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Abstract

Tropical dry forests (TDF) are highly threatened ecosystems that are often fragmented due to land-cover change. Using plot inventories, we analyzed tree species diversity, community composition and aboveground biomass patterns across mature (MF) and secondary forests of about 25 years since cattle ranching ceased (SF), 10–20-year-old plantations (PL), and pastures in a TDF landscape in Ecuador. Tree diversity was highest in MF followed by SF, pastures and PL, but many endemic and endangered species occurred in both MF and SF, which demonstrates the importance of SF for species conservation. Stem density was higher in PL, followed by SF, MF and pastures. Community composition differed between MF and SF due to the presence of different specialist species. Some SF specialists also occurred in pastures, and all species found in pastures were also recorded in SF indicating a resemblance between these two land-cover types even after 25 years of succession. Aboveground biomass was highest in MF, but SF and *Tectona grandis* PL exhibited similar numbers followed by *Schizolobium parahyba* PL, *Ochroma pyramidale* PL and pastures. These findings indicate that although species-poor, some PL equal or surpass SF in aboveground biomass, which highlights the critical importance of incorporating biodiversity, among other ecosystem services, to carbon sequestration initiatives. This research contributes to understanding biodiversity conservation across a mosaic of land-cover types in a TDF landscape.

Keywords

aboveground biomass, pasture, plantations, secondary forest, tree diversity, tropical dry forest

Introduction

Global biodiversity is declining at alarming rates (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES], 2019) and land-cover change is the main cause (Daskalova et al., 2020; IPBES, 2019). The relationship between land-cover change and biodiversity loss is particularly evident in biodiversity hotspots in tropical dry forests (TDFs e.g., Sloan et al., 2014). TDFs are among the most highly threatened ecosystems on Earth, with the largest remnants located in South America (Miles et al., 2006) which is particularly understudied relative to other TDF regions (Sanchez-Azofeifa et al., 2005).

TDFs in South America were mostly cleared for agriculture, particularly cattle ranching (Aide et al., 2013; Miles et al., 2006). Despite a long history of land use change in the region, our understanding about the regeneration ecology and conservation value of fragments that remain, including old-growth and secondary forests,

as well as the managed land-cover types that now characterize TDF landscapes is limited. Some studies suggest that species richness in regenerating TDF could reach similar values to those of old-growth forest. This regeneration could happen at similar or even greater rates than those observed in wet forests because of the

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resprouting capacity and dominance of wind-dispersed species in TDF (Chazdon, 2014; Chazdon et al., 2007; Hilje et al., 2015; Kennard, 2002; Lebrija-Trejos et al., 2008). In Mesoamerica, TDF in the intermediate stages of regeneration from pasture were found to be richer in species than older forests (Hilje et al., 2015), and in Bolivia species richness in TDF reached mature forest levels a couple of decades after cessation of slash-and-burn agriculture (Kennard, 2002). In regards to stem densities, adult tree densities tends to decrease as regeneration progresses but that of saplings could show different pattern (Dupuy et al., 2012). While these findings are promising for TDF regeneration, other studies suggest that due to soil damage, TDF recovery after shifting cultivation can be slow (Lawrence et al., 2007). In TDF regenerating from pastures, persistent alien grasses can limit tree regeneration (Cabin et al., 2000; Lyons-Galante & Haro-Carrión, 2017). Rainfall patterns and the presence of established trees also affect succession rates and trajectories (Derroire et al., 2016; Kennard et al., 2002). Despite these differences in species recovery, there is agreement that, as in wet forests, species composition recovery lags behind changes in species densities and forest structural changes (e.g. biomass, stem density) in TDF (Chazdon, 2014; Chazdon et al., 2007). These findings indicate that documenting species richness and community composition in mature and secondary TDF is still needed to improve our knowledge of how diversity is maintained over a broad range of land-cover types and across various TDF landscapes within the Neotropics.

Few evaluations of biodiversity in TDF managed land-uses (e.g. agriculture, plantations) exist, probably because it is expected that most managed land-uses host fewer tree species than forest. A study by Mora et al. (2016) in Mexico reported trade-offs between tree species richness and fodder production, but observed no trade-off between tree species richness and aboveground biomass in old-growth forests and pastures. In landscapes where tree plantations occur, these biomass – species richness relationship could be different because plantations, like forests, accumulate high amounts of biomass but are less diverse than forests. Few studies have directly compared biomass in natural and plantation forests in TDF landscapes. One study in India indicates that plantation forests store more biomass than natural forests (Guha et al., 2019). In the Neotropics, comparisons across studies suggest a similar trend (Kirby & Potvin, 2007; Kraenzel et al., 2003; Read & Lawrence, 2003; Wishnie et al., 2007). Tree plantations can have a broad range of management objectives in TDF landscapes. Some could have restoration purposes and involve native species while others involve introduced species for timber production (Assis et al., 2013; Kirby & Potvin, 2007; Maneschy et al., 2010;

Vleut et al., 2013; Wishnie et al., 2007). For instance, teak (*Tectona grandis*), an introduced species in the Americas, grows in TDF regions and has even been proposed as a climate mitigating strategy to sequester atmospheric carbon (Kirby & Potvin, 2007; Kraenzel et al., 2003). Because of these varied objectives, careful attention is needed to understand the ecological role of plantations. For example, if carbon sequestration is considered, other ecosystem services and biodiversity could be in jeopardy (Coomes et al., 2008). Given this complexity, it seems critical to document both biomass and the richness and composition of species over natural and managed land-cover types in TDF.

This research investigates variation in tree species diversity, community composition, and aboveground biomass across the main land-cover types of a highly fragmented TDF landscape in Ecuador. We aim to fill gaps in knowledge about biodiversity conservation over a broader range of land-cover types, including managed land-uses, and to provide critical information about floristic composition and species diversity for a TDF region less documented in the scientific literature.

Methods

Study Area

The study landscape encompasses an area of about 36,000 ha of semi-deciduous tropical vegetation between the towns of Pedernales (0°4'20"N 80°3'0"W) and Jama (0°12'07"S 80°15'49"W) (Figure 1), considered the largest remnant of this vegetation type in Ecuador (Neill, 1999). Lowland semi-deciduous tropical vegetation extends along the coast approximately 20 km inland with elevations of 100–400 m. This vegetation type is characterized by temperatures around 25°C with little seasonal variation, annual precipitation of about 1500–2500 mm with a dry season of around 4 months with precipitation as low as 3 mm per month (Josse & Balslev, 1994; Neill, 1999). The terrain includes steep slopes with valleys used for agriculture and cattle ranching. Semi-deciduous forest canopy cover varies; some forests have relatively open canopies and dense understories while others have more closed canopies with lower understory development. Some tree species are thorny and some lose their leaves during the dry season (e.g., *Cochlospermum vitifolium* and *Tabebuia chrysantha*). Species characteristic of this vegetation type include *Gallesia integrifolia* (Phytolacaceae), *Triplaris cumingiana* and *Cocoloba mollis* (Polygonaceae), *Pseudolmea rigida* (Moraceae), and *Eugenia* spp. (Myrtaceae) (Sierra, 1999).

The landscape is about 40% forested, with about half relatively well-preserved forests while the other half is either severely degraded (i.e. selectively logged) or

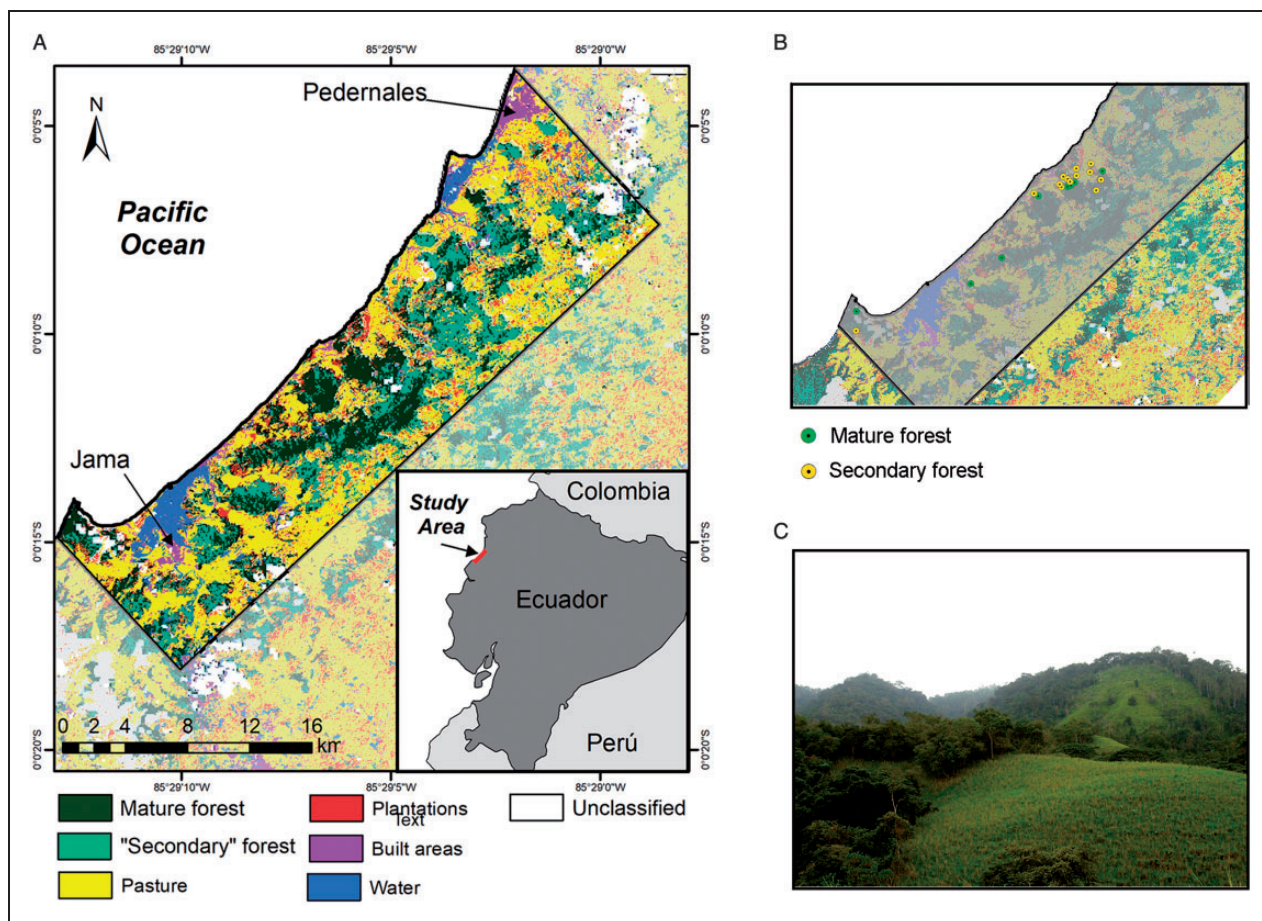


Figure 1. Study area in coastal Ecuador. A: Land-cover classification from Haro-Carrión & Southworth (2018), "Secondary forest" includes secondary and degraded forests; B: Location of sampling sites for mature and secondary forests; C: Detail of forest – pasture edges.

secondary. The major land-cover types in the study area include mature forest (MF), secondary (SF) and degraded forest, pasture, and forestry plantation (PL) (Haro-Carrión & Southworth, 2018) (Figure 1A). MF with many old-growth characteristics but some previous anthropogenic disturbances (e.g., light selective logging) accounts for about 15% of the landscape. Some MF occurs in slopes, likely because these areas are less suited for cattle, but some occur in relatively flat areas and by the coastline because of land-management choices. A couple are now protected in private reserves. SF results from pasture abandonment or pasture-fallow cycles. They are reported to be about 25 years old by landowners, which in the majority of cases was corroborated by remote sensing (Haro-Carrión & Southworth, 2018). The extent of SF in the landscape is not fully known because degraded and SF are difficult to differentiate using Landsat data, but together they account for about 25% of the landscape (Haro-Carrión & Southworth, 2018). Accounting for about 50% of the study area, pasture dominates the landscape and is

planted with exotic grass species used in cattle ranching. Typically, pastures have scattered trees of several different species that provide shade for the cattle (Figure 1B and C). Even-aged mono-cultural PL of teak (*Tectona grandis*), pachaco (*Schizolobium parahyba*), and balsa (*Ochroma pyramidale*) cover about 10% of the landscape. Teak and pachaco PL were estimated to be 15–20, and balsa PL 10–15 years old. The study area is considered a biodiversity hotspot because of low cover of native vegetation and its exceptionally high species diversity and endemism (Myers et al., 2000).

Field Data Collection

Field inventories during the summers of 2010 and 2012 were used to estimate aboveground biomass and tree diversity in all major land-cover types. The entire study area is characterized by privately owned property. We attempted to sample across the entire study area, but site selection was constrained by the ability to secure permission to access and sample sites. An average distance of approximately 7,500 m separates MF and SF

sites from one another, but some are less than 500 m apart. SF typically bordered both pastures and MF while PL of all types were typically embedded in the pasture matrix (Figure 1B).

In MF, SF, and pastures at random locations, we established 60 × 60 m plots to sample trees >20 cm DBH (stem diameter at 1.3 m or above buttresses) with a nested 20 × 20 m plot for trees 10–20 cm DBH (modified after Magnusson et al., 2005; Phillips et al., 2003). Only the smaller plots were used to sample PL because tree species richness and variation in stem density was low and did not require a more complex sampling approach. To avoid the effect of edges, we located sampling plots at distances >50 m from edges, which was facilitated by characteristically sharp edges in most forest (both MF and SF) – pasture edges (Figure 1C). Less pronounced edges were found of some SF. In these cases, we tried to locate our plots in the middle of the patch. We sampled a total of eight MF, 13 SF, 10 pastures, four *Tectona grandis* PL, and three *Schizolobium parahyba* and *Ochroma pyramidale* PL. Species were categorized as endemic, native, or introduced to Ecuador and noted for their conservation status based on IUCN criteria. Taxonomy is based on <https://www.tropicos.org/> (2020). Specimen processing was undertaken in the facilities of the QCA Herbarium and specialists assisted with species identification in the QCA and QCNE Herbaria in Quito. Voucher specimens were deposited at QCA and QCNE.

Tree Species Diversity and Composition

To compare land-cover types on the basis of tree diversity, we used individual-based rarefaction curves and the Mao Tao estimator computed with EstimateS software (V.8.2) to correct for differences in stem densities (e.g., Colwell et al., 2004; Gotelli & Colwell, 2001). The significance of observed differences in species richness between land-cover types (at $P < 0.05$) was evaluated by visually comparing rarefaction curves and their associated 95% confidence intervals (CIs). PL of *Schizolobium parahyba*, *Ochroma pyramidale* and pastures did not have enough individuals to be included in rarefaction analysis.

To assess tree community similarities of the eight MF and 13 SF, we examined patterns in assemblage composition using a multidimensional scaling analysis (NMDS; Saeed et al., 2018). To deal with rarely sampled species, the species abundance by site matrix was transformed using a Wisconsin double standardization (Bray & Curtis, 1957). Then, we used the transformed matrix to create a Bray-Curtis dissimilarity matrix and used this matrix to generate an NMDS of tree species composition by site. To understand separate sites in terms of their species composition, we report which tree species

had high and low positive loadings on both axes of the NMDS.

Prior to conducting the NMDS, to examine if proximity of plots among sample sites influenced similarity of tree species compositions, we conducted a Mantel test (Dutilleul et al., 2000; Rossi, 1996). To do this, we generated distance matrices based on geographic distance (i.e. Euclidean distance) and tree composition matrices using the Jaccard index. We rejected the hypothesis that spatial distance affected similarities in tree species composition (Mantel statistic based on Pearson's product-moment correlation = 0.09126; $p = 0.157$) and proceeded with the NMDS. The statistical significance of community composition differences between MF and SF was tested using a PERMANOVA (Permutational Multivariate Analysis of Variance) (McArdle & Anderson, 2001). We focused this analysis on MF and SF because species stem density and species richness were too low in pastures and PL to produce meaningful results.

Biomass Estimation

Aboveground biomass estimations for MF, SF, pastures and all three PL types were calculated using an equation for 'moist forests' based DBH and wood density. This equation was selected because it fits well the annual and seasonal precipitation patterns of the study area (Chave et al., 2005)

$$AGB_{est} = p \times \exp\left(-1.499 + 2.148 \ln(D) + 0.207 \left(\ln(D)\right)^2 - 0.0281 \left(\ln(D)\right)^3\right)$$

where:

AGB – Aboveground biomass

p – Wood density

D – Diameter at breast height (DBH)

For wood density we used the average of reported values for South America for each species (Zanne et al., 2009); if the species was not found in the database we used values for the genus; if the genus was not represented we used the average value for the family (1 species). For 4 species, values from other regions of the world were used because no reported data were found from South America. AGB estimations were scaled up to megagrams per hectare (Mg/ha) for easier interpretation and comparison among land-cover types. We compared land-cover types on the basis of AGB with one-way analysis of variance (ANOVA) after testing for normality with the Shapiro-Wilks method and checked graphically for homoscedasticity by plotting the residuals versus fitted values of the ANOVA model. Statistics were done using R 4.0.2 (R Core Team, 2020), with

'vegan' (Oksanen et al., 2019) for community composition, 'tidyverse' (Hadley Wickham et al., 2019) for data manipulation, and 'ggplot2' (H. Wickham, 2016) for graphing.

Results

Species Diversity

A total of 124 tree species were recorded, including 10 endemic to Ecuador and 15 with IUCN conservation status (Table 1). Species of conservation concern occurred mostly in MF, but half of the species present in MF also occurred in SF and one species was only found in SF. Tree species in pastures and PL were all native with the exception of *Tectona grandis* (Table 1).

Tree species richness was highest in MF followed by SF, pastures and PL (Table 2). The same sequence was found for rarefaction curve-based estimates of diversity, but excluding PL of *Schizolobium parahyba* and *Ochroma pyramidale*, and pastures that did not have enough individuals to be included (Figure 2). Species richness numbers indicate that a similar diversity pattern to that of *Tectona grandis* PL is expected in PL of the other two species. Pastures were richer in species than PL, with 10 species recorded among 30 trees sampled in 10 pasture sites. Stem densities of trees >10 cm DBH standardized to per hectare values were highest in PL, followed by MF, SF, and pastures (Table 2).

Community Composition

Tree species composition in MF and SF plots differed significantly (PERMANOVA $F = 2.3345$, $p < 0.001$). The NMDS produced a solution with a stress value of 0.13, indicating a good representation of the data when reduced to two dimensions. The NMDS indicates that community differences are due to the presence of unique species in each. NMDS MF plots clustered closely while SF were more dispersed, with one (SF13) more similar to MF than SF. This site was classified as MF through remote sensing analysis (Haro-Carrión & Southworth, 2018), so it is possible that it was just miss-reported by landowners as SF when it is actually a selectively-logged forest. On the first NMDS axis, rare MF species had the most negative loadings while rare SF species had the most positive loadings. On the second axis, rare SF species contributed the most to both the higher and lower ends of the axis (Figure 3).

Aboveground Biomass

AGB differed among land-cover types ($F = 19.12$, $p < 0.001$); a Tukey post-hoc revealed that MF supported higher AGB on average than any other land cover type. Twenty-five-year-old SF and 15-20-year-old

Tectona grandis PL were similar in AGB followed by 15–20-year-old *Schizolobium parahyba* PL with lower but not significantly different values to those of SF or teak PL. Pastures supported the lowest AGB, but not significantly lower than 10–15-year-old *Ochroma pyramidale* PL (Figure 4).

Discussion

Land-cover change is driving massive losses of biodiversity globally (Daskalova et al., 2020, IPBES, 2019). Given the irreplaceable regulating, material, and spiritual services of biodiversity, understanding species diversity and community composition patterns across mosaics of land-cover types is of paramount importance, especially in landscapes such as tropical dry forests.

Our data from a TDF in Ecuador on tree species diversity, stem density and community composition indicate that it is possible that SF are in earlier or intermediate stages of succession compared to other TDFs of similar age. Although, it is difficult to make cross-study comparisons with the existing literature because of different sampling methodologies (i.e. different minimum tree size sampled), findings from other regions could offer some insights. In Mesoamerica, 32 year-old SF regenerating from pastures were richer in species than forests both older and younger than them by decades (Hilje et al., 2015), and chronosequence data indicate species characteristic of MF could start dominating forest composition about 40 years of succession after agricultural abandonment (Lebrija-Trejos et al., 2008). While these findings might suggest that after an additional 5–15 years of succession, what were 25-year old SF at the time of this study could reach species richness numbers comparable to MF, tree stem density and community assemblages patterns indicate otherwise. We found lower tree stem density of trees >10 DBH in SF than in MF, which does not correspond to patterns expected for mid-succession SF (Chazdon, 2014; Chazdon et al., 2007; Dupuy et al., 2012). The absence of MF specialists in SF communities is also characteristic of early or intermediate stages of regeneration (Chazdon, 2014; Hilje et al., 2015; Lebrija-Trejos et al., 2008). However, we acknowledge that successional patterns of both stem density and species composition could vary when trees <10 cm DBH (not considered in this study) are included in the analysis (Dupuy et al., 2012). Finally, SF specialists, absent in MF communities, were found in pastures indicating a close resemblance between pasture and SF after 25 years of succession. Floristic inventory details show that all 10 species found in pastures were also recorded in SF in equal or higher numbers. In contrast, only seven of these 10 species were recorded in MF and in equal or lower numbers than in SF. Some of these species include *Guazuma ulmifolia* and *Cochlospermum*

Table 1. Species Stem Density, Status in Ecuador Accompanied by IUCN Conservation Status If Available, and Wood Densities for Tree Species in Mature Forest (MF; N = 8), Secondary Forest (SF; N = 13), Pastures (Pa; N = 10), and Forestry Plantations (PI; N = 10).

Family	Species	Density (ind >10 cm DBH/ha)				Status	Wood Density (g/cm ³)
		MF	SF	Pa	PI		
Achariaceae	<i>Mayna odorata</i>	1	–	–	–	Native	0.61
Anacardiaceae	<i>Mauria suaveolens</i>	2	2	<1	–	Native	0.31
	<i>Spondias mombin</i>	9	1	1	–	Native	0.40
Annonaceae	<i>Annona muricata</i>	<1	4	–	–	Native and cultivated	0.32
	<i>Klarobelia megalocarpa</i>	3	–	–	–	Endemic vulnerable	0.59
	<i>Mosannonna pacifica</i>	4	2	–	–	Endemic endangered	0.59
	<i>Rollinia mucosa</i>	–	2	–	–	Native	0.32
Apocynaceae	<i>Rauvolfia littoralis</i>	<1	–	–	–	Native	0.48
Arecaceae	<i>Phytelephas aequatorialis</i>	8	4	–	–	Native	0.43
Asteraceae	<i>Fulcaldea laurifolia</i>	20	3	–	–	Native	0.60
	<i>Vernonanthura patens</i>	–	13	–	–	Native	0.60
Bignoniaceae	<i>Tabebuia chrysantha</i>	2	1	–	6	Native	1.00
	<i>Tabebuia guayacan</i>	44	44	–	–	Native	0.82
	<i>Tecoma castaneifolia</i>	–	18	–	–	Native	0.79
Bixaceae	<i>Cochlospermum vitifolium</i>	6	17	<1	–	Native	0.22
Burseraceae	<i>Bursera graveolens</i>	<1	2	–	–	Native	0.32
Capparaceae	<i>Capparidastrum cf. pachaca</i>	3	–	–	–	Native	0.68
Celastraceae	<i>Maytenus octogona</i>	4	–	–	–	Native	0.72
Chrysobalanaceae	<i>Licania sp.</i>	1	–	–	–	Unknown	0.82
Cordiaceae	<i>Cordia alliodora</i>	1	21	–	–	Native	0.52
	<i>Cordia hebeclada</i>	–	5	–	–	Native	0.52
Erythroxylaceae	<i>Erythroxylum ruizii</i>	4	–	–	–	Native	0.79
Euphorbiaceae	<i>Adelia triloba</i>	3	–	–	–	Native	0.54
	<i>Alchornea leptogyna</i>	13	–	–	–	Native near threatened	0.42
	<i>Croton fraseri</i>	–	2	–	–	Endemic endangered	0.46
	<i>Croton glabellus</i>	54	2	–	–	Native	0.46
	<i>Sapium laurifolium</i>	2	<1	<1	–	Native	0.41
Fabaceae	<i>Acacia macracantha</i>	–	2	–	–	Native	0.73
	<i>Acacia sp.</i>	3	–	–	–	Native	0.66
	<i>Bauhinia aculeata</i>	3	2	–	–	Native	0.64
	<i>Bauhinia sp.</i>	25	–	–	–	Unknown	0.64
	<i>Brownea coccinea</i> subsp. <i>angustiflora</i>	1	–	–	–	Native	1.21
	<i>Caesalpinia sp.</i>	3	–	–	–	Native	1.01
	<i>Centrolobium ochroxylum</i>	5	<1	–	–	Native	0.69
	<i>Cynometra cf. bauhiniifolia</i>	6	–	–	–	Native	0.84
	<i>Erythrina smithiana</i>	<1	<1	–	–	Endemic endangered	0.19
	<i>Geoffroea spinosa</i>	1	1	–	–	Native	0.67
	<i>Inga sp.</i>	4	3	–	–	Unknown	0.58
	<i>Leucaena trichodes</i>	–	4	–	–	Native	0.65
	<i>Lonchocarpus atropurpureus</i>	6	12	–	–	Native	0.73
	<i>Machaerium millei</i>	20	17	–	–	Native	0.24
	<i>Ormosia sp.</i>	<1	–	–	–	Native	0.61
	<i>Prosopis cf. pallida</i>	2	2	<1	–	Native	0.88
	<i>Prosopis juliflora</i>	–	<1	<1	–	Native	0.74
	<i>Pseudosamanea guachapele</i>	–	11	<1	–	Native	0.51
	<i>Pterocarpus cf. rohrii</i>	1	–	–	–	Native	0.46
<i>Samanea saman</i>	–	2	1	–	Native	0.50	
<i>Schizolobium parahyba</i>	–	–	–	333	Native	0.35	
<i>Senna alata</i>	<1	–	–	–	Native and cultivated	0.56	
<i>Senna spectabilis</i>	–	3	–	–	Native and cultivated	0.56	
<i>Swartzia littlei</i>	5	1	–	–	Endemic endangered	0.83	

(continued)

Table 1. Continued.

Family	Species	Density (ind >10 cm DBH/ha)				Status	Wood Density (g/cm ³)	
		MF	SF	Pa	PI			
Lamiaceae	<i>Aegiphila alba</i>	–	21	–	–	Native	0.66	
	<i>Tectona grandis</i>	–	–	–	963	Introduced and cultivated	0.60	
Lauraceae	<i>Licaria cf. triandra</i>	<1	–	–	–	Native	0.47	
Lecythidaceae	<i>Gustavia angustifolia</i>	3	6	–	–	Native endangered	0.65	
	<i>Gustavia serrata</i>	<1	–	–	–	Endemic endangered	0.65	
Malpighiaceae	<i>Bunchosia cf. cornifolia</i>	–	2	–	–	Native and cultivated	0.65	
Malvaceae	<i>Ceiba trischistandra</i>	5	–	–	–	Native	0.32	
	<i>Eriotheca ruizii</i>	<1	<1	–	–	Native	0.39	
	<i>Herrania balaensis</i>	<1	–	–	–	Native endangered	0.44	
	<i>Guazuma ulmifolia</i>	8	92	<1	–	Native	0.51	
	<i>Ochroma pyramidale</i>	–	<1	–	725	Native and cultivated	0.14	
	<i>Pachira rupicola</i>	1	<1	–	–	Native	0.45	
	<i>Pseudobombax millei</i>	3	1	–	–	Endemic data deficient	0.27	
	Meliaceae	<i>Guarea glabra</i>	19	–	–	–	Native	0.60
		<i>Ruagea glabra</i>	<1	–	–	–	Native	0.47
		<i>Trichilia hirta</i>	<1	–	–	–	Native	0.60
<i>Trichilia</i> sp.		–	4	–	–	Unknown	0.66	
Moraceae	<i>Brosimum alicastrum</i>	37	2	–	–	Native	0.63	
	<i>Castilla elastica</i>	2	4	–	–	Native	0.82	
	<i>Clarisia biflora</i>	1	–	–	–	Native	0.48	
	<i>Ficus</i> sp.	1	<1	–	–	Unknown	0.41	
	<i>Maclura tinctoria</i>	<1	<1	–	–	Native	0.79	
	<i>Piratinera guianensis</i>	<1	–	–	–	Native	0.84	
	<i>Trophis racemosa</i>	1	2	–	–	Native	0.56	
	Myristicaceae	<i>Virola sebifera</i>	<1	–	–	–	Native	0.46
Myrtaceae	<i>Calyptanthes fusca</i>	1	–	–	–	Native	0.78	
	<i>Eugenia aff. florida</i>	1	–	–	–	Unknown	0.68	
	<i>Eugenia aff. oerstediana</i>	1	–	–	–	Unknown	0.76	
	<i>Eugenia cf. oerstediana</i>	1	–	–	–	Native	0.76	
	<i>Eugenia florida</i>	1	6	–	–	Native	0.68	
	<i>Myrcia cf. fallax</i>	1	–	–	–	Native	0.82	
	<i>Psidium guajava</i>	–	1	–	–	Native and cultivated	0.63	
	Nyctaginaceae	<i>Neea</i> sp.	10	2	–	–	Native	0.68
Olacaceae	<i>Heisteria cf. acuminata</i>	<1	–	–	–	Native	0.70	
Petiveriaceae	<i>Gallesia integrifolia</i>	6	1	–	–	Native	0.51	
Picramniaceae	<i>Picramnia latifolia</i>	3	–	–	–	Native	0.40	
Polygonaceae	<i>Coccoloba cf. densifrons</i>	<1	–	–	–	Native	0.58	
	<i>Coccoloba cf. obovata</i>	13	–	–	–	Native	0.61	
	<i>Triplaris cumingiana</i>	5	<1	<1	–	Native	0.52	
Primulaceae	<i>Jacquinia sprucei</i>	–	<1	–	–	Native	0.61	
Rhamnaceae	<i>Ziziphus thyrsoiflora</i>	5	–	–	–	Native	0.85	
Rubiaceae	<i>Alibertia</i> sp.	3	–	–	–	Native	0.73	
	<i>Alseis eggersii</i>	10	<1	–	–	Native	0.75	
	<i>Faramea occidentalis</i>	3	–	–	–	Native	0.58	
	<i>Guettarda acreana</i>	20	4	–	–	Native	0.87	
	<i>Guettarda hirsuta</i>	<1	–	–	–	Native	0.71	
	<i>Joosia</i> sp.	<1	–	–	–	Unknown	0.65	
	<i>Randia carlosiana</i>	<1	2	–	–	Endemic endangered	0.67	
	<i>Simira cordifolia</i>	<1	–	–	–	Native	0.66	
	<i>Simira rubescens</i>	7	–	–	–	Native	0.80	
	Rutaceae	<i>Zanthoxylum martinicense</i>	<1	–	–	–	Native	0.60
<i>Zanthoxylum riedelianum</i> subsp. <i>kellermanii</i>		7	1	–	–	Native	0.61	
Sabiaceae	<i>Meliosma occidentalis</i>	<1	–	–	–	Native	0.52	

(continued)

Table 1. Continued.

Family	Species	Density (ind >10 cm DBH/ha)				Status	Wood Density (g/cm ³)
		MF	SF	Pa	PL		
Salicaceae	<i>Casearia sylvestris</i>	<1	2	–	–	Native	0.72
Sapindaceae	<i>Cupania americana</i>	–	22	–	–	Native	0.73
	<i>Exothea paniculata</i>	5	9	–	–	Native	0.73
Sapotaceae	<i>Sapindus saponaria</i>	<1	1	–	–	Native	0.67
	<i>Talisia setigera</i>	23	–	–	–	Native endangered	0.84
	<i>Chrysophyllum</i> aff. <i>argenteum</i>	<1	1	–	–	Native	0.78
	<i>Chrysophyllum</i> sp.	<1	–	–	–	Native	0.76
	<i>Pouteria brevipetiolata</i>	<1	–	–	–	Endemic endangered	0.78
	<i>Pouteria cordiformis</i>	<1	–	–	–	Endemic	0.78
	<i>Pradosia montana</i>	15	–	–	–	Native	0.73
Solanaceae	<i>Pradosia</i> sp.	3	–	–	–	Native	0.73
	<i>Acnistus arborescens</i>	–	1	–	–	Native and cultivated	0.50
Ulmaceae	<i>Solanum</i> sp.	–	<1	–	–	Unknown	0.50
	<i>Ampelocera longissima</i>	1	–	–	–	Native least concern	0.67
Unidentified	<i>Ampelocera macphersonii</i>	–	1	–	–	Native	0.67
		<1	–	–	–	Unknown	0.61
Urticaceae		–	8	–	–	Unknown	0.35
	<i>Cecropia</i> sp.	–	8	–	–	Unknown	0.35
Zamiaceae	<i>Urera baccifera</i>	6	2	–	–	Native	0.17
	<i>Zamia poeppigiana</i>	1	–	–	–	Native least concern	0.61

Taxonomy based on Tropicos.org (2020).

Table 2. Total Tree Species Richness, Number of Endemics, Number of Species With IUCN Status, and Average Stem Density Among Analysed Land-Cover Types for Trees >10 cm DBH.

Land-use	Species richness	No. endemic species	No. species with IUCN status	Area sampled (ha)	Av. stem density (ind/ha)
Mature forest	99	9	14	3.2	183 ± 49
Secondary forest	68	6	7	5.2	130 ± 57
Pasture	10	0	0	7.47	4 ± 4
<i>Tectona grandis</i>	2	0	0	0.16	969 ± 120
<i>Schizolobium parahyba</i>	1	0	0	0.12	333 ± 14
<i>Ochroma pyramidale</i>	1	0	0	0.12	725 ± 189

vitifolium, two species previously reported as typical of early stages of post-agricultural succession (Hilje et al., 2015). We believe that given the continuous perturbations from cattle and the presence of exotic grasses in many of the SF we studied (Lyons-Galante & Haro-Carrión, 2017), succession is happening at a slower pace comparable to that found in other TDF with similar histories of grazing (Cabin et al., 2000).

As expected, tree species richness was lower in pastures and all PL types, but documenting this finding is important for assessing species richness across land-cover types and, in the case of PL, for analysing tree species richness in conjunction with aboveground biomass. *Ochroma pyramidale* is a native species used in restoration and reforestation projects, and in cases its use has been aligned with biodiversity conservation

objectives (Vleut et al., 2013; Wishnie et al., 2007). The *Ochroma pyramidale* PL studied in this research were considered by landowners as examples of “reforestation” but our findings indicate low species richness and a limited carbon storage when compared to the other analysed land-cover types. Less is known about the use of *Schizolobium parahyba* for restoration in TDF landscapes, but a similar pattern to that of *Ochroma pyramidale* might be expected based on its use elsewhere in the Neotropics (Assis et al., 2013; Maneschy et al., 2010). *Tectona grandis* is an introduced species. Its cultivation has been analyzed in reforestation initiatives in other TDF landscapes (Kraenzel et al., 2003). In the studied landscape, landowners reported limited environmental benefits to its cultivation, did not associate it with carbon sequestration initiatives, and mostly gave

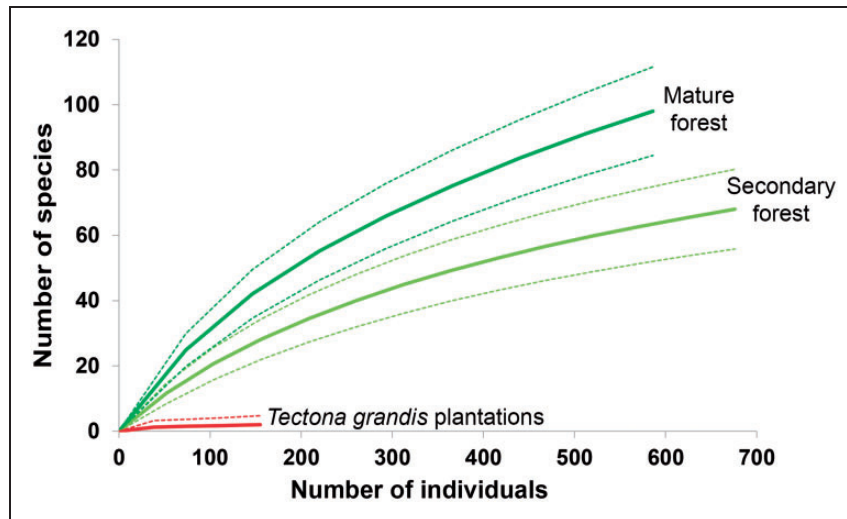


Figure 2. Individual-Based Species Rarefaction Curves for Trees >10 cm DBH. Land-uses analysed include mature forest (N = 8); secondary forest (N = 13); and *Tectona grandis* plantations (N = 4). *Schizolobium parahyba*, *Ochroma pyramidale*, and pastures were excluded because low stem density did not allow rarefaction analysis. Dashed lines indicate 95% CI.

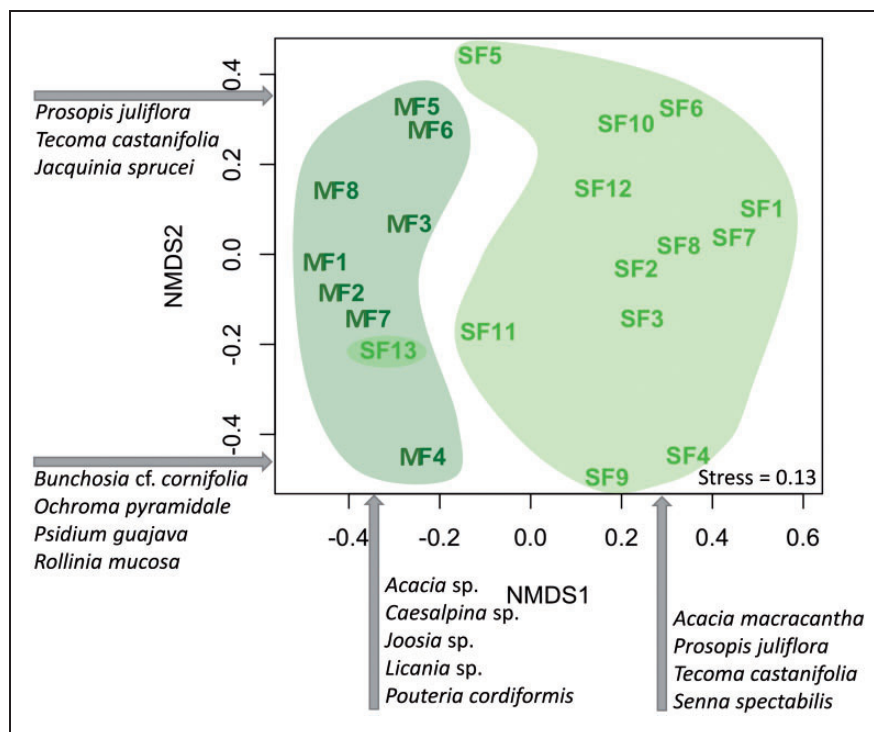


Figure 3. Non-Metric Multidimensional Scaling (NMDS) in Two-Dimensional Space of Mature Forest (MF) and Secondary Forest (SF) Sites. Results are based on tree assemblage composition using abundance data from each site.

financial objectives as the reasons for its planting. Despite these characteristics, findings from this research indicate that *T. grandis* could store as much carbon in aboveground biomass as SF, indicating it may compete and possibly outperform SF in carbon-based initiatives. In other TDF landscapes, synergies between forest

conservation and carbon storage have been reported (Mora et al., 2016). Our findings suggest that aboveground biomass in many of the studied PL types could reduce these synergies, potentially creating a trade-off between biodiversity conservation and carbon sequestration initiatives.

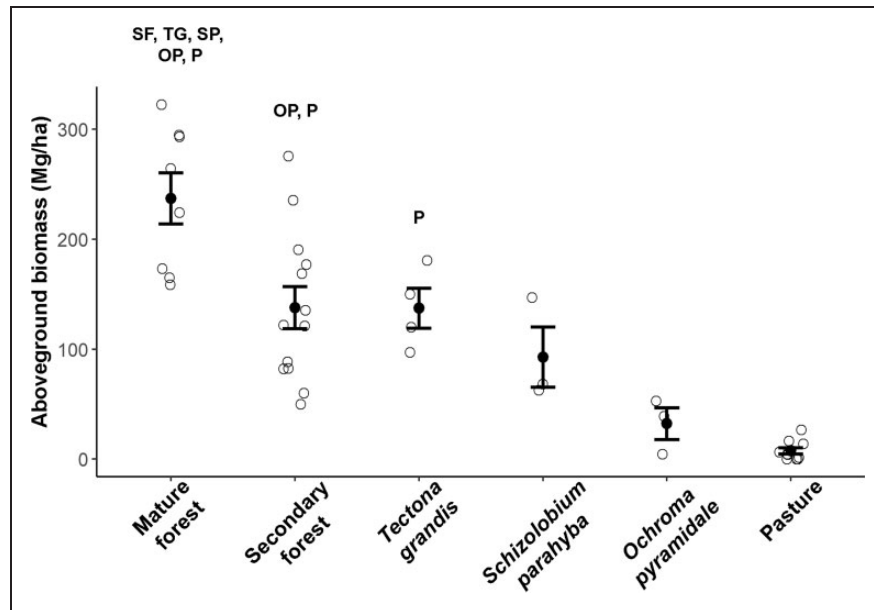


Figure 4. Average Aboveground Biomass for Mature Forest (MF, N = 80), Secondary Forest (SE, N = 13), Pasture (P, N = 10), and Plantations of *Tectona grandis* (TG, N = 4), *Schizolobium parahyba* (SP, N = 3), and *Ochroma pyramidale* (OP, N = 3). Acronyms above each whisker indicate land-cover types with significantly lower aboveground biomass based on Tukey post hoc pairwise comparisons.

This research provides a critical understanding of tree diversity, composition and aboveground biomass across the major land-cover types in a dry forest landscape in coastal Ecuador. However, results should be interpreted cautiously considering that a full understanding of landscape characteristics including matrix structure and configuration, forest patch size and shape is lacking and represent a limitation of this research. Likewise, our floristic inventory provides a reliable comparisons of tree species richness, diversity and aboveground biomass across land-cover types, but longer temporal evaluations of community composition and aboveground biomass are needed to fully understand the dynamics of carbon storage and sequestration and community composition change over time. Incorporating seedling and sapling into future research could also help understand tree diversity and community composition differences across land-cover types and clarify patterns of secondary succession. Finally, perhaps the single most significant variable not accounted in this research is land tenure and associated land-management decisions. Many sites challenge documented landscape – species diversity patterns and rather reflect unique land management choices. Species-rich MF are found adjacent to pastures, SF occurs near roads and forest (MF and SF) are in areas less steep than many pastures. These are just some examples that reflect unique management choices with direct implications for biodiversity conservation that require further analysis.

Implications for Conservation

We analysed tree species diversity, community composition and aboveground biomass across mature forests (MF), secondary forests (SF), three types of plantations (PL), and pastures in a TDF landscape in Ecuador. The following are key findings related to forest and biodiversity conservation:

1. MF were more diverse than SF, but detailed analyses indicate that while most endemic and IUCN-categorized species were found in MF (15 total), half of them were also present in SF. This finding agrees with broader findings that recognize the importance of SF in biodiversity conservation, especially in highly fragmented landscapes (Chazdon, 2014; Chazdon et al., 2007).
2. It is critical to evaluate richness and diversity patterns across major land-cover types to fully understand tree diversity and forest succession patterns. In this research, SF resemble pastures in tree species composition, and succession is probably delayed because of the effects of pasture grasses, suggesting some challenges when planning for reforestation.
3. Aboveground biomass and tree diversity were the highest in MF, indicating potential synergies between forest conservation and carbon storage and sequestration initiatives. However, species-poor *Tectona grandis* PL could host as much as or more aboveground biomass as SF, raising awareness of the importance of

aligning biodiversity conservation (or other ecosystem services) and carbon storage and sequestration in reforestation efforts.

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