



Land use legacy effects on structure and composition of subtropical dry forests in St. Croix, U.S. Virgin Islands



Emily E. Atkinson*, Erika Marín-Spiotta

Department of Geography, University of Wisconsin-Madison, 550 N. Park St., Madison, WI 53706, United States

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ABSTRACT

Tropical dry forests are subject to intense human pressure and land change, including conversion to agricultural crops, pasture or agroforestry, and urban encroachment. Decades, and even centuries, of conversion, expansion, regrowth, and changing land-use practices can result in a mosaic of secondary growth patches with different land-use histories. Whereas post-agricultural landscapes may appear as contiguous areas of forest regeneration, the successional trajectory of forest patches from historic land cover to their current state may differ substantially, with consequences for species composition and ecosystem structure and function. We examined the effect of different land-use histories on current forest structure, biomass, and composition in subtropical dry forests in St. Croix, U.S. Virgin Islands. We sampled three types of secondary forests that followed different regeneration pathways after centuries of sugarcane agriculture: 40-year old secondary forests that naturally regenerated after sugarcane abandonment, 40-year old secondary forests that were reforested with timber plantations before management ceased and they were overtaken by natural succession, and 10-year old secondary forests that were intensive pasture prior to recent forest regeneration. Secondary forests that naturally regenerated after sugarcane had similar structural characteristics, in terms of basal area, stem density, aboveground biomass, and species diversity compared to secondary forests of the same age that were former plantations. Species composition, however, remained distinct. Compositional differences between the two types of 40-year old secondary forests could be partially attributed to plantation species, specifically *Swietenia mahagoni*, whereas naturally regenerated forests were dominated by common secondary forest species, such as *Melicoccus bijugatus* and *Cordia alba*. The effects of hurricane damage helped to explain structural similarity and compositional dissimilarity between naturally regenerated secondary forests and former plantations. Forest age had a significant effect on forest structure and composition. Differences between 10-year old and both types of 40-year old secondary forests were driven by a dominance of the nitrogen-fixing species *Leucaena leucocephala*, which rapidly established in 10-year old secondary forests and resulted in greater stem density and lower basal area, biomass, and species richness. Our results show that land-use history plays an important role in shaping species composition, especially in post-agricultural tropical dry forests. Although forests with differing land-use histories may structurally resemble one another within decades of abandonment, species composition may remain distinct for much longer. Understanding the legacy of human land use is important for dry forests that have a long history of disturbance and for predicting their response to future environmental change.

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1. Introduction

Tropical dry forests are the most perturbed, heavily used, fragmented, and threatened tropical forests (Janzen, 1988; Miles et al., 2006; Quesada et al., 2009). Compared to all other biomes of the world, tropical dry forests have experienced the greatest habitat loss and land conversion due to increasing human population

growth and have one of the lowest proportions of area under protection and conservation (Hoekstra et al., 2004; Janzen, 1988; Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). Subtropical and tropical dry forest life zones, characterized by strong seasonality in rainfall and several months of drought, occupy 42% of the global tropics (Brown and Lugo, 1990) and about 50% of land in Central America and the Caribbean (Murphy and Lugo, 1995). Nearly 80% of tropical land with mean annual rainfall ≤ 1500 mm has experienced $> 50\%$ conversion from natural vegetation to human use (Powers et al., 2011).

* Corresponding author. Tel.: +1 608 262 1855.

E-mail address: eeatkinson@wisc.edu (E.E. Atkinson).

Caribbean dry forests are the least conserved (Molina Colón et al., 2011; Lugo et al., 2006) and have undergone significant deforestation due to colonial plantation economies and high densities of human population in lowland, coastal areas. After centuries of agricultural use, abandonment of plantation agriculture in many Caribbean islands has led to widespread secondary forest regeneration (Aide et al., 2012; Álvarez-Berríos et al., 2013). A prime example of extensive land change and subsequent shift to secondary forest is the Caribbean island of St. Croix, U.S. Virgin Islands. Prior to Danish colonization in 1733, the U.S. Virgin Islands had 90% forest cover (Brandeis and Oswalt, 2007; The Nature Conservancy, 2003; Haagensen, 1995). Following colonization, more than half (54%) of the island of St. Croix was converted to sugarcane agriculture, particularly in the flat central lowlands. Sugarcane cultivation lasted there for over 200 years until the early 20th century, with some areas continuing in production until the mid-1950s (Weaver, 2006). The decline of the sugarcane industry led to island-wide pasture establishment and agroforestry development. By 1917, an estimated 90% of St. Croix had been cleared for agriculture and logged for valuable timber (Ward et al., 2000). During the mid- to late-20th century much of the intensive pasture and agroforestry activities ceased. Whereas there are currently some parts of the island in active pasture, post-agricultural forests now cover approximately 50% of land on St. Croix (Brandeis et al., 2009; Brandeis and Oswalt, 2007). This secondary forest cover is predominantly composed of relatively young forests with only 3% in mature forest stands (Brandeis and Oswalt, 2007). Early successional forests consist of mostly small diameter trees and reflect centuries of past and recent land use.

The result of this dynamic history has been a mosaic of secondary forests that have followed different pathways to their current state – some secondary forests regenerated almost immediately after sugarcane abandonment, while others only recently regenerated after extensive pasture or agroforestry use. The objective of our study was to examine whether differences in land-use history led to differences in forest structure, aboveground biomass, composition, and species diversity in subtropical dry forests. Our approach was to measure the effect of land-use history and successional trajectories by controlling for climate and soil type. Thus, we compared common post-agricultural secondary forest types found in St. Croix, including naturally regenerated secondary forests, former timber plantations, and younger recently regenerated secondary forests.

2. Methods

2.1. Site description

We conducted this research in subtropical dry forests of St. Croix, U.S. Virgin Islands (17°44'N, 64°43'W). Three replicate post-sugarcane secondary forest types were identified with the following land-use histories: (1) cessation of sugarcane followed by a short period of low intensity pasture use (7–20 years) and 40 years of natural forest regeneration, hereafter referred to as 40-year old secondary forests; (2) cessation of sugarcane followed by low intensity pasture use and managed reforestation with timber plantations, which are no longer being managed and have regenerated to secondary forests, hereafter referred to as 40-year old former plantations; and (3) cessation of sugarcane followed by a long period of high intensity pasture use (30 years) and recent natural forest regeneration, hereafter referred to as 10-year old secondary forests (Table 1). The former timber plantation sites were experimental sites that had been planted with mahogany (*Swietenia mahagoni*), teak (*Tectona grandis*) or mastic (*Sideroxylon foetidissimum*). The first two were part of the USDA Estate Thomas

Experimental Forest, where planting occurred during 1954–1972 (Weaver, 2006). Early measurements from Estate Thomas showed that some of the densest stands, mostly *S. mahagoni*, had basal areas of 45 m²/ha (Wadsworth, 1947). The third plantation site was privately owned property adjacent to the University of the Virgin Islands. While management practices at the three former plantation sites differed, they were all planted, harvested, and then abandoned at comparable times. Harvesting began in 1963 and continued regularly until abandonment (Weaver, 2006). All sites were identified by reconstructing land-use history through the use of documented land-use history records, archived maps, and personal communication with local farmers, government officials, landowners, and researchers affiliated with the University of the Virgin Islands and the Virgin Islands Department of Agriculture.

All sites were located in the subtropical dry life zone (Fig. 1). Mean annual precipitation at sites was approximately 1060 mm with a mean annual temperature of 26.4 °C (1971–2001 from climatic stations located in Christiansted Fort and Bethlehem Upper New Works) (Weaver, 2006). Sites were chosen in order to control for parent material, soil order and slope. Soils at all sites are classified as Mollisols and are part of either the Sion soil series, consisting of shallow, well-drained, slowly permeable soils formed in material weathered from soft limestone bedrock (*Typic Haplustolls*) or the Arawak soil series, consisting of very deep, well-drained, moderately slowly permeable soils formed in alkaline marine deposits (*isohyperthermic Typic Calciustolls*) (Soil Survey NRCS). All sites were located on flat topography at 9–127 m above sea level.

2.2. Forest structure and composition

Sites were sampled during January and June 2013. At each site, we established four 1 × 25 m parallel transects to measure and identify all live, rooted trees with diameter at breast height (dbh) <10 cm and ≥1 cm and stem length of at least 1.3 m (Fig. 2), following the methods of Aide et al. (2000). The trees in this size class will hereafter be referred to as “small” trees. Two 8 × 25 m parallel transects were overlain on top of the small tree transects to measure dbh for all trees ≥10 cm and stem length of at least 1.3 m, hereafter referred to as “large” trees (Fig. 2). All multiple stems from a single base that satisfied the dbh and height requirements were measured. Trees were identified to the species level according to Little and Wadsworth (1964, 1974) and with assistance from researchers at the University of the Virgin Islands and the director of the St. George Village Botanical Garden. Voucher specimens were collected and deposited at the St. George Village Botanical Garden in St. Croix.

For each site, stems and basal area were summed for the small tree (total of 100 m²) and large tree (total of 400 m²) transects. Basal area (m²/ha) and stem density (n stems/ha) were calculated for all small and large stems. Importance values (IV) were calculated as the sum of relative stem abundance and relative basal area per site for each species (Marín-Spiotta et al., 2007). For each tree species, IV ranged from 0 (no species present at site) to 2 (site is comprised entirely of a single species).

2.3. Diversity and dissimilarity

Shannon-Weiner diversity (H') and evenness (E_H) were calculated for individuals:

$$H' = - \sum_{i=1}^R p_i \ln p_i \quad (1)$$

$$E_H = H' / \ln S \quad (2)$$

Table 1
Site history for secondary forests in St. Croix, U.S. Virgin Islands.

Forest type	Age (yrs)	Site	Latitude	Longitude	Elevation (m)	Sugarcane	Pasture	Timber plantation	Secondary Forest
10-yr Secondary Forests	8–10	Woodson (WOD)	17° 44.512' N	64° 47.124' W	45	1800s–1954	1954–mid-2000	–	Mid-2000–2014
	8–10	Woodson II (WOJ)	17° 44.425' N	64° 47.029' W	32	1800s–1954	1954–mid-2000	–	Mid-2000–2014
	8–10	Estate Bethlehem (BET)	17° 44.141' N	64° 47.123' W	52	1800s–1954	1954–mid-2000	–	Mid-2000–2014
40-yr Former Plantations	42	Estate Thomas E (ETE)	17° 44.644' N	64° 44.318' W	127	1800s–1928	1928–1953	1954–1972	1972–2014
	42	Estate Thomas D (ETD)	17° 44.792' N	64° 44.254' W	111	1800s–1928	1928–1953	1954–1972	1972–2014
	39–44	Estate Bethlehem L. (BEL)	17° 43.221' N	64° 47.065' W	56	1800s–1928	1928–1950	1950–1970	1970–2014
40-yr Secondary Forests	44	Estate Little Princess (ELP)	17° 45.519' N	64° 43.593' W	9	1750–1950	1950–1970	–	1970–2014
	41	Estate Adventure (EAD)	17° 43.086' N	64° 48.156' W	32	1792–1966	1966–1973	–	1973–2014
	39–44	Estate Canaan (CAN)	17° 45.486' N	64° 47.738' W	34	1800s–1940	1940–1970	–	1970–2014

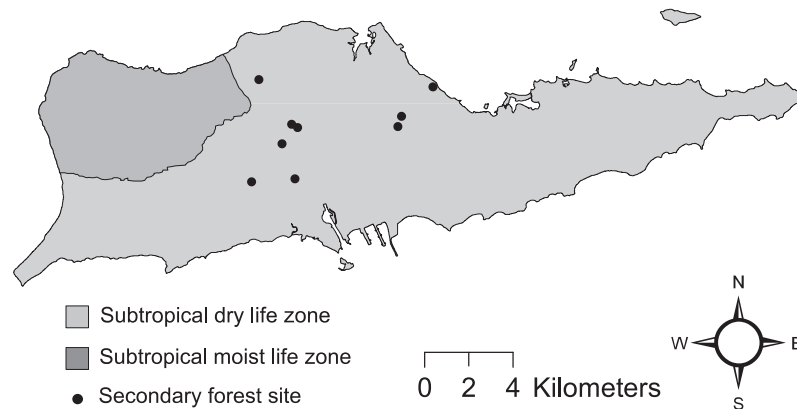


Fig. 1. Map of secondary forest sites in St. Croix, U.S. Virgin Islands.

where p is the proportion of individuals of a given species compared to the total number of species per site. S is the total number of individuals per site.

Dissimilarity of tree species between secondary forest types was compared using Sorensen's quantitative dissimilarity index (C_N) (Magurran, 1988). Index C_N was based on species occurrence and species importance:

$$C_N = 1 - [2N_j / (N_a + N_b)] \quad (3)$$

where N_a and N_b are the abundance (total number of individuals) found in site A and site B , respectively, and N_j is the sum of the lower of the two abundances for species found in both sites.

2.4. Biomass estimates

Aboveground biomass (AGB) was calculated using previously published allometric equations. We used two equations for young (<50 years) secondary forests (van Breugel et al., 2011) since many published allometric equations are created for mature forests. The first equation only used measures of dbh while the second equation incorporated wood specific gravity (WSG) (Reyes et al., 1992), which has been shown to be an important factor in calculating AGB (van Breugel et al., 2011):

$$AGB = \exp(-1.863 + 2.208 \times \ln(\text{DBH})) \quad (4)$$

$$AGB = \exp(-1.130 + 2.267 \times \ln(\text{DBH}) + 1.186 \times \ln(\text{WSG})) \quad (5)$$

We also used an equation meant for tropical dry forests from a commonly cited paper that focuses on forest types in calculating AGB (Chave et al., 2005):

$$AGB = \text{WSG} \times \exp(-0.667 + 1.784 \ln(\text{DBH}) + 0.207(\ln(\text{DBH}))^2 - 0.281(\ln(\text{DBH}))^3) \quad (6)$$

Wood specific gravity values for each species were used as reported by Reyes et al. (1992). For each equation we calculated AGB for small trees, large trees, and all trees separately.

Since *Leucaena leucocephala*, an n-fixing, early successional species, was clearly dominant in 10-year secondary forests, we tested a separate biomass model for those forests using a species-specific allometric model developed by Kumar et al. (1998). We found no significant differences in the biomass results from this model compared to the van Breugel et al. (2011) model that incorporated WSG. For this reason, we chose not to present the species-specific allometric model results nor include them in other analyses.

2.5. Data analysis

Small tree, large tree, and all tree datasets for basal area, stem density, species richness, and species evenness were tested for normality and equal variance. In the case of normality, a one-way ANOVA to test for significant differences ($p < 0.05$) among sites was performed, and if all requirements for normality were not met, a nonparametric Kruskal–Wallis test was performed. Parametric and nonparametric analyses were performed in JMP version 11.0 (SAS Institute, 2013).

AGB data were tested for differences among forest type (treatment), AGB models, and their interactions by analyzing data with Mixed Model Personality in JMP version 11.0 (SAS Institute, 2013). We used a split-plot 2-way ANOVA with forest type (treatment) as the whole plot factor (as a randomized complete block) and AGB model as the subplot factor.

Species composition was analyzed with nonmetric multidimensional scaling (NMS) analysis, using importance values. Pearson and Kendall correlation coefficients were calculated and used to identify which tree species significantly contributed to differences

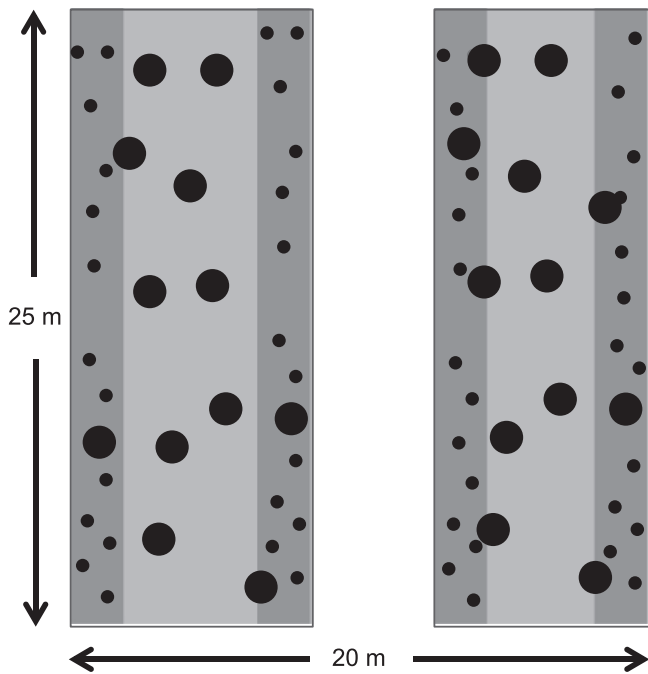


Fig. 2. Transect design for measurement of large and small trees at secondary forest sites.

in species composition among sites. Ordination analyses were performed in PC-ORD (McCune and Mefford, 2011).

3. Results

3.1. Forest structure and basal area

We measured a total of 1574 stems, including 1353 stems (86% of total stems) in the small tree size class (dbh <10 cm and ≥ 1 cm) and 221 stems (14% of total stems) in the large tree size class (≥ 10 cm). In general, small stems accounted for the majority of stems across all forest types. In 10-year old secondary forests small stems accounted for 99% of all stems, whereas in 40-year old secondary forests and 40-year old former plantations small stems made up 87% and 95% of all stems, respectively.

Stem density was significantly greater in 10-year old secondary forests ($23,350 \pm 2,754$ stems/ha) ($p < 0.05$) followed by 40-year old former plantations ($14,883 \pm 3,004$ stems/ha) and 40-year old secondary forests ($8,708 \pm 2,771$ stems/ha) (Fig. 3). When separated by tree size class, the same pattern was true for small trees and the inverse was true for large trees, where stem density of large trees was greatest in 40-year old secondary forests ($1,142 \pm 361$ stems/ha) followed by 40-year old former plantations (683 ± 360 stems/ha) and 10-year old secondary forests (17 ± 17 stems/ha) (Fig. 3).

Basal area was greater in the 40-year old secondary forests and 40-year old secondary forests that were former plantations (28.5 ± 9.8 m²/ha and 24.7 ± 5.8 m²/ha, respectively) compared to 10-year old secondary forests (14 ± 0.8 m²/ha) (Fig. 3). When separated by tree size class, approximately half of the basal area in 40-year old secondary forests and former plantations came from large trees, whereas 10-year old secondary forests had almost no large trees (Fig. 3). Small trees made up approximately 55% of total basal area at all sites, and large trees made up approximately 45% of total basal area at all sites.

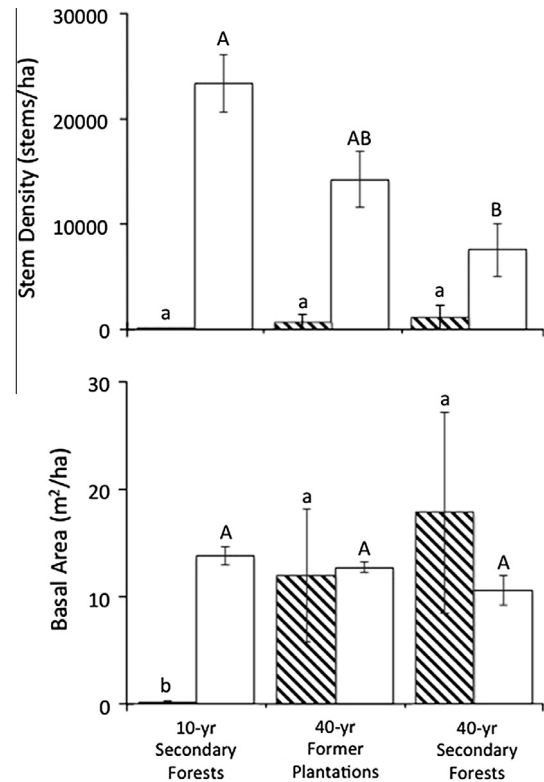


Fig. 3. Mean relative stem density $\pm$ SE (n stems/ha) (top) and mean relative basal area $\pm$ SE (m²/ha) (bottom) of small trees (white bars) and large trees (hatched bars) across secondary forest types (three replicate field sites per forest type) in the dry life zone of St. Croix, U.S. Virgin Islands. Capital letters represent significant differences for small trees across secondary forest types and lowercase letters for large trees.

3.2. Aboveground biomass

There was no interaction between the effect of forest type and model choice on AGB estimates for small trees ($p = 0.4021$), large trees ($p = 0.9993$), and all trees combined ($p = 0.8587$) (Table 2). Across all models, aboveground biomass estimates were greatest in 40-year old secondary forests and former plantations compared to 10-year old secondary forests (Fig. 4). The AGB model from van Breugel et al. (2011) that included WSG yielded the greatest AGB estimates for both types of 40-year old secondary forests, whereas there were no significant differences between van Breugel et al. (2011)'s model that did not include WSG and the Chave et al. (2005) dry forest specific model for total biomass (Fig. 4).

3.3. Forest composition

We identified a total of 30 species, from 29 genera and 16 families (Table 3). Fabaceae was the most speciose family followed by Myrtaceae and Rubiaceae. The one species all forest types had in common was *L. leucocephala*, which was also the most important species across all sites (Fig. 5), according to importance values. *L. leucocephala* made up 94% of all stems in the 10-year old secondary forests, 18% of all stems in 40-year old secondary forests, and 9% in 40-year old former plantations. *L. leucocephala* was the most important tree in the small-tree size class across all sites, whereas *S. mahagoni* was the most important large tree species across all sites but was absent in the 10-year old secondary forests.

In former small-leaf mahogany (*S. mahagoni*) and teak (*T. grandis*) plantations, *S. mahagoni* was the most important large tree species, whereas no live *T. grandis* was measured in our survey.

Table 2
Results of a 2-way split-plot ANOVA showing the significance of forest type, AGB model, and their interaction on aboveground biomass estimates of secondary forests in the dry life zone of St. Croix, U.S. Virgin Islands.

	Factor					
	Forest type		AGB model		Forest type × AGB model	
	F	P	F	P	F	P
<i>Aboveground biomass (Mg/ha)</i>						
All trees	10.1226	0.0011	6.1681	0.0091	0.3233	0.8587
Small trees	7.7507	0.0037	165.2985	<0.0001	1.0656	0.4021
Large trees	11.0353	0.0019	0.6451	0.5419	0.0171	0.9993

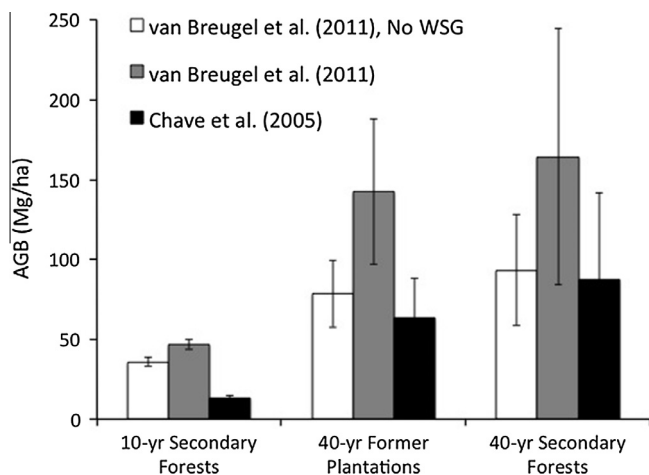


Fig. 4. Mean aboveground biomass estimates $\pm$ SE (three replicate field sites per forest type) across secondary forest types using three different allometric models in the dry life zone of St. Croix, U.S. Virgin Islands. WSG = wood specific gravity.

The greatest occurrence of *S. foetidissimum* was in the former mastic plantation, but this species was present in all 40-year old former plantations and all 40-year old secondary forests.

Species composition and importance differed among secondary forest types. The 40-year old secondary forests were dominated by *Melicoccus bijugatus*, *L. leucocephala*, and *Cordia alba*, in order of importance and across size class. In these forests, *M. bijugatus* was the most important species in both the small tree and large size class. The 40-year old former plantations were dominated by *Triphasia trifolia*, *Bourreria succulenta*, and *L. leucocephala*, in order of importance and across size class. In these forests, *T. trifolia* was the most important small tree species while *S. mahagoni* was the most important large tree species. The 10-year old secondary forests contained only three species: *L. leucocephala*, *Albizia lebbbeck*, and *Acacia macracantha*. In these forests, *L. leucocephala* was the most important small tree species, making up 94% of all stems, while *A. macracantha* was the most important large tree species, represented by only 6 individuals.

Ordination analysis on importance values separated sites into three main groups: 40-year old secondary forests, 40-year old former plantations, and 10-year old secondary forests (Fig. 6). The primary difference in tree species composition along Axis 1 ($r^2 = 0.77$), separating 10-year old secondary forests from both types of 40-year old secondary forests, was the importance of *L. leucocephala* (Kendall's tau = -0.97 , Pearson's $r = -0.94$). The difference in tree species composition along Axis 2 ($r^2 = 0.15$), which separated 40-year old secondary forests from former plantations, was driven by *Eugenia ligustrina* (Kendall's tau = -0.57 , Pearson's $r = -0.54$) in the small-tree size class and *S. mahagoni* (Kendall's tau = -0.47 , Pearson's $r = -0.46$) in the large-tree size class. *E. ligustrina* and *S. mahagoni* were either absent or of minor importance in the 40-year old naturally regenerated secondary forests.

3.4. Diversity indices

Shannon-Weiner diversity indices were significantly greater in 40-year old secondary forests (2.11 ± 0.19) and 40-year old former plantations (2.09 ± 0.38) compared to 10-year old secondary forests (0.17 ± 0.08) (Table 4). Similarly, species evenness was greater in 40-year old secondary forests (0.49 ± 0.01) and 40-year old former plantations (0.42 ± 0.01) compared to 10-year old secondary forests (0.03 ± 0.02). There were no significant differences in diversity or evenness among 40-year old secondary forests and former plantations of the same age. Sorensen's dissimilarity index showed that 10-year old secondary forests differed from both types of 40-year secondary forests, ranging from 76% to 100% dissimilarity for individual site comparisons based on abundance (Table 5). The two types of 40-year secondary forests also differed from each other, with dissimilarity at the site level ranging from 52% to 91% (Table 5).

4. Discussion

4.1. No structural effects of land-use history in similarly aged secondary forests

Historical land-use legacies can influence successional pathways of dry forests with different effects on structure and composition. In subtropical dry forests in St. Croix, land-use history did not significantly affect vegetation structure in secondary forests of similar ages. Over a period of 40 years, plantations left unmanaged structurally resembled naturally regenerated forests in terms of basal area (for small, large, and all trees), stem density (for small, large, and all trees), and aboveground biomass estimates.

During secondary forest regrowth, recovery of structural characteristics of reference (undisturbed) or primary forests can occur in as little as 30–40 years of succession (Guariguata and Ostertag, 2001; Chazdon, 2003; Marín-Spiotta et al., 2007). Fewer studies have compared structural characteristics between secondary forests and former tree plantations (but see Lugo, 1992), but there is evidence that over time the two can become structurally similar. Vegetation structure and species richness in tree plantations can be affected by management intensity, plantation size, distance to seed sources, and site conditions (Lugo, 1992). However, management intensity in small tropical plantations tends to be highest during site preparation, planting, and tree establishment. After trees are established and grow above competing vegetation, plantations often grow unmanaged, and other plant species have the opportunity to establish. In many cases, structural similarities between paired secondary forests and former tree plantations may then come from similarities in canopy species, and compositional similarities or differences may come from understory species, which we will discuss in the next section.

Former timber plantations and naturally regenerated secondary forests can also resemble each other in terms of aboveground biomass. In early stages, planting woody species can increase

Table 3
Species traits, mean relative stem density (stems/ha), and basal area (m²/ha) of all stems ≥ 1 cm in diameter at breast height per species across secondary forest types of the dry life zone of St. Croix, U.S. Virgin Islands.

Family	Species ^a	Plant type ^a	Successional status ^b	Functional type ^a	Dispersal mode ^{b,c,d}	Shade tolerance ^{b,c,e,f,h}	Wood density ^g (g/cm ³)	Mean relative basal area (stems/ha)			Mean relative stem density (m ² /ha)				
								10-yr Forests	Secondary	40-yr Former Plantations	40-yr Forests	Secondary	10-yr Forests	Secondary	40-yr Former Plantations
Boraginaceae	<i>Bourreria succulenta</i>	N	P	NL	B	PG	0.73			0.1873	0.0549			0.1853	0.0419
Boraginaceae	<i>Cordia alba</i>	N	P	NL	B	SI	0.53			0.0155	0.2884			0.0011	0.2177
Capparaceae	<i>Capparis indica</i>	N	P	NL	B	SI	0.68			0.0259	0.0081			0.0433	0.0009
Erythroxylaceae	<i>Erythroxylum rotundifolium</i>	N	LS	NL	B	SI	0.86			0.0042	0.0069			0.0008	0.0021
Euphorbiaceae	<i>Adelia ricinella</i>	N	P	NL	B	SI	0.87			0.0020				0.0008	
Fabaceae	<i>Acacia macracantha</i>	N	P	L	B	SI	0.73	0.0419				0.0033			
Fabaceae	<i>Albizia lebeck</i>	L	P	L	A	SI	0.55	0.3257		0.0039	0.0197	0.1495		0.0004	0.0215
Fabaceae	<i>Hymenaea courbaril</i>	N	LS	L	B	SI	0.70				0.0005				0.0014
Fabaceae	<i>Inga laurina</i>	N	P	L	B	SI	0.62				0.0077				0.0028
Fabaceae	<i>Leucaena leucocephala</i>	L	P	L	A	SI	0.64	0.8496		0.2396	0.3356	0.9103		0.2631	0.2643
Fabaceae	<i>Tamarindus indica</i>	L	LLP	L	B	SI	0.80			0.1715				0.0473	
Flacourtiaceae	<i>Casearia decandra</i>	N	LS	NL	B	SI	0.56				0.0274				0.0239
Flacourtiaceae	<i>Casearia guianensis</i>	N	LS	NL	B	SI	0.70				0.0079				0.0084
Meliaceae	<i>Swietenia mahagoni</i>	L	LLP	NL	A	SI	0.75			0.1534	0.1367			0.0444	0.0009
Myrsinaceae	<i>Ardisia obovata</i>	N	LS	NL	B	SI	0.60				0.0008				0.0042
Myrtaceae	<i>Eugenia spp.</i>	N	LS	NL	B	PG	0.65			0.0200				0.0031	
Myrtaceae	<i>Eugenia ligustrina</i>	N	LS	NL	B	PG	0.98			0.0312				0.0032	
Myrtaceae	<i>Eugenia rhombea</i>	N	LS	NL	B	PG	0.80			0.0083	0.0085			0.0023	0.0068
Nyctaginaceae	<i>Guapira fragrans</i>	N	LLP	NL	B	SI	0.83			0.1342	0.0583			0.3541	0.0160
Nyctaginaceae	<i>Pisonia subcordata</i>	N	LLP	NL	B	SI	0.50				0.1383				0.1350
Rhamnaceae	<i>Krugiodendron ferreum</i>	N	LS	NL	B	SI	1.35			0.0181				0.2745	
Rubiaceae	<i>Chiococca alba</i>	N	P	NL	B	ST	0.90				0.0008				0.0014
Rubiaceae	<i>Psychotria nervosa</i>	N	LS	NL	B	ST	0.65			0.0005	0.0006			0.0003	0.0056
Rubiaceae	<i>Randia aculeata</i>	N	P	NL	B	SI	0.72			0.0018				0.0003	
Rutaceae	<i>Amyris elemifera</i>	N	LS	NL	B	SI	1.05			0.0402				0.0017	
Rutaceae	<i>Triphasia trifolia</i>	L	P	NL	B	ST	0.84			0.0370	0.0076			0.0069	0.0072
Sapindaceae	<i>Melicoccus bijugatus</i>	L	LLP	NL	B	SI	0.86			0.0546	0.3229			0.0533	0.2921
Sapotaceae	<i>Manilkara zapota</i>	N	LS	NL	B	PG	0.89			0.2386	0.0173			0.0671	0.7384
Sapotaceae	<i>Sideroxylon foetidissimum</i>	N	LS	NL	B	PG	0.90			0.0355	0.0248			0.0146	0.0126
Zygophyllaceae	<i>Guaiacum officinale</i>	N	LS	NL	B	SI	1.25			0.0035				0.0003	

Plant type: N = Native, L = Naturalized.

Successional status: P = Pioneer, LLP = Long-lived Pioneer, LS = Late successional.

Functional type: NL = Non-legume, L = Legume.

Dispersal mode: B = Biotic, A = Abiotic.

Shade tolerance: SI = Shade Intolerant, ST = Shade Tolerant, PG = Phase-Gap.

^a Little and Wadsworth (1964, 1974).

^b Kirk (2009).

^c Howard (1988, 1989).

^d Saracco et al. (2005).

^e Liogier (1988).

^f Liogier and Martorell (2000).

^g Reyes et al. (1992).

^h Francis (1992).

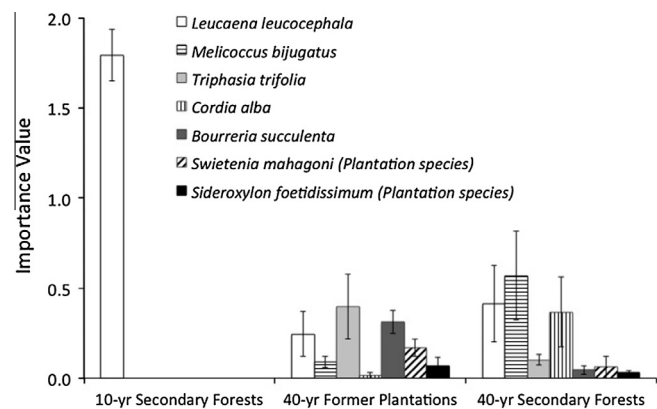


Fig. 5. Top five most important species for all diameter size classes based on importance values, plus planted timber plantation species in secondary forests of the dry life zone of St. Croix, U.S. Virgin Islands. Legend lists species in order of importance with the plantation species last.

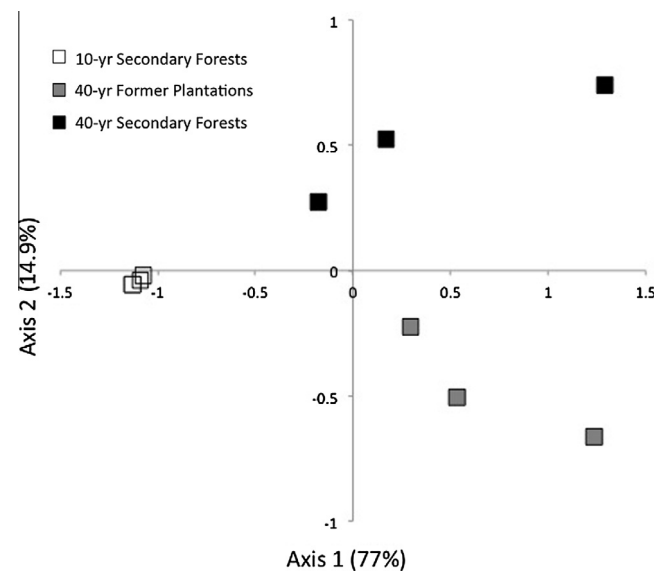


Fig. 6. Nonmetric multidimensional scaling (NMS) analysis results for importance values of all tree species in three replicate field sites for secondary forest types of the dry life zone of St. Croix, U.S. Virgin Islands: 40-year old secondary forests that naturally regenerated shortly after sugarcane abandonment (black), 40-year old secondary forests that were reforested with experimental timber plantations before forest management ceased and were overtaken by natural successional processes (gray), and 10-year old secondary forests that experienced an intermediate period of intensive pasture use prior to recent forest regeneration (white).

Table 4
Shannon–Weiner diversity and evenness across secondary forest sites of the dry life zone of St. Croix, U.S. Virgin Islands.

	Diversity	Evenness
10-yr Secondary Forests		
WOD	0.08	0.01
WOJ	0.13	0.02
BET	0.33	0.06
40-yr Former Plantations		
BEL	2.54	0.53
ETD	2.41	0.49
ETE	1.33	0.24
40-yr Secondary Forests		
ELP	2.02	0.50
CAN	2.48	0.51
EAD	1.83	0.47

aboveground biomass accumulation relative to natural succession (Lugo, 1992; Aide et al., 1995; Cusack and Montagnini, 2004; Holl and Zahawi, 2014), particularly since plantation species are often selected for rapid growth. Biomass accumulation in naturally regenerated secondary forests, especially those regrowing on abandoned agricultural land, tends to occur in later successional stages (Brown and Lugo, 1990; Guariguata and Ostertag, 2001; Holm et al., 2012), though rates depend on the intensity of previous land-use activities (Holl and Zahawi, 2014; Silver et al., 2000). Although a disparity in biomass accumulation may occur in early stages, evidence suggests that with time the biomass in former timber plantations and naturally regenerated secondary forests may converge. In a global meta-analysis of biomass accumulation rates for tropical secondary forests and former plantations, Bonner et al. (2013) found that biomass accumulation was higher in former plantations for sites <18 years since establishment, whereas there were no significant differences between former plantations and secondary forests for older sites (>18 years).

The pattern of aboveground biomass accumulation in timber plantations and naturally regenerated secondary forests is drawn from work in wet life zones since far fewer studies have compared such patterns in dry or seasonally dry tropical forests (Aide et al., 1995; Lugo, 1992; Cusack and Montagnini, 2004; Bonner et al., 2013; Chazdon, 2003). We suggest that the pattern of aboveground biomass convergence is applicable to dry forests. Dry forests are generally slower growing and tend to have slower rates of biomass accumulation (Vieira and Scariot, 2006; Silver et al., 2000) but can recover their relatively simple mature structure more rapidly after disturbance compared to wet forests (Murphy and Lugo, 1986). Our results from different AGB models also lend support to the convergence of structural characteristics between former plantations and naturally regenerated secondary forests. Although one model (van Breugel et al., 2011 with WSG included) clearly showed higher AGB estimates compared to the other two models, when each of the three models was considered individually, there was no significant difference in AGB between former plantations and naturally regenerated secondary forests.

Similarities in structural characteristics such as biomass and basal area between secondary forests on former plantations and those naturally regrowing after a short history of pasture use after sugarcane suggest that successional processes overcame the legacy of forest management in dry forests in St. Croix. The convergence of structural components between former tree plantations and natural secondary forests has been used to “jump start” forest regeneration on abandoned agricultural land and pave the way for mixed-species secondary forests (Vieira et al., 2009; Carnevale and Montagnini, 2002; Lugo, 1997; Parrotta et al., 1997; Powers et al., 1997).

4.2. Land-use history affects species composition of similarly aged secondary forests

Land-use history has been shown to have a significant long-term effect on species composition in subtropical dry forests (Molina Colón and Lugo, 2006; Molina Colón et al., 2011; Gillespie et al., 2000). The effect of a long period of intensive human land use can cause an ecosystem response that results in new combinations or abundances of species that are different enough from what was there before human use to be called novel ecosystems (Lugo and Helmer, 2004; Hobbs et al., 2006; Lugo, 2009). Previous work on novel ecosystems in dry forests of Puerto Rico has shown that after 45 years of forest recovery following agriculture, the emerging novel forests differed from original native forests in terms of species composition (Molina Colón and Lugo, 2006) and that over time the resultant species succession

Table 5

Sorenson dissimilarity matrix across secondary forests types and sites based on species abundance.

	10-yr Secondary Forests			40-yr Former Plantations			40-yr Secondary Forests		
	WOD	WOJ	BET	BEL	ETD	ETE	ELP	CAN	EAD
<i>10-yr Secondary Forests</i>									
WOD									
WOJ	0.13								
BET	0.33	0.21							
<i>40-yr Former Plantations</i>									
BEL	0.92	0.90	0.87						
ETD	0.92	0.91	0.88	0.45					
ETE	1.00	1.00	1.00	0.72	0.67				
<i>40-yr Secondary Forests</i>									
ELP	0.89	0.87	0.82	0.52	0.78	0.61			
CAN	1.00	1.00	0.99	0.68	0.61	0.66	0.77		
EAD	0.86	0.83	0.76	0.90	0.81	0.91	0.43	0.86	

appears to be a new mix of native and introduced species (Molina Colón et al., 2011).

In dry forests in St. Croix, we found that secondary forests with different land-use histories had distinct species composition, despite similarities in age and forest structure. Differences in species composition may be influenced by the lasting presence of former plantation species and their high importance values long after management has ceased, even 60 years after planting (Silver et al., 2004). The dominance of former plantation species can influence species composition through remnant trees and species interactions (Cusack and Montagnini, 2004). We found evidence that remnant trees from former timber plantations may indeed contribute to unique species composition when compared to naturally regenerated secondary forests. Although *L. leucocephala*, has a high importance value in both former plantations and naturally regenerated secondary forests in our study, there are strong differences in the abundance of other secondary forest species. Species that have high abundances in naturally regenerated secondary forests include the naturalized species *M. bijugatus* and the native species *C. alba*, both as small and large trees. Both species are common pioneer species in St. Croix (with *M. bijugatus* as a long-lived pioneer) and grow best in full sunlight (Table 3) (Choat et al., 2007; Francis, 1992; Little and Wadsworth, 1964). These species, although important in naturally regenerated secondary forests, did not have high importance values in any of the former plantations, which suggests that they may not have been able to establish in the shaded understory of *S. mahagoni* or *S. foetidissimum*. Instead, former plantations have high species abundances of *S. mahagoni* as large trees (and, *S. foetidissimum* in former plantations of this species) and of *B. succulenta* and *T. trifolia* as small trees, indicating that the latter species developed in the understory of plantation species since they had a higher shade tolerance. Plantation species did appear to facilitate the growth of native species such as *B. succulenta* and the species *Amyris elemifera*, *Krugiodendron ferreum*, and *Randia aculeata*, which were not present in naturally regenerated secondary forests, as well as of naturalized species such as *T. trifolia*.

Plantation species can facilitate the regeneration of a diverse set of species in dry forests (Griscom and Ashton, 2011). For example, in dry forests in Uganda, enrichment planting following pine plantations was not necessary to obtain a rich tree community with a large number of new recruits (Omeja et al., 2009). However, the ability to facilitate complex species composition does not necessarily mean this will result in the same set of species that would arise in a naturally regenerated forest.

As regeneration proceeds, plantation species may become less important even though they may act as catalysts in influencing species composition. Tropical tree plantations can allow for the establishment of high concentrations of native tree species in their

understory after human management ceases (Lugo, 1997). Planted species can fail to regenerate under their own shade or become less dominant at the site following abandonment of management practices, allowing other species to reach the canopy and reproduce (Lugo, 1997; Sansevero et al., 2011). Our results suggest that the dynamics of this process may not necessarily lead a former plantation to promote the growth of the same type of native species as a naturally regenerated secondary forest, nor similar abundances of such native species, which may lead to secondary forests of differing compositions, and novel species assemblages.

An important element to consider in St. Croix and other Caribbean forests is the effect of hurricanes, since these disturbance events can play an important role in shaping tropical dry forest structure (Van Bloem, 2005). In the case of St. Croix, the effects of hurricane damage may help to explain structural similarity and compositional dissimilarity between former plantations and naturally regenerated secondary forests. Hurricane Hugo struck St. Croix in 1989, as a Category 4 hurricane (winds 130–150 mph). At this time, naturally regenerating secondary forests were undergoing early succession and former plantations had been recently left unmanaged. Hurricanes can have strong influences on forest structure due to tree mortality, which can affect stem density and basal area (Scatena et al., 1996; Weaver, 1994). However, depending on mortality and sprouting, the structure of a forest may change but hurricane damage may not necessarily affect species composition. For instance, low mortality and abundant sprouting may lead to higher stem density without changing species composition (Van Bloem, 2005). Reviews of hurricanes in wet versus dry forests have shown that, in general, dry forests have lower mortality and damage (2–14% stem mortality and 7–22% loss in basal area) compared to wet forests (1–58% stem mortality, 10–58% loss in basal area) (Whigham et al., 1999). Previous studies have shown that plantations dominated by a single species of the same age can provide continuous canopy resistance to wind and therefore experience less damage and mortality during hurricanes (Van Bloem, 2005). Studies have also shown that there are low damage rates in the case of mahogany (Francis and Alemany, 2003; Van Bloem, 2005). Taken together, Hurricane Hugo in St. Croix may have contributed to rapid convergence of forest structure in the abandoned tree plantations and naturally regenerated forests without convergence of species composition. Depending on sprouting following Hurricane Hugo, the structure of both types of secondary forests may have been similarly affected, particularly if naturally regenerated forest stands had some large stems and similarly aged trees. However, species composition may not have been affected in the case of Hurricane Hugo. Other studies have shown persistence of historical legacies of land use on species composition through damaging hurricanes (Flynn et al., 2010;

Comita et al., 2010; Uriarte et al., 2004; Thompson et al., 2002; Boucher et al., 2001).

4.3. Age influences structural and compositional differences of secondary forests

In subtropical dry secondary forests in St. Croix, age played a significant role in the structure and composition of post-agricultural forests. Structurally, the 10-year old forests in our study were characteristic of early successional forests in the tropics, having a high density of small trees and a smaller basal area with nearly no large trees (Denslow and Guzman, 2001; Guariguata and Ostertag, 2001). Chronosequence studies have shown that forest age is a good predictor of forest structure, especially of basal area (Aide et al., 1996; Becknell and Powers, 2014; Chazdon et al., 2007; Madeira et al., 2009; Marín-Spiotta et al., 2008; Pascarella et al., 2000). In the first decade of tropical forest succession, vegetation is typically characterized by short-lived, light-demanding pioneer species, in particular by Fabaceae in dry life zones (Kalacska et al., 2004) and Rubiaceae and Melastomataceae in wet life zones (Guariguata and Ostertag, 2001).

Past human activities can explain the prevalence of non-native species in post-agricultural landscapes (Lugo and Helmer, 2004; Aide et al., 2000). At our study sites, *L. leucocephala* (Fabaceae) dominated 10-year old secondary forests. This species was first introduced to St. Croix during the Spanish colonial trade (1565–1825) and later became naturalized throughout the West Indies, eventually being used as cattle feed in pastures (Parrotta, 1992; Brandeis and Oswalt, 2007; Kirk, 2009). The dominance of this species is consistent with recent island-wide forest inventories that found *L. leucocephala* was the most dominant species across all of the U.S. Virgin Islands (Brandeis and Oswalt, 2007) and with other dry forest studies that showed dominance correlated with intensity or frequency of disturbance (Parrotta, 2000; Molina Colón and Lugo, 2006). The non-native legume establishes in highly degraded areas and forms persistent, mono-dominated stands, where slow growth of native saplings contribute to the dominance of *L. leucocephala* in successional forests (Wolfe and Van Bloem, 2012).

In highlighting the differences in structure and species composition between the 10-year old and 40-year old forests, it is important to note that the degree of disturbance plays a strong role in determining regeneration processes (Chazdon, 2003). Compared to both types of 40-year forests, the 10-year forests dominated by *L. leucocephala* underwent a longer, more intensive pasture period. However, the greater degree of disturbance in the younger forests also shows the potential of *L. leucocephala* to restore ecosystem function and structure. *L. leucocephala* creates a thin canopy with a moderately shaded understory, fixes nitrogen, and has readily decomposed leaf litter that provides an N-rich mulch on the forest floor, which some contend supports a diversity of natural regeneration (Parrotta, 1999; Santiago-García et al., 2008). Although this species is considered highly invasive, it is not known to replace native tropical dry forest species nor does it regenerate under itself without the aid of repeated disturbance (Molina Colón and Lugo, 2006). Furthermore, *L. leucocephala* fosters understory re-establishment of native species by shading out grasses, thereby reducing fuel loads that would increase fire intensity and allow it to establish instead of native species (Santiago-García et al., 2008; Wolfe and Van Bloem, 2012). Currently, the 10-year forests dominated by *L. leucocephala* are structurally and compositionally distinct from older forests. The long-term trajectory of these sites remains to be seen but their extended intense disturbance history and distinct land-use history compared to other forest types in St.

Croix suggests they may remain compositionally distinct in the future.

Tropical dry forests in St. Croix have not only developed on land that was heavily used for centuries but they continue to grow within a currently urbanizing human-dominated landscape, exposed to further conversion, species introductions and environmental pollution. Their sensitivity to seasonality in rainfall and drought, and encroaching human population growth make them increasingly vulnerable to future disturbance. In the face of such severe threats, we must recognize that these traditionally understudied forests can provide valuable ecosystem services such as reducing surface runoff and increasing infiltration for aquifer recharge (Weaver, 1996), protecting offshore marine habitat from soil erosion (Rogers, 1998), and serving as biological refuges for endangered species (Weaver, 2006). Understanding how land-use history may affect their regeneration in the form of structure and composition will allow us to better protect and manage these forests as well as predict how they might respond to future disturbance.

5. Conclusion

This study highlights different legacies of past land use and disturbance on forest structure and species composition in tropical dry forests. Former plantations and secondary forests that regenerated following sugarcane agriculture had similar structural characteristics, in terms of basal area, stem density, and aboveground biomass after 40 years of plantation abandonment. These forests also had similar species diversity, despite tree planting and different management histories, providing evidence for the role of plantation trees in promoting establishment of diverse understories and canopies during forest succession. Species composition, however, remained distinct between the two types of 40-year old secondary forests and the legacies of former land use persist through hurricane disturbance. Younger successional forests with a longer history of intensive land use differed in structure and species composition, with very low species richness. Although forests with differing land-use histories may structurally resemble one another within a few decades of regeneration, species composition may remain distinct for much longer periods of time, which may have implications for the management of plantations in dry forest post-agricultural landscapes. Knowing how land-use history affects regeneration in some of the most heavily used and fragmented tropical forests will allow us to predict how they might respond to future human and climatic disturbance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.09.033>.

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