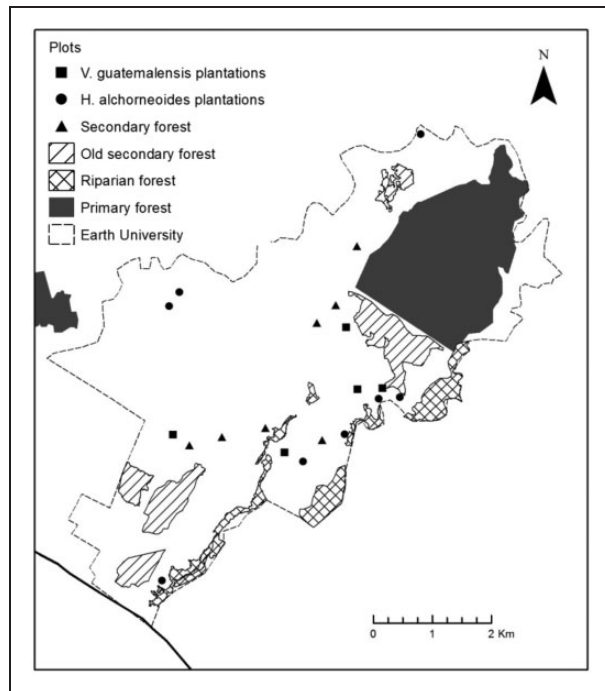
Figure 1. Map of plots at Universidad Earth in Pocora, Limón in the Caribbean lowlands of Costa Rica. The dotted line represents boundaries of the university campus. The forested areas marked inside and outside of the university campus are surrounded by banana plantations, pastures, tree plantations, and young secondary forest (<20 years). Each symbol represents a 30 × 30 m forest plot.

for at least 30 years and much longer in some areas. When cattle-grazing operations ceased in 1993, some portions of these pastures were abandoned and grew into secondary forest, whereas others were converted to tree plantations for carbon sequestration and timber production. Site histories were determined from aerial photos (1960, 1971, 1992, 1998, and 2002) and interviews with employees of the university.

Study Plots

Twenty 30 × 30 m plots were established and sampled between May 2013 and October 2014 in tree plantations and secondary forest sites (Figure 1). *Vochysia guatemalensis* and *Hieronyma alchorneoides* plantations were chosen for this study because they are native species commonly planted in the region in small- to medium-scale plantations for timber production and restoration (Piotto et al., 2003; Zahawi et al., 2013). Eight plots were established in *H. alchorneoides* plantations, five in *V. guatemalensis* plantations, and seven in secondary forests. Tree plantations were selected if they were monocultures planted for carbon fixation and were undisturbed since 5 years after planting. We selected secondary forest plots across the landscape that matched the age range and distribution of selected tree plantations. Plots were placed

centrally within each site to avoid edge effects (>10 m from edges).

Secondary forests ranged in age from 11.5 to 21 years and ranged in size between 5.0 and 20.5 ha. Selected plantations ranged in age from 8 to 15.5 years and ranged in size from 0.54 to 4.8 ha. Since secondary forest sites were 4 years older on average than the tree plantations, we sampled half of the tree plantation plots again in June 2016, 3 years after the initial census in 2013. We observed statistically significant changes in stem density, basal area, and some compositional variables, but not in diversity. However, none of the results in this study changed when using data from the second census instead of the first for tree plantations. Therefore, in the subsequent analysis, only data from the initial census were used, to maximize sample size.

The purpose of these plantations was primarily carbon fixation and they were managed using practices intermediate between typical timber plantations and pure restoration plantings. Timber plantations in the region are typically monocultures, thinned twice in the first 10 years to approximately 30% of the original density, and cleared of natural regeneration annually. Restoration plantings, on the other hand, are typically mixed species and lack any thinning or clearing. In general, the tree plantations in our study were of a single species, either *V. guatemalensis* or *H. alchorneoides*, with occasional other species interspersed (83% to 100% of one species). Plantations in our study typically were planted with 3 × 3 m spacing. Only one thinning of planted individuals occurred between 3 and 5 years, although not all sites were thinned. As a result, planted tree density at the time of this study ranged between 200 and 755 trees/ha^{-1}. Understory regeneration was cleared with machetes in tree plantations only for 5 years following planting. After 5 years, natural regeneration in these plantations was not disturbed.

Data Collection

In each plot, all woody stems >2 cm dbh (diameter at breast height) were measured and identified to species between May 2013 and October 2014 with help from an experienced field assistant who identified species in the field as well as from vouchers. When identification to species was not possible, genus or morphotype was used. Lianas and palms were rare and not included when they occurred. Species abundances in each plot are shown in Table S1.

Species were classified according to demographic and morphological criteria. According to maximum adult height, species were classified into two growth forms: understory species (<15 m) and canopy species (>15 m). Each species was also classified by regeneration guild (short-lived pioneer, long-lived pioneer, or shade-tolerant)

and by dispersal agent (wind, ballistic, bat, bat and bird, bird, bird and mammal [non-bat], or mammal [non-bat]). Information on maximum adult height and dispersal agent were obtained from the Digital Flora database at La Selva Biological Station (Castro, 2013). Regeneration guilds for Costa Rican tree species have been subjectively assigned based on observations by experienced forest ecologists and made available by the national forest resources agency (Sistema de Información de Recursos Forestales, 2010). These classifications match those used by other ecologists (Finegan & Delgado, 2000). Species classifications are shown in Table S2.

Distance from the edge of each plot to primary forest, secondary forest, tree plantations, and riparian forest was measured using plot coordinates and hand-digitized forest areas from 2011 satellite imagery, and subsequently ground truthed. We included forested areas outside University lands when taking these measurements. Distances to other forest types besides primary forest were not used in the analysis because they did not add explanatory power beyond the effect of distance from primary forest. However, distance from primary forest was understood to integrate the effects of other forest types, since amount of general forest cover tended to be lower in areas farther from primary forest.

Two environmental factors were measured to determine if there was any systematic bias in the type of site selected by land managers for tree plantations or secondary forests. First, percent slope of each plot was measured along the steepest edge of the plot using a clinometer. Second, soil texture was measured by using a basic sedimentation technique. Nine topsoil samples (0–20 cm) were collected at evenly spaced points in each plot. Samples were mixed together for each site, air dried, sieved, placed in 0.5 L uniform jars with 15 g of detergent and 300 mL of distilled water, and shaken for 10 min to disperse soil aggregates. Following shaking, height of sedimentation in the jar (2 subsamples per site) was observed at uniform intervals as relative measures of the amount of sand, silt, and clay, respectively. This measurement is understood to be only a rough estimate of soil particle size distribution.

We characterized vegetation structure of each plot with several metrics. Stem density and basal area were calculated for both all individuals and only natural regeneration (planted individuals excluded). Canopy height was measured at six evenly spaced points within each plot and averaged. Canopy openness was measured as the percentage of light passing through the canopy. Light (photosynthetic photon flux density, $\mu mol\, m^{-2}\, s^{-1}$) was measured at a height of 4 m using a light meter composed of 10 separate quantum sensors spaced over a 50-cm line (MQ-301, Apogee, Logan, UT), and simultaneously in a nearby clearing. Canopy openness in each plot was then calculated as percent of the reference light measurement, averaged across the nine points.

Data Analysis

Planted trees were excluded from all diversity and composition analyses. To examine species composition of natural regeneration, a nonmetric multidimensional scaling ordination was performed with an abundance-based Bray-Curtis similarity index. Abundance data were ln $(x+1)$ transformed to reduce influence of the most abundant species. "MetaMDS" function in the R package "vegan" was used for ordination with automatic transformation disabled (Oksanen et al., 2015). Species scores were produced as weighted averages of the sites. We used the permutation test *adonis* within vegan to test for significant effects of forest type, distance to primary forest, and their interaction on species composition. Since this permutation test confounds dispersion effects with location effects, we also tested for homogeneity of dispersion across forest types with the *betadisper* test in "vegan."

Multiple regression with model selection was used to evaluate the effects of forest type and distance from primary forest on 12 dependent variables describing natural regeneration. Each of the dependent variables described later was regressed against forest type (*H. alchorneoides* plantation, *V. guatemalensis* plantation or secondary forest), distance to primary forest, and the interaction between the two variables. Dummy variables were used to represent forest type in the multiple regression. All possible models were considered and the best was selected based on the AICc criteria, a small sample-corrected version of AIC (Burnham & Anderson, 2002). Model selection was performed using the R package "MuMIn" version 1.15.6 (Barton, 2016).

The 12 dependent variables were rarefied species richness and abundances of 11 ecological categories. Rarefied species richness for each plot was the number of species at 70 individuals (lowest number found in any plot) estimated using rarefaction. This measure of species richness is independent of sample size. Abundances of different ecological categories for each plot were also calculated: understory species, canopy species, short-lived pioneers, long-lived pioneers, shade-tolerant, and the seven dispersal categories. Ballistic dispersal was not analyzed further as it was infrequently found at our sites.

Influential observations, variance inflation, homogeneity of variance, and normality of the residuals were examined for full and reduced models. Abundances of bat-dispersed and mammal-dispersed species were ln $(y+1)$ transformed to meet statistical assumptions. Although there was spatial autocorrelation in some of the dependent variables, we found no autocorrelation in the residuals of any models using a Moran's I test, a result validating independence of observations in the

regression (Diniz-Filho, Bini, & Hawkins, 2003). If only forest type was found to have an effect on a dependent variable, a post hoc Tukey honest significant difference test was used to test all pairwise comparisons. Finally, analysis of variance (ANOVA) and post hoc Tukey honest significant difference were used to test for differences in environmental and structural variables between forest types.

Results

Forest Structure and Soil Properties

Tree plantations differed significantly from secondary forests in stem density, basal area, and canopy openness (ANOVA, $p < .04$; Table 1), but not canopy height ($p = .14$). Our measurements of stem density and basal area in tree plantations included both planted and naturally regenerating trees. Generally, tree plantations had a lower stem density, higher basal area, and lower canopy openness than secondary forests. In *Vochysia guatemalensis* plantations, planted trees made up 92.9% of basal area and 21.0% of stems. Similarly, in *Hieronyma*

alchorneoides plantations, planted trees made up 91.7% of basal area and 24% of stems. Forest types exhibited no significant differences in % soil clay, % soil sand, or plot slope (ANOVA, $p > .08$; Table 2).

Species Composition

Of 3,889 individuals sampled, 99.4% were identified to species. Of 97 different species found, 92 were identified to species, 1 to genus, and 4 species to morphotype. Species composition of naturally regenerating woody plants was significantly affected by forest type (*adonis* test, $p = .02$) and distance from primary forest ($p = .002$). The interaction between the effect of forest type and distance on composition was not significant ($p = .37$). Tree plantations were separated from secondary forest plots along Axis 2 of the ordination, whereas plots near to primary forest were separated from those far from primary forest along Axis 1 (Figure 2). Three tree plantations, located far (>3 km) from primary forest, did not follow these trends and fell in with secondary forests in the ordination. The two forest types showed similar levels of multivariate dispersion (*betadisper*, $p = .94$).

Table 1. Means (SD) and ANOVAs of Forest Structure Variables by Forest Type: *Vochysia guatemalensis* Plantations (VG), *Hieronyma alchorneoides* Plantations (HA), and Secondary Forests (SF).

	HA	VG	SF	$F(2, 17)$	p
N	8	5	7		
Stem density (stems/plot)	171.8 (47.5) a	161.0 (29.5) a	244.3 (50.9) b	7.0	.006*
Stem density (excluding planted)	130.6 (50.6) a	127.2 (30.8) a	244.3 (50.9) b	13.7	<.001*
Basal area (m²/ha)	18.5 (5.4) ab	25.5 (3.5) a	12.2 (6.4) b	8.9	.002*
Basal area (excluding planted)	1.53 (1.07) a	1.80 (1.37) a	12.2 (6.4) b	16.4	<.001*
Canopy height (m)	24.6 (4.5)	23.5 (1.3)	20.4 (3.3)	2.3	.14
Canopy openness (%)	15.0 (5.0) ab	13.3 (4.9) a	21.3 (5.3) b	4.2	.035*

Note. ANOVAs = analyses of variance; HSD = honest significant difference. Letters indicate results of Tukey's HSD tests.
*ANOVA $p < .05$.

Table 2. Means (SD) and ANOVAs of Site Characteristics by Forest Type: *Vochysia guatemalensis* Plantations (VG), *Hieronyma alchorneoides* Plantations (HA), and Secondary Forests (SF).

	HA	VG	SF	$F(2, 17)$	p
N	8	5	7		
Distance to primary forest (km)	2.5 (1.6)	1.9 (1.4)	1.9 (1.4)	0.36	.70
Age	12.0 (2.7) a	12.4 (2.9) ab	16.6 (4.2) b	4.1	.03*
% sand	46.6 (18.3)	50.4 (11.7)	56.1 (18.5)	0.52	.61
% clay	15.0 (5.7)	12.1 (3.4)	9.4 (2.7)	3.0	.08
% slope	1.5 (1.1)	2.7 (2.6)	1.1 (1.0)	1.5	.25

Note. ANOVAs = analyses of variance; HSD = honest significant difference. Letters indicate results of Tukey's HSD tests.
*ANOVA $p < .05$.
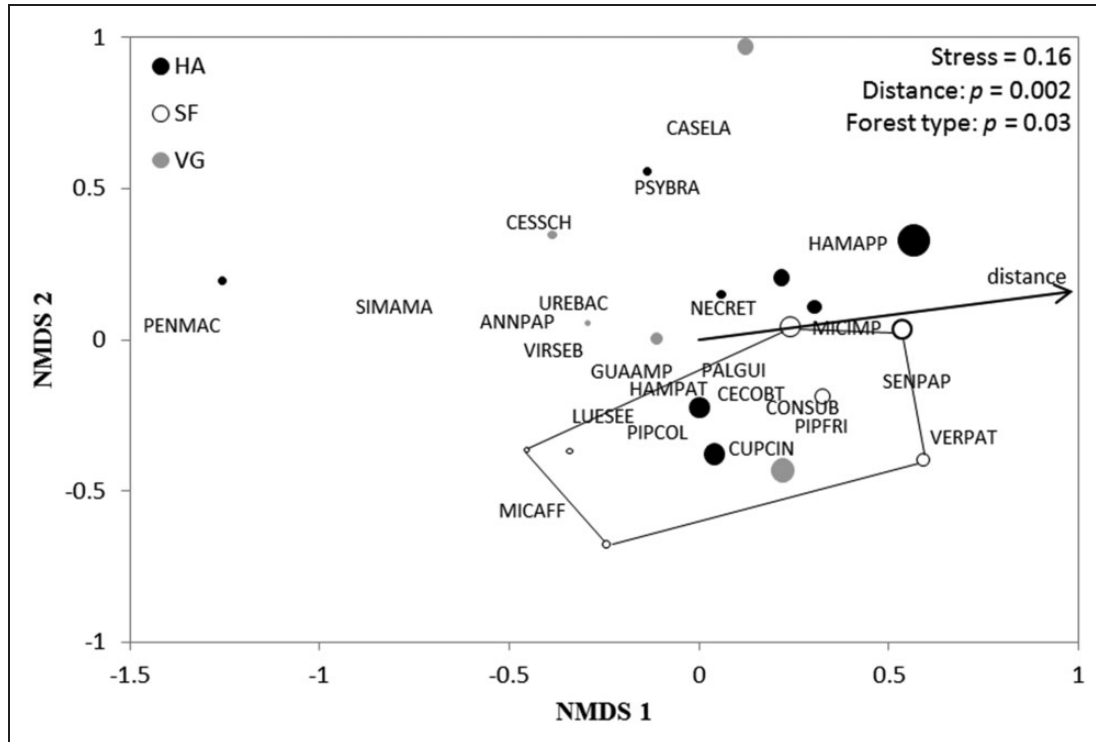
Figure 2. NMDS ordination plot of naturally regenerating woody plants in *V. guatemalensis* plantations (VG), *H. alchorneoides* plantations (HA), and secondary forests (SF). Each circle represents a different forest plot and circle size is scaled to distance from primary forest (larger means farther from PF). The distance from primary forest vector is shown by the arrow. Species with ≥ 24 individuals are shown. For full species names, see Table S2. Polygon connects secondary forest plots for clarity.

Axis 2 represents a shift from understory species dispersed by small birds or bats (e.g., *Cecropia obtusifolia*, various Melastomataceae, *Piper* spp.) in secondary forests to canopy species dispersed by larger birds or non-bat mammals in tree plantations (e.g., *Castilla elastica*, *Nectandra reticulata*, *Simarouba amara*). Axis 1 represents a shift from long-lived pioneers and shade-tolerant species near primary forest (e.g., *Annona papilionella*, *Guatteria amplifolia*, *Virola sebifera*) to short-lived pioneers far from primary forest (e.g., *Hampea appendiculata*).

Growth Forms

Plants identified to species level included 51 canopy species (adult height > 15 m; 36.0% of individuals) and 41 understory species (63.8% of individuals). Forest type but not distance from primary forest was included as an explanatory variable in the best model for abundance of understory species (Table S3). Abundance of understory species was significantly higher in secondary forests (161.7 ± 30.9 stems / plot) than in *H. alchorneoides* plantations (69.3 ± 27.4) and *V. guatemalensis* plantations (87.2 ± 31.1), $F(2, 17) = 1.0$, $p = .0009$ (Figure 3 and Table S4). Abundance of canopy species was not affected by forest type or distance from primary forest (Table S3).

Average canopy species abundance was 74.0 ± 16.7 stems/plot in secondary forests, 54.4 ± 29.6 in *V. guatemalensis* plantations, and 60.8 ± 20.2 in *H. alchorneoides* plantations.

Regeneration Guilds

Twenty-five species of those identified were short-lived pioneers (68.9% of individuals), 51 were long-lived pioneers (24.7% of individuals), and eight were shade tolerant (3.9% of individuals). The best model for abundance of short-lived pioneers was forest type only, $F(2, 17) = 8.3$, $p = .003$. Significantly more short-lived pioneers were found in secondary forests (173.9 ± 44.4) than in *H. alchorneoides* plantations (83.3 ± 31.6) and *V. guatemalensis* plantations (80.4 ± 24.8; Figure 3). This difference is driven by understory species because forest type did not have an effect on abundance of short-lived canopy pioneers, $F(2, 17) = 1.2$, $p = .32$.

Distance from primary forest but not forest type was included in both best models for abundance of long-lived pioneers and shade-tolerant species (Table S3). Abundance of long-lived pioneers decreased significantly as distance to primary forest increased (−9.7 stems/km), $F(1, 18) = 12.2$, $p = .003$ (Figure 4). Abundance of shade-tolerant species also decreased significantly as distance to
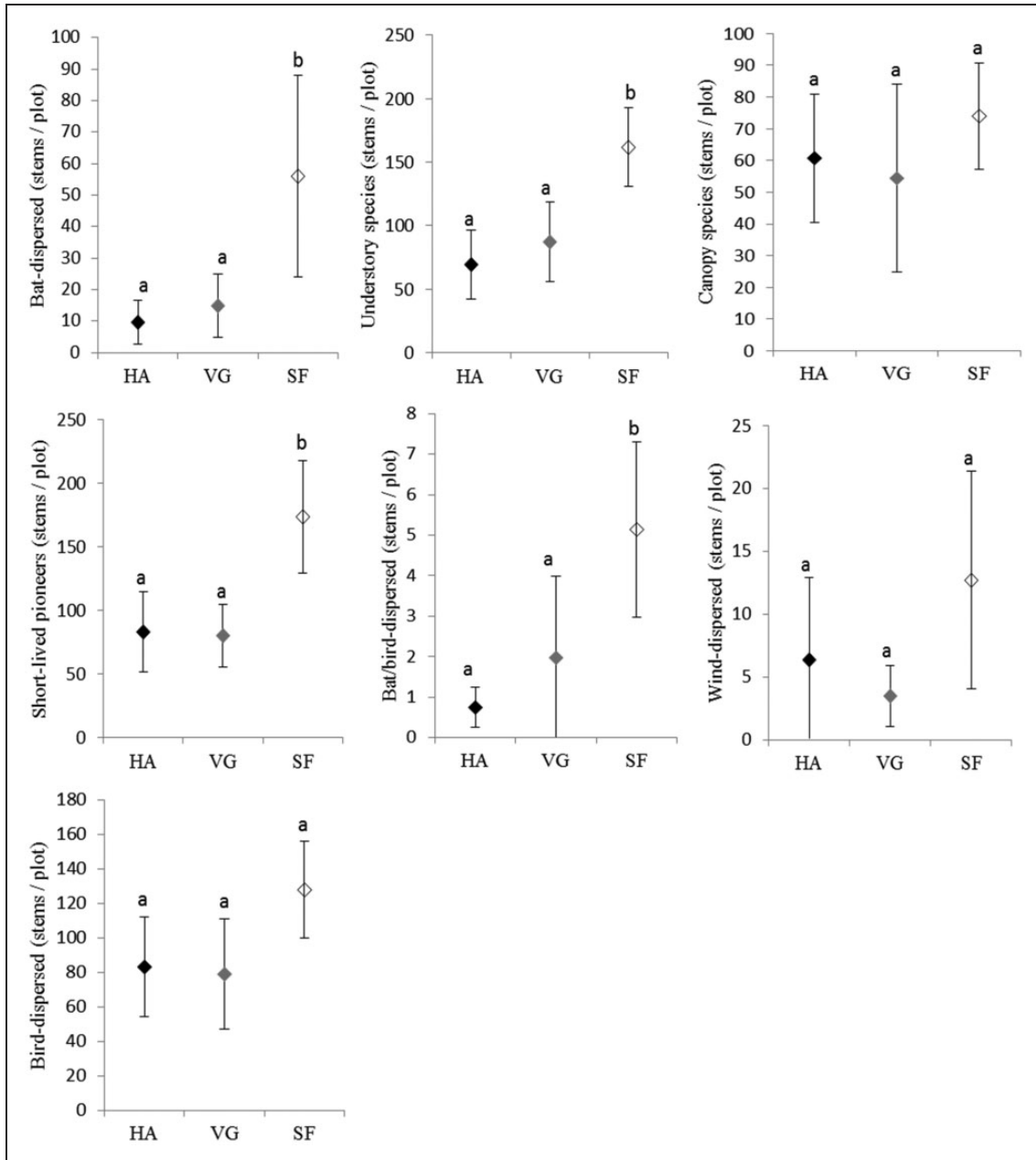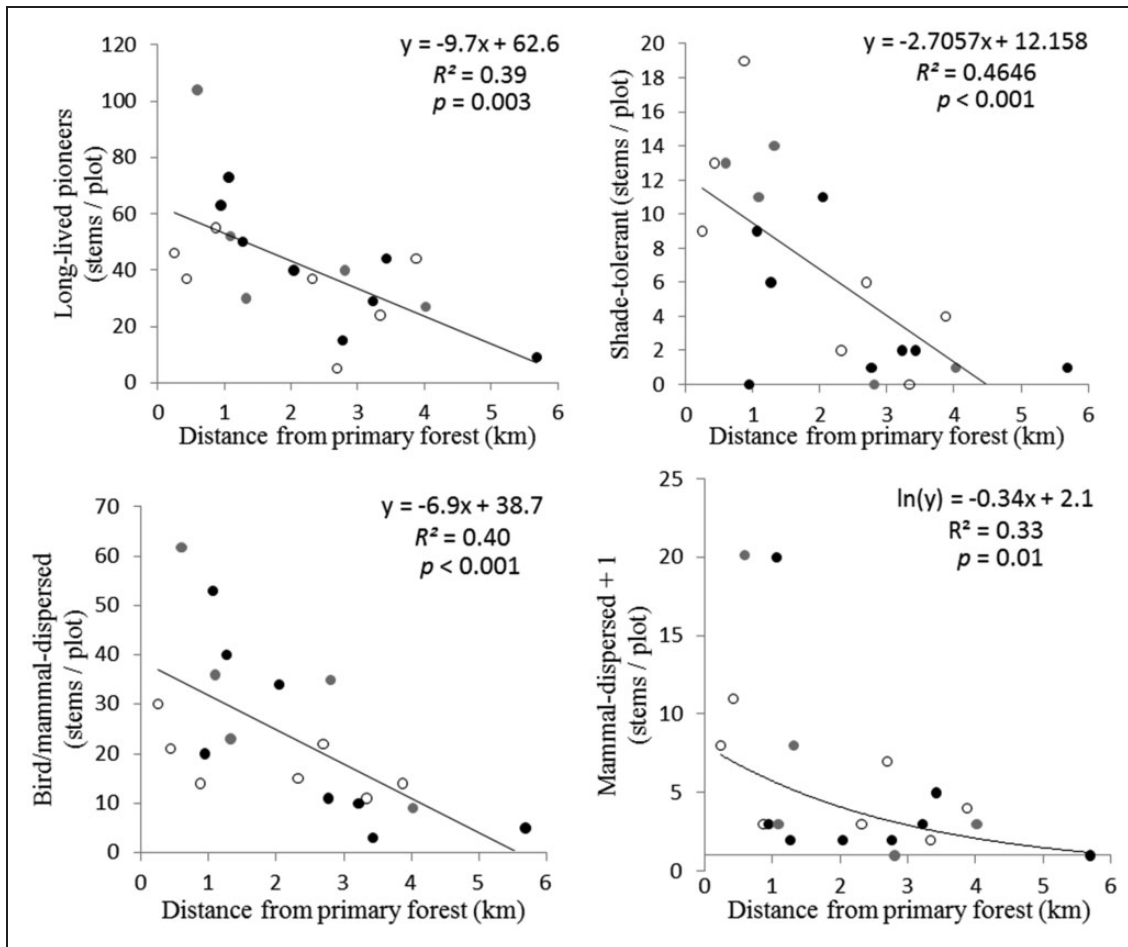
Figure 3. Abundance of different ecological categories of woody plants in different forest types. These categories were not significantly related to distance to primary forest (Table S2). Forest types are secondary forest (SF), *H. alchorneoides* tree plantations (HA), and *V. guatemalensis* tree plantations (VG). Letters indicate significant differences ($p < .05$) between forest types from Tukey's HSD tests.

primary forest increased (-2.7 stems/km), $F(1, 18) = 15.6$, $p = .0009$ (Figure 4).

Dispersal Vector

Ten species were wind-dispersed (4.0% of individuals), 3 were ballistically dispersed (1.8% of individuals), 8 were only bat-dispersed (16.5% of individuals), 3 were both bat- and bird-dispersed (1.5% of individuals), 27 were only bird-dispersed (58.6% of individuals), 23 were

both bird and mammal-dispersed (13.7% of individuals), and 12 were only mammal-dispersed (2.8% of individuals). Wind-dispersal abundance was not related to forest type or distance from primary forest (Table S3). Abundances of bat-dispersed and bat/bird-dispersed species were best explained by forest type alone ($p < .007$, Table S3). Both categories were at least twice as abundant in secondary forests than in both types of tree plantations (Figure 3). Abundance of bird-dispersed species followed a similar trend but the difference between forest types was

Figure 4. Relationship between distance to primary forest and abundance of different ecological categories of woody plants. None of these variables were affected by forest type (Table S2). Forest types are secondary forest (open symbols), *H. alchorneoides* tree plantations (black), and *V. guatemalensis* tree plantations (gray). Variables which were log-transformed for analysis are shown with a nonlinear trendline.

not statistically significant, $F(2, 17) = 3.1$, $p = .07$. Abundances of bird or mammal-dispersed and mammal-dispersed species were best explained by distance from primary forest alone (Table S3) and decreased significantly as distance from primary forest increased ($p < .01$, Figure 4).

Species Richness

Variation in rarefied species richness (species / 70 individuals) of natural regeneration was most effectively explained by a model with only distance from primary forest ($r^2 = .63$, Table S3). Distance had a significant negative effect on rarefied richness (−1.9 species/km), $F(1, 18) = 14.4$, $p = .001$ (Figure 5(a)). Mean rarefied richness was not affected by forest type and was 14.4 ± 3.9 in *H. alchorneoides* plantations, 19.0 ± 4.3 in *V. guatemalensis* plantations, and 17.6 ± 3.7 in secondary forest. Across all forest types, mean species density was 23.7 ± 3.1 species/900 m^2. The interaction between forest type and

distance was not significant in this model or any other variable tested. Individual-based species accumulation curves showed slightly slower species accumulation in *H. alchorneoides* plantations than in secondary forest and *V. guatemalensis* plantations (Figure 5(b)).

Discussion

Effects of Forest Type on Species Composition

Species composition of natural regeneration in tree plantations was different from secondary forests, and we identified ecological groups associated with this difference. Secondary forests had substantially more short-lived pioneers, understory species, and bat-dispersed species than tree plantations. However, secondary forests and tree plantations had similar abundances of mid- to late-successional categories (long-lived pioneers, shade-tolerant, bird-dispersed, and mammal-dispersed). Previous experimental studies in tropical forests have
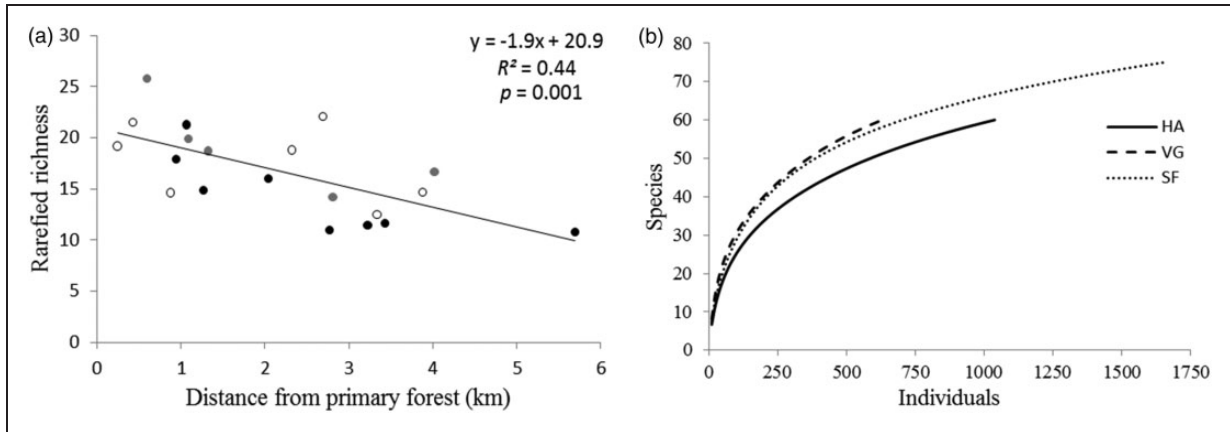
Figure 5. Diversity of naturally regenerating woody plants in tree plantations and secondary forests. (a) Relationship between rarefied species richness (per 70 individuals) in each plot and distance from primary forest. There was no significant difference between forest types: secondary forest (SF; open circles), *H. alchorneoides* tree plantations (HA; black circles), and *V. guatemalensis* tree plantations (VG; gray circles). (b) Individual-based species accumulation curves for each forest type.

found differences in species composition between tree plantations and secondary forest at 10 and 15 years old (Butler et al., 2008; Holl et al., 2017), although a study of 5-year-old sites did not (Gilman et al., 2016). Although regeneration in tree plantations is often dominated by early successional species (Cusack & Montagnini, 2004; Zahawi et al., 2013), it has been shown to resemble the composition of mature forest more than secondary forest does (Holl et al., 2017). This may be due to increased dispersal of large-seeded species in tree plantations compared with secondary forests (Reid, Holl, & Zahawi, 2015). Also, germination and survival of early-successional species, which are inhibited by both shade and litter (Dupuy & Chazdon, 2008), may be lower in tree plantations than in early secondary growth. Since these tree plantation sites had a shorter period of undisturbed regeneration and lower overall stem density than secondary forest, it was difficult to determine whether recruitment of early-successional species was suppressed or whether recruitment of mid- to late-successional species was enhanced. Regardless, our results suggest that tree plantations may catalyze succession of species composition in areas of extended land use and habitat fragmentation.

We found substantially fewer understory species in tree plantations than in secondary forest, a group made up mostly of shrubs and treelets in the Melastomataceae, Piperaceae, and Rubiaceae families. In the lowland forests of Costa Rica, shrub density decreases with forest age (Laska, 1997), and this shift is correlated with a decline in light availability (Capers, Chazdon, Brenes, & Alvarado, 2005). Lower light availability in tree plantations compared with pastures may have inhibited germination and growth of many shade-intolerant understory species.

Forest type effects on species composition may also be attributable to habitat preferences of seed dispersers. The most common bat-dispersed plants in our sites were pioneer species *Cecropia obtusifolia, Piper colonense, Piper friedrichsthallii*, and *Senna papillosa*, all of which were more abundant in secondary forests. These results are consistent with a study from wet forests in Mexico, which showed that bats are more important than birds for seed dispersal of pioneer tree and shrubs into open, grassy areas (de la Peña-Domene, Martínez-Garza, Palmas-Pérez, Rivas-Alonso, & Howe, 2014). Another study showed that birds, not bats, are responsible for increased tree seed rain in 2- to 4-year-old tree plantations compared with natural regeneration in Costa Rica (Cole, Holl, & Zahawi, 2010). Our result adds to mounting evidence that tree plantations impact seed disperser assemblages during early secondary succession (Holl et al., 2017), although importance of disperser groups may shift in different regions.

Tree plantations had similar abundances of a mid-successional category (long-lived pioneers) as secondary forests. Also, abundances of late-successional categories (shade-tolerant and mammal-dispersed species) were quite low in all forest types (<6% of individuals). Recruitment of mature forest species is typically a slow process in natural regeneration (Aide, Zimmerman, Pascarella, Rivera, & Marcano-Vega, 2000; Finegan, 1996; Norden et al., 2009), and a lack of seed dispersal of these species is considered the major obstacle. Our study does not suggest that tree plantations substantially enhance recovery of mature forest species during the first two decades of succession.

Guild categories in our study are coarse distinctions based on subjective assessments by ecologists. To gain a more complete understanding of successional stages of these forests, an objective classification based on habitat preferences or functional traits would be useful. An objective classification of tree species of the region

based on habitat preferences (old-growth specialists, secondary growth specialists, and generalists) has been conducted (Chazdon et al., 2011); however, habitat preferences of about 40% of species at our sites have not been determined.

Effect of Forest Type on Species Richness

We found that rarefied species richness of woody plants was similar in tree plantations grown for carbon sequestration and secondary forests. Recovery of plant diversity in tropical forest is highly limited by seed dispersal (Holl, 1999; Hooper, Legendre, & Condit, 2005), and seed rain diversity is enhanced in tree plantations compared with abandoned pastures (Cole et al., 2010; Zamora & Montagnini, 2007). Comparisons of tropical forest restoration in planted and unplanted plots have shown that tree planting either enhanced plant diversity (Guariguata et al., 1995; Parrotta, 1995; Powers et al., 1997) or resulted in similar species richness as naturally regenerating forest (Bone et al., 1997; Butler et al., 2008; Healey & Gara, 2003; Lugo, 1992). Tree plantations are thought to be most effective in landscapes with intermediate levels (~30%) of forest cover (Tambosi, Martensen, Ribeiro, & Metzger, 2014) similar to our sites. However, tree plantations in our study had a more intense management (e.g., planted tree thinning and 5-year period of manual understory clearing) than in most comparisons of diversity. Given the landscape and management context, we suspect that in our sites, tree plantations could have enhanced diversity of seed rain, but that diversity of recruitment did not exceed secondary forest perhaps because understory clearings delayed the period of natural regeneration.

Our findings show that single-species tree plantations with native species and moderate management practices can still support levels of diversity comparable to secondary forests. While mixed-species plantings are preferable for forest restoration (Rodrigues, Lima, Gandolfi, & Nave, 2009; Stanturf, Palik, & Dumroese, 2014), single-species plantations of common timber species are often used due to convenience in restoration and carbon sequestration projects. Also, other studies have shown variation between native plantation species in their ability to enhance abundance and diversity of recruitment in the understory (Carnevale & Montagnini, 2002). Our findings are consistent with studies that show that *Vochysia guatemalensis* and *Hieronyma alchorneoides* perform well in supporting regeneration of woody plants (Guariguata et al., 1995; Powers et al., 1997). This is likely due to these species creating a relatively dense canopy, which shades out grasses that compete with woody plants (Butler et al., 2008). Careful selection of species for tree plantations could enhance the conservation value of forest planted for carbon sequestration.

Effect of Landscape on Forest Regeneration

As distance from primary forest increased, species richness declined and species composition shifted. Abundances of bird- and mammal-dispersed species, only mammal-dispersed species, shade-tolerant species, and long-lived pioneers declined as distance to primary forest increased. The recovery rate of diversity and composition of both tree plantations and secondary forests is related to surrounding landscape (Crouzeilles & Curran, 2016; Goosem et al., 2016; Parrotta & Knowles, 2001; Zanne & Chapman, 2001). As noted previously, distance from primary forest in our study is correlated with a decline in forest cover of all forest types. Seed sources for sites that were closer to primary forest were probably more diverse and composed of later successional species than for sites far from primary forest.

The interaction between forest type and distance from primary forest was not significant for any variables tested. However, the effect of distance from primary forest on species richness, long-lived pioneers and bird/mammal-dispersed species seemed to be larger in tree plantations than secondary forests (see scatterplots in Figures 4 and 5). We may have lacked the statistical power to identify the interaction. Contrary to our expectations, tree plantations may have been affected more by amount of surrounding forest cover than secondary forests. Large frugivorous bats, which appear to be dispersing more seeds in our secondary forests sites than tree plantations, can disperse seeds over distances of several kilometers and in fragmented landscapes in the tropics (Corlett, 2009). Whereas mobility of bird and mammal seed dispersers is known to be greatly limited by forest fragmentation (McConkey et al., 2012). Active restoration is often considered more necessary in regions degraded by intense land-uses and forest fragmentation (Chazdon & Guariguata, 2016; Holl & Aide, 2011). However, if this finding is supported by further evidence, it may suggest that tree plantations provide larger conservation benefits in landscapes with less forest fragmentation.

Implications for Conservation

Differences in species composition between tree plantations and secondary forests may have implications for both carbon sequestration and successional trajectories. Fewer early-successional species in tree plantations than in secondary forests may result in greater rates of carbon sequestration in tree plantations. There is some evidence that the rate of aboveground biomass accumulation in wet tropical forest trees is lower in light-demanding species than in shade-tolerant species (Keeling, Baker, Vasquez-Martinez, Monteagudo, & Phillips, 2008). Also, these compositional differences demonstrate that

succession in secondary forest is delayed compared with tree plantations. And the fact that tree plantations had lower canopy openness than secondary forests suggests that, in the coming years, light-demanding species are more likely to be inhibited in tree plantations than in secondary forests. As with other neotropical secondary successions (Longworth et al., 2014; Myster & Malahy, 2008), the initial colonization is likely to impact the species composition of further successional stages through priority effects. However, long-term research of tree plantations is needed since the majority of studies have been of tree plantations younger than 20 years old. It remains unknown if differences in species composition between tree plantations and secondary forest are persistent and whether the legacy of the planted trees inhibits successional dynamics at later stages.

Land managers interested in reforestation of agricultural land in Costa Rica and across the tropics often choose between allowing natural regeneration and planting tree plantations. Public and private organizations directing carbon sequestration projects also makes decisions regarding reforestation strategy. Government policies and cultural views often encourage tree plantations (Chazdon & Guariguata, 2016), which are regarded as a more active measure than secondary forest. In Costa Rica, it is not uncommon for tree plantations to be used as a restoration method instead of for timber production (Piotto et al., 2003; Redondo-Brenes, 2007). Our results demonstrate that tree plantations may represent a slightly more advanced succession stage than secondary forest, and therefore greater conservation value at this forest age. However, it should be noted that these plantations used native species and had a light management. Use of native species is more common in Costa Rica than many other tropical countries (Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008). Efforts to encourage light management of tree plantations and use of native species when consistent with tree plantation goals would favor conservation goals.

Supplemental Material

Supplementary material for this article is available online.

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