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Effects of historical land use and recovery pathways on composition, structure, ecological function, and ecosystem services in a Caribbean secondary forest

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ABSTRACT

Regenerated secondary forests in the tropics are resilient ecosystems. Differences in land-use history and disturbance, abiotic and biotic site conditions, and successional pathways can influence secondary forest biodiversity, structure, ecological functions, and ecosystem services. However, studies assessing the supply of ecosystem services of secondary forests are limited. We examined trees in plots located across late successional stage secondary forest in the Luquillo Experimental Forest, Puerto Rico with three combinations of historical canopy cover (circa 1936) and post-agricultural recovery pathways: (1) > 50% canopy cover and passive regeneration (>50 P), (2) < 50% canopy cover and passive regeneration (<50 P), and (3) < 50% canopy cover and assisted + passive regeneration (<50 A+P). Using i-Tree Eco methodology, we investigated if differences in historical cover and passive vs assisted natural regeneration resulted in differences in composition and structure, hydrological functions, and estimated regulating ecosystem services, and compared the results between native and non-native species. The <50 P plots had greater species richness than the >50 P and <50 A+P plots, while the <50 A+P plots had significantly greater DBH, height, basal area, aboveground biomass, and estimated quantities of evaporation and transpiration, carbon storage, and removal of airborne contaminants compared to the other recovery pathways. Differences among plot groups can be attributed to historical management actions in concert with successional trajectories characteristic of novel secondary forests. Native species dominated throughout these secondary forests and cumulatively exhibited services that were 1.3 to 3.5 times greater than those of non-native species. However, non-native trees contributed disproportionally to basal area and aboveground biomass, and thus to some ecosystem services. Both natives and non-natives exhibited service provision that varied significantly with diameter size class and service type, and large trees were observed to be dominant service providers irrespective of species origin. Our study marks the first landscape-scale quantitative assessment of forest composition, structure and ecological functioning that is explicitly linked to exploring regulating ecosystem services within the montane secondary forest in Puerto Rico and expands representation of this research from the Caribbean. The findings underscore the role of historical land use and recovery pathways in driving services of tropical forests and show how ecosystem functions can vary in accordance with dynamic structural attributes of individual trees. This research can provide a useful point of comparison for analysis of biomass accumulation, ecosystem service provision, and evaluating service tradeoffs associated with forest structure in other recovering and old-growth tropical landscapes.

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1. Introduction

Tropical forests around the world are heavily influenced by anthropogenic disturbances such as clearing for intensive agriculture, industrial logging, fires and habitat fragmentation (Lewis et al., 2015, Spracklen et al., 2015). Socioeconomic shifts toward urbanization and industrialization have also triggered forest re-growth facilitating successional transitions in many tropical landscapes (Aide et al., 2013). This has resulted in the growth of post-disturbance secondary forests (*sensu* Brown and Lugo, 1990) that have regenerated naturally following land use. Extensive research examining successional processes that occur following anthropogenic disturbance has documented different patterns of tropical forest regeneration and biomass accumulation (Brown and Lugo, 1990, Aide et al., 2000, Chazdon, 2003). Recovery pathways can be highly variable at both stand and landscape levels due to factors like functional traits and their interactions with resource use and abiotic conditions (Poorter et al., 2021b), the spatiotemporal overlap of anthropogenic with natural disturbance (e.g., landslides, hurricanes, tree falls) and succession dynamics (e.g., dispersal dynamics, recruitment rates) (Foster et al., 1999, Arroyo-Rodríguez et al., 2017).

Recent studies have advanced our understanding about tropical forest succession, ecosystem functions, and the delivery of ecosystem services in recovered secondary forests (Ferraz et al., 2014). Land use change affects tropical forest biomass accumulation, carbon sequestration and storage (Silver et al., 2000, Chazdon et al., 2016, Poorter et al., 2016), water yield and ecohydrological processes related to climate regulation (Sun et al., 2017), maintenance of biodiversity for ecological functioning (Poorter et al., 2015), as well as human well-being (Cardinale et al., 2012) and vulnerability to climate change (Locatelli et al., 2015). Tropical secondary forests are resilient systems that can recover many elements of pre-disturbance biodiversity, ecosystem functions, and services, whether through natural regeneration or direct planting (Poorter et al., 2016, Poorter et al., 2021a, Zimmerman et al., 2021b). The extenat to which restoring secondary forests may provide comparable levels of ecosystem services as the undisturbed forests they replaced is largely determined by abiotic site conditions (e.g., climate and soil), the degree of forest degradation following prior land use, the surrounding landscape composition and structure, and the desired service outcomes (Chazdon, 2008, Poorter et al., 2021a, Poorter et al., 2021b). Time after disturbance is particularly important (Chazdon, 2008, Poorter et al., 2021a). For example, secondary tropical forests in early stages of natural succession have been found to supply higher values of individual services such as carbon storage and timber production than late successional stages; meanwhile, late secondary tropical forests can exhibit a greater diversity and more balanced distribution of multiple service types (e.g., biodiversity, timber, global climate regulation) with fewer tradeoffs among individual services (Zeng et al., 2019). Both native and non-native trees can contribute to

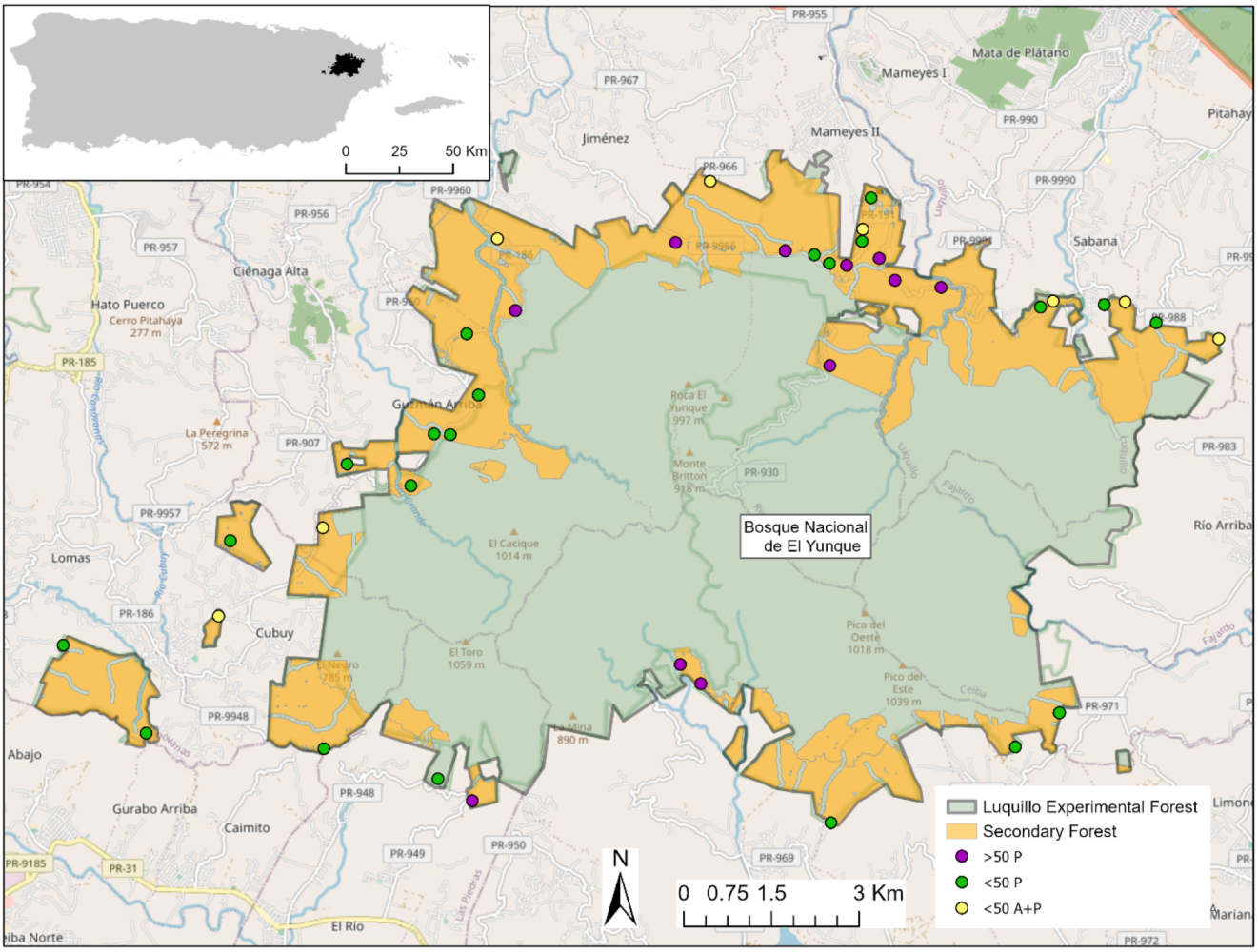

Fig. 1. Location of the Luquillo Experimental Forest (LEF; coterminous with Bosque Nacional El Yunque) within the island of Puerto Rico (inset) and map of the LEF showing areas classified as secondary forests and the locations of monitoring plots used in this study, identified by plot groups as described in the Methods.

Table 1
Ecological characteristics of secondary forest monitoring plots in the Luquillo Experimental Forest. < 50 and > 50 refer to historical canopy cover percentage in 1936. A = assisted natural regeneration, P = passive natural regeneration, DW = dead wood, G = grass & herbaceous, L = leaf litter & mulch, LT = live tree, R = rock, S = shrub. Plots with dominant ground cover of equal value in more than one category have symbols separated by a "/".

Plot	Forest type	Elevation (m asl)	Plot group	Canopy cover (%)	Understory density (%)	Dominant ground cover (%)
1	Secondary submontane moist	417	<50 P	29.3	83.8	DW, 28.8
2	Secondary montane wet	393	<50 P	49.3	82.1	S, 31.3
3	Secondary submontane moist	301	>50 P	39.3	75.2	L/G, 17.5
4	Secondary montane wet	272	<50 A+P	59.3	90.8	S, 53.8
5	Secondary montane wet	240	<50 P	36.8	87.4	G, 27.5
6	Secondary montane wet	320	>50 P	21.8	88.2	G, 28.8
7	Secondary montane wet	196	>50 P	19.3	93.1	G/L, 17.5
8	Secondary montane wet	178	>50 P	29.3	86.2	L, 36.3
9	Secondary montane wet	115	>50 P	25.5	87.9	L, 57.5
10	Secondary submontane moist	265	<50 A+P	64.0	87.9	G, 40.0
11	Secondary montane wet	431	>50 P	29.3	91.9	DW/G/S, 18.8
12	Secondary montane wet	269	<50 P	28.0	89.7	L, 40.0
13	Secondary montane wet	510	>50 P	24.3	85.2	G, 43.8
14	Secondary montane wet	531	>50 P	50.5	88.9	L, 48.8
15	Secondary montane wet	443	>50 P	36.8	89.0	G/R, 23.8
16	Tabonuco montane wet	452	<50 P	43.0	89.2	G, 35.0
17	Secondary montane wet	398	>50 P	51.8	94.8	S, 26.3
18	Secondary montane wet	477	<50 P	23.0	88.4	G, 63.8
19	Secondary submontane moist	344	<50 P	53.0	92.4	L, 42.5
20	Secondary montane wet	555	<50 P	45.5	94.1	L, 41.3
21	Secondary montane wet	439	<50 P	60.5	86.5	LT, 27.5
22	Secondary montane wet	523	<50 P	49.3	78.6	G, 38.8
23	Secondary montane wet	305	>50 P	25.5	85.0	G, 31.3
24	Secondary montane wet	432	<50 P	26.8	85.7	G, 36.3
25	Secondary montane wet	484	<50 P	29.3	90.4	S, 30.0
26	Secondary montane cloud	639	<50 A+P	28.0	92.9	S, 26.3
27	Secondary montane wet	149	<50 A+P	40.5	88.0	L, 30.0
28	Secondary montane wet	588	<50 A+P	19.3	90.3	S, 42.5
29	Secondary montane wet	134	<50 P	59.3	90.8	S, 21.3
30	Secondary montane wet	114	<50 A+P	71.8	93.6	L, 28.8
31	Secondary montane wet	286	<50 A+P	31.8	94.8	DW/G/L, 21.3
32	Secondary montane wet	202	<50 A+P	73.0	94.3	L, 40.0
33	Secondary montane wet	183	<50 P	21.8	94.3	L, 42.5
34	Secondary montane wet	144	<50 P	51.8	88.4	S, 27.5
35	Secondary montane wet	493	<50 P	44.3	94.8	L, 36.3
36	Secondary submontane moist	535	<50 P	49.3	87.2	L, 28.8
37	Secondary montane wet	555	<50 P	54.3	81.1	L, 33.8
38	Secondary montane wet	313	<50 P	33.0	81.8	L, 26.3
39	Secondary montane wet	288	<50 P	34.3	89.9	L, 45.0
40	Secondary montane wet	160	<50 P	28.0	87.9	G, 32.5

the restoration of ecosystem functions and services (Chazdon, 2008), including increasing local biodiversity (Brockerhoff et al., 2017), regulating climate, building soil fertility, controlling soil erosion, and providing timber and fibers (Castro-Díez et al., 2019). In some cases, non-native tree species can help restore ecosystem functions following loss of native forests, providing habitat, shelter or food resources (Schlaepfer et al., 2011), facilitating restoration of degraded sites (Lugo, 2004) and filling functional roles on par with native species in terms of aboveground biomass and productivity, nutrient cycling, and soil carbon storage (Mascaro et al., 2012). However, differences in service provision of native and non-native trees are highly context specific, and vary across species type, environmental conditions (e.g., climate, soils, topography) and structural traits of individual trees (e.g., canopy structure, phenology, water and light use efficiency) (Eviner et al., 2012, Castro-Díez et al., 2019). From the perspective of managing secondary forests in recovering tropical landscapes, promoting multifunctional forests requires improved understanding about how particular forest attributes influence ecosystem service provision and tradeoffs among distinct restoration practices (Felipe-Lucia et al., 2018, Zeng et al., 2019). Across Caribbean islands, there has been limited study of ecosystem services in forested areas (Nelson et al., 2020). Prior research has looked at forest ecosystem structure, function and service supply across distinct forest types (Forero-Montaña et al., 2019) or examined services provided by a specific forest ecosystem type in multiple geographic locations (e.g., Bhomia et al., 2016). Yet given the dominance and variability of tropical secondary forests globally (FAO, 2020), there remains a need for analysis among stands of a similar landscape context to elucidate the effects of environmental factors, historical land use, and regeneration pathways on secondary forest structure, functions, and ecosystem service provision.

The Luquillo Experimental Forest (LEF) in Puerto Rico is one of the best studied sites in the Neotropics (Lugo and Heartsill-Scalley, 2014, Zimmerman et al., 2021b). Many of the LEF lands below 600 m asl are comprised of secondary forest heavily influenced by agricultural and agroforestry land uses up through the first four decades of the 20th century (García-Montiel and Scatena, 1994, Thompson et al., 2002). From the 1930s to the early 1980s, the USDA Forest Service conducted a multitude of land rehabilitation and silvicultural improvement activities (Zimmerman et al., 2021b), introducing >100 native and non-native plant species (Marrero, 1947, Francis, 1995). >30 non-native species have become naturalized (Francis and Liogier, 1991). Commercial logging in the LEF ceased in 1955, yet select forest enrichment of mahogany and other species continued through the 1970s within passively regenerating stands, resulting in assisted natural regeneration (*sensu* Shono et al., 2007) in areas designated for timber stand improvements. By the 1980s public opinion and management objectives had shifted from resource extraction toward conservation priorities, such that timber production areas were never harvested and assisted regeneration of those lands ceased altogether (McGinley, 2017), giving way entirely to passive regeneration in the decades that followed. Other abandoned agricultural and pasture lands and disturbed forested areas were never managed and reverted to secondary forest exclusively through

Table 2
Results of one-way ANOVAs for plot characteristics, composition, structure, hydrologic functions (evaporation, transpiration) and ecosystem services (carbon storage and sequestration, pollution removal, oxygen production) as estimated using i-Tree Eco, according to plot group for trees with DBH ≥ 5 cm. < 50 and > 50 refer to historical canopy cover percentage in 1936. A = assisted natural regeneration. P = passive natural regeneration. Values in bold denote groups with significant differences ($\alpha < 0.05$) according to Tukey Kramer test. Dagger (†) denotes significance for trees with DBH ≥ 10 cm as well. Asterisk (*) indicates variables that were transformed to fulfill statistical assumptions. Note that all variables that were transformed for analysis are back-transformed here for ease of interpretation.

Source		Plot group	Mean	95% CI	*df*	*F* value	*p* value
PLOT CHARACTERISTICS	Canopy cover (%)	>50 P	32.1	25–40	2,37	3.156	0.055
		<50 P	40.5	35–46			
		<50 A+P	48.5	31–66			
	Understory density (%)	>50 P	87.8	84–91	2,37	2.312	0.113
		<50 P	87.3	86–90			
		<50 A+P	91.6	89–94			
COMPOSITION	Richness*†	>50 P	16.3	13–19	2,37	**3.659**	**0.036**
		<50 P	18.6	17–20			
		<50 A+P	14.6	11–19			
STRUCTURE AND BIOMASS	Tree density* (trees ha^{-1})	>50 P	882.7	692 – 1,073	2,37	**4.734**	**0.015**
		<50 P	1,229.5	1,033– 1,425			
		<50 A+P	861.3	638 – 1,084			
	DBH† (cm)	>50 P	14.9	13–17	2,37	**10.501**	**0.0002**
		<50 P	13.8	13–15			
		<50 A+P	18.4	15–21			
	Total height† (m)	>50 P	8.92	8–10	2,37	**8.984**	**0.0007**
		<50 P	8.77	8–10			
		<50 A+P	11.2	9–13			
	Basal area*† (m^2 ha^{-1})	>50 P	24.0	18–30	2,37	**3.688**	**0.034**
		<50 P	27.9	23–32			
		<50 A+P	40.0	27–53			
	Leaf area* (m^2 ha^{-1})	>50 P	45,260.5	31,162–59,359	2,37	2.681	0.052
		<50 P	61,153.8	49,252–73,055			
		<50 A+P	84,516.7	56,505–112,528			
	Leaf biomass* (kg ha^{-1})	>50 P	4,213.7	3,016–5,411	2,37	2.362	0.054
		<50 P	5,465.6	4,387–6,543			
		<50 A+P	6,892.6	5,011–8,773			
	Total AG biomass*† (kg ha^{-1})	>50 P	115,461	78,457–152,464	2,37	**6.217**	**0.004**
		<50 P	138,790	107,349–170,230			
		<50 A+P	312,719	162,010–463,427			
HYDROLOIC FUNCTIONS AND ECOSYSTEM SERVICES	Evaporation*† m^3 yr^{-1}	>50 P	400.8	276–525	2,37	**4.383**	**0.019**
		<50 P	541.6	436–647			
		<50 A+P	748.4	500–996			
	Transpiration*† m^3 yr^{-1}	>50 P	98.3	68–129	2,37	**4.373**	**0.019**
		<50 P	132.7	107–159			
		<50 A+P	183.4	123–244			
	Carbon storage*† (kg)	>50 P	6,494.4	4,367–8,622	2,37	**4.478**	**0.018**
		<50 P	7,356.9	5,792–8,921			
		<50 A+P	14,951.4	7,785–22,118			
	Carbon sequestration* (kg yr^{-1})	>50 P	463.9	352–576	2,37	0.450	0.640
		<50 P	578.8	435–723			
		<50 A+P	534.8	311–758			
	Pollution removal*† (g yr^{-1})	>50 P	8,409.4	5,790–11,029	2,37	**4.380**	**0.019**
		<50 P	10,362.3	9,151–13,574			
		<50 A+P	15,702.9	10,498–20,908			
	Oxygen production* (kg yr^{-1})	>50 P	1,237.8	940–1,535	2,37	0.449	0.641
		<50 P	1,543.9	1,159–1,928			
		<50 A+P	1,426.4	831–2,022			

Table 3
Diversity metrics for all plots together and per plot group. < 50 and > 50 refer to historical canopy cover percentage in 1936. A = assisted natural regeneration, P = passive natural regeneration. Numbers in parentheses represent subsets of non-native species classified as invasive species.

Diversity metric	All plots	>50 P	<50 P	<50 A+P
Total richness	109	62	90	43
Native	93	57	78	34
Non-native (Invasive)	16(6)	5(2)	12(4)	9(3)
Shannon index	3.413	3.123	3.273	3.021
Simpson index	0.940	0.926	0.933	0.931

mechanisms of passive regeneration and species sorting following abandonment (Lugo and Helmer, 2004). Over time, anthropogenic influences have resulted in the emergence of novel forest communities, with unique combinations (relative to historical forests) of native and non-native species (Lugo, 2009). Today, all secondary forest in the LEF is in a late secondary successional stage, with a minimum of 70–80 years since agricultural clearing.

These differences in land-use history and regeneration pathways in the LEF present a unique opportunity to assess the long-term recovery trajectories of secondary forest and the effects on ecological functions in a tropical environment. Numerous studies from Puerto Rico have compared forest composition and structure along temporal chronosequences examining stands of secondary vs primary forest. After several decades post-disturbance, parameters such as tree species richness, diversity, and structural attributes such as density, basal area, and aboveground biomass often return to levels analogous to those of undisturbed forests with similar site conditions (Aide et al., 1995, Zimmerman et al., 1995, Lugo and Helmer, 2004, Marin-Spiotta et al., 2007). Species composition of secondary forests, on the other hand, frequently remains distinct compared to native forests of similar age, with fewer rare, endemic, and native species and large trees (Aide et al., 2000, Rojas-Sandoval et al., 2022). Furthermore, legacies of historical

land use do not occur in isolation; in the LEF long-term research has documented the effects of hurricane disturbance on forest composition and structure including survival, regeneration and subsequent thinning of secondary species (Weaver, 2002, Hogan et al., 2016, Uriarte et al., 2019). Several studies suggest that land use legacies persist through time, interacting with successive hurricanes to influence patterns of species distribution, successional trajectories, and forest structure (Zimmerman et al., 1995, Thompson et al., 2002, Hogan et al., 2016).

Our study builds on this rich research history and aims to fill an important knowledge gap regarding the effects of historical land use and management on forest composition, structure, ecological functions, and their associated services in late secondary tropical forests. In this work, we initiated a vegetation monitoring project in the LEF following Hurricane María in 2017. We applied the i-Tree Eco (https://www.itreetools.org/tools/i-tree-eco) methodology to this tropical setting and collected data on mature trees from 40 monitoring plots located in advanced secondary forest with plot groups representing distinct combinations of historical canopy cover and recovery pathways (see Methods below). We examined these data to evaluate if differences in canopy cover at the time of agricultural abandonment and subsequent passive vs assisted natural regeneration are driving differences in (1) the composition and structure of trees in advanced secondary forests, and (2) some of the hydrologic functions and regulating services (as estimated from structural attributes) these secondary forests provide to local human communities. We also evaluated differences between native and non-native species and among distinct size classes within stands from each plot group, focusing on the ecology of forest trees, their biophysical effects on the surrounding ecosystem. We do not address the economic valuation component of the services provided, as that is beyond the scope of this work. The results of this study provide the first landscape-scale quantitative assessment of forest composition, structure and ecological functioning that is explicitly linked to examining regulating ecosystem services within the montane secondary forest (*sensu* Beard, 1944, 1955) in Puerto Rico. We discuss the findings in the context of structural and functional attributes of native vs. non-native species, historical land-use legacies, and the effects of passive vs assisted ecological restoration on successional trajectories both among plot groups and more broadly within the LEF. We also consider the implications of tropical forest dynamics for human communities and highlight the need for robust data at the individual tree and stand levels to adequately assess service provision and tradeoffs within forested ecosystems.

2. Methods

2.1. Site description

The study was performed within the LEF, which is coterminous with the Bosque Nacional de El Yunque (El Yunque National Forest in English). The LEF encompasses 11,540 ha in the Luquillo Mountains of eastern Puerto Rico, of which 3,170 ha (28%) are classified as recovering secondary forest with multiple historic land uses (EYNF, 2018). Secondary forests in the LEF are designated as submontane and montane (Beard, 1944, 1955), have mean canopy heights of 20–30 m, and occur at elevations ranging from 100 m to 600 m asl within the subtropical moist and wet life zones (Ewel and Whitmore, 1973, Gould et al., 2006, Weaver and Gould, 2013, EYNF, 2018). These secondary forests serve as a buffer zone between privately-owned properties outside the LEF that have a history of human intervention and management, and primary forests at higher elevation inside the LEF that escaped historical clearing. Previous analyses (e.g., Scatena, 1989, García-Montiel and Scatena, 1994, Zimmerman et al., 1995, Foster et al., 1999) have established the mid-1930s as an important reference point marking a distinct change in land management practices in the LEF; by the late 1930s, >85% of the LEF's present-day land area had been acquired by the United States government, including the vast majority of lands now designated as secondary forest (Weaver, 2012). Analysis of historical aerial photographs has shown that approximately 23% of the LEF was composed of secondary forest lands in 1936 and that 55% of that secondary forest area had forest canopy cover < 50% at that time (Foster et al., 1999).

2.2. Monitoring plots and data collection

To assess the influence of historical canopy cover and passive vs assisted natural regeneration on current forest composition, structure, functions, and services, 40 circular plots (area = 0.1 ha) were located within the secondary forest (Fig. 1). Plot locations were randomly distributed in areas with slopes < 30% and in proximity to roads and/or trails (minimum distance > 20 m and maximum < 250 m) to facilitate data collection. The minimum distance between plots was set to 250 m to ensure spatial independence among sampling points. Using spatial datasets produced by Foster et al. (1999) detailing 1936 canopy cover in the LEF together with visual analysis of 1936 aerial orthophotos of the LEF, Forest Service reports of the LEF landscape and land use practices during the past century (Harris et al., 2012, Weaver, 2012), and published analyses of land cover in eastern Puerto Rico (including the LEF) during the past four decades (i.e., Gonzalez, 2001, López-Marrero, 2003, Gould et al., 2012), plots were classified into three groups based on combinations of their historical canopy cover and post-agricultural regeneration pathways. The first group corresponds to secondary forest plots with > 50% canopy cover in 1936 (i.e., they were predominantly forested at that time) that have continued to recover via passive natural regeneration (hereafter referred to as the ">50 Passive" (or > 50 P) plots). The second group corresponds to secondary forest plots with < 50% canopy cover in 1936 (i.e., they were predominantly deforested and in early to mid-successional stages at that time) that have continued to recover via passive natural regeneration (hereafter the "<50 Passive" (or < 50 P) plots). The third group corresponds to secondary forest plots that also had < 50% cover in 1936 (i.e., they were predominantly deforested an in earlier successional stages at that time) and are located in areas that experienced a combination of both assisted and passive natural regeneration (hereafter the "<50 assisted + passive" (or < 50 A+P) plots). Assisted regeneration occurred in the LEF up to the early 1980s in the form of understory line plantings for enrichment of desirable timber, including both native and non-native species (see Marrero, 1947, Francis, 1995, Weaver, 2012 for lists of introduced species), which we observed in the field as straight rows of trees at the time of our monitoring. Since the 1980s this third group of plots has only undergone exclusively passive natural restoration, as confirmed by Forest Service staff. Eleven plots (total area = 1.1 ha) were classified as > 50 P, 21 plots (total area = 2.1 ha) were classified as < 50 P, and 8 plots (total area = 0.8 ha) as < 50 A+P.

Data collection protocols were based on methodologies outlined in the i-Tree Eco User's Manual (i-Tree Team, 2021a) and Field Manual (i-Tree Team, 2021b) for analysis of urban and rural forests and assessment of ecosystem services. i-Tree Eco is part of a peer-reviewed suite of tools that have been effectively used for analysis of urban and rural forests and assessment of ecosystem services, including carbon storage and sequestration (Nowak et al., 2013) and removal of air pollution (Wu et al., 2019). The protocols were adapted to omit parameters that are typically collected in urban inventories (e.g., anthropogenic structures), and to include vegetative elements common in tropical forests (e.g., abundance of palm trees or the presence of lianas in tree canopies), as well as structural changes in forest parameters related to Hurricane María disturbance (e.g., broken limbs, lost treetops, and fallen trees).

Ground cover (0–1 m above ground surface) was analyzed for nine categories estimated in percentage intervals of 5% including: (1) leaf litter, (2) shrubs and small trees with diameter at breast height (hereafter DBH) < 5 cm, (3) grasses and herbs, (4) dead wood, (5) lianas and vines, (6) live trees with DBH ≥ 5 cm, (7) rocks, (8) bare soil, and (9) water (i.e., streams, rivers, and ponds). Plot canopy cover was assessed

Table 4
Compositional summary of the top 10 dominant species for all plots together and per plot group regardless of origin. < 50 and > 50 refer to historical canopy cover percentage in 1936. A = assisted natural regeneration, P = passive natural regeneration. Species are arranged in rank descending order based on abundance. Orig = Origin (N = Native, NN = Non-native), Freq = Frequency (count plots^{-1}), Dens = Density (trees ha^{-1}), BA = Basal area (m^2/ha), Rel Freq = Relative frequency (%), Rel Dens = Relative density (%), Rel Dom = Relative dominance (% of total BA), IV = Importance value ((Relative Frequency + Relative Density + Relative Dominance)/3).

All plots									>50 P								
Species	Orig	Freq	Dens	BA	Rel Freq	Rel Dens	Rel Dom	IV	Species	Orig	Freq	Dens	BA	Rel Freq	Rel Dens	Rel Dom	IV
Prestoea acuminata	N	622	155.5	2.6	14.7	3.7	8.9	9.1	*Prestoea acuminata*	N	386	183.8	1.6	14.9	7.1	5.6	9.2
Cecropia schreberiana	N	564	141.0	0.9	13.3	3.3	3.2	6.6	*Cecropia schreberiana*	N	374	178.1	0.6	14.5	6.9	2.1	7.8
Swietenia macrophylla	NN	307	76.8	6.8	7.2	1.8	23.1	10.7	*Tabebuia heterophylla*	N	230	109.5	2.1	8.9	4.2	7.4	6.9
Tabebuia heterophylla	N	275	68.8	2.9	6.5	1.6	9.8	6.0	*Calophyllum antillanum*	N	139	66.2	0.7	5.4	2.6	2.5	3.5
Ocotea leucoxylon	N	197	49.3	0.7	4.6	1.2	2.3	2.7	*Swietenia macrophylla*	NN	127	60.5	1.9	4.9	2.3	6.9	4.7
Casearia arborea	N	156	39.0	*0.3*	3.7	0.9	1.2	1.9	*Ocotea leucoxylon*	N	121	57.6	0.4	4.7	2.2	1.5	2.8
Calophyllum antillanum	N	144	36.0	0.7	3.4	0.8	2.5	2.2	*Myrcia deflexa*	N	97	46.2	0.2	3.8	1.8	0.7	2.1
Guarea guidonia	N	130	32.5	1.7	3.1	0.8	5.9	3.2	*Guarea guidonia*	N	91	43.3	1.3	3.5	1.7	4.6	3.3
Myrcia deflexa	N	122	30.5	0.1	2.9	0.7	0.4	1.3	*Casearia arborea*	N	83	39.5	0.6	3.2	1.5	2.2	2.3
Cyathea arborea	N	120	30.0	0.3	2.8	0.7	1.1	1.6	*Inga laurina*	N	76	36.2	0.5	2.9	1.4	1.8	2.1

via visual observation of tree crowns and estimated in intervals of 5% using forest density charts, and understory density of shrubs and trees ≥ 1 m in height was evaluated using a concave spherical densiometer.

Within each plot, all self-supporting woody stems with DBH ≥ 5 cm were tagged with a unique number and determined to be alive or dead based on the visual observation of living tissue. If alive, they were identified to species or genus level following Liogier and Martorell (2000) and Axelrod (2011). The DBH of each stem and total height of individual trees was recorded. Palm crown live frond ratios were assessed following Blair et al. (2019). Percent crown missing and percentage of crown dieback were estimated in 5% intervals, while crown light exposure (CLE) was evaluated on a scale from 0 to 5, following i-Tree Eco protocols. Some crown parameters required by the i-Tree Eco model could not be collected due to an abundance of dense coarse woody debris, tangling vines, and saturated soils that inhibited movement or visibility within the plots. Missing values for tree height (<0.1% of individuals) were estimated by calculating average height values of all live conspecific individuals with diameter within +/-2 cm. Similarly, missing values for height to crown base (10% of individuals) were estimated by calculating based on the average proportion of live crown ratio for all live trees in all plots. Missing values for percent crown missing and percent crown dieback (0.3% of individuals) were estimated by calculating average values for all live trees in the same plot. Crown widths for all trees were estimated based on regression data published by Westfall et al. (2020) for tropical/subtropical hardwoods and by Korom et al. (2016) for palms.

2.3. Citizen science approach

All data used in this study were collected as part of a citizen science project led by the Fundación Amigos de El Yunque in collaboration with the USDA Forest Service, the University of Puerto Rico-Río Piedras Campus, and other partners. Participants were trained in tree dentification and implementation of the adapted i-Tree Eco protocol. Fieldwork and data collection described above occurred from January 2019 through April 2021, led by a core team of scientists that participated throughout the entire project. Data were digitalized and reviewed by experts and entered into the project database (data available at: https://portal.edirepository.org/nis/mapbrowse?packageid=edi.1484.1).

2.4. Structural analysis, hydrologic functions and ecosystem services

We compiled a dataset containing all live trees with DBH ≥ 5 cm. Individual trees were identified as native or non-native following Francis and Liogier (1991). Native species were further identified as endemic to the Puerto Rican archipelago following Axelrod (2011). Non-native species were classified as invasive or not following Rojas-Sandoval and Acevedo-Rodríguez (2015) and Zimmerman et al. (2021a). Overall richness was tallied per plot group according to origin (native or non-native). Analyses of forest structure and hydrologic functional values and select ecosystem services were calculated using i-Tree Eco (v6.1.36; i-Tree Team, 2021c). The i-Tree Eco program is a tool in the suite designed to use standardized field data collected from individual trees, together with local hourly air pollution and meteorological data to quantify forest structure and its numerous functional effects (i.e., ecosystem services) and values for human communities (Nowak and Crane, 2000, Nowak et al., 2008). The i-Tree database includes species and meteorological data specific to municipalities located in Puerto Rico.

Basal area (BA), leaf area (LA), and leaf biomass (LB) for each tree were calculated in i-Tree Eco. BA was calculated based on the combined diameters of the six largest stems whereas LA and LB were calculated using measurements of crown dimensions and percentage of crown canopy missing, which helped adjust for biomass losses incurred due to wind damage from Hurricane María. Total aboveground biomass (AGB) was calculated per tree using published regression equations for lower elevation broadleaf species (Weaver and Gillespie, 1992) and palms (Frangi and Lugo, 1985) in the LEF, which have been applied and validated in previous studies (see Marín-Spiotta et al., 2007, Weaver, 2010). Broadleaf regression equations included variables for diameter and total height, while palm biomass was based on total height alone.

Estimation of ecological functions and associated regulating ecosystem services by i-Tree Eco was limited to several quantifiable effects relevant to trees in rural tropical forest settings that could extrapolated from the structural data we collected. The model calculated two hydrologic functions, evaporation from a wet canopy and transpiration (evaporation from a dry canopy), and estimated three regulating services, total carbon stored, gross carbon sequestered annually, oxygen production, and air pollution removed. Below we provide a summary of the methods used by i-Tree Eco for estimating these ecological functions and services. Additional information about the Eco models for estimating the biophysical attributes of tree ecosystem services is summarized in Nowak (2021) and references within.

Hydrologic functions – Evaporation and transpiration were calculated using process-based models that incorporate leaf and bark area data and crown conditions to estimate tree cover area, and local weather data. Specific equations are detailed in Hirabayashi (2013, 2015, 2016), and Wang et al. (2008). Precipitation data was acquired from the San Juan International Airport for the years 2013, the wettest year (2,260 mm of recorded rainfall) among available datasets in the Eco model,

<50 P									<50 A+P								
Species	Orig	Freq	Dens	BA	Rel Freq	Rel Dens	Rel Dom	IV	Species	Orig	Freq	Dens	BA	Rel Freq	Rel Dens	Rel Dom	IV
Prestoea acuminata	N	167	151.8	0.8	17.2	15.6	3.2	12.0	*Swietenia macrophylla*	NN	108	135.0	3.9	15.7	19.6	9.7	15.0
Cyathea arborea	N	119	108.2	0.3	12.3	11.1	1.4	8.3	*Cecropia schreberiana*	N	76	95.0	0.6	11.0	13.8	1.4	8.7
Cecropia schreberiana	N	114	103.6	0.2	11.7	10.7	1.0	7.8	*Prestoea acuminata*	N	69	86.3	0.3	10.0	12.5	0.7	7.7
Swietenia macrophylla	NN	72	65.5	1.0	7.4	6.7	4.0	6.0	*Hibiscus elatus*	NN	45	56.3	0.7	6.5	8.2	1.7	5.4
Andira inermis	N	39	35.5	0.2	4.0	3.7	0.9	2.8	*Alchornea latifolia*	N	44	55.0	0.2	6.4	8.0	0.6	5.0
Ocotea leucoxylon	N	35	31.8	0.4	3.6	3.3	1.7	2.9	*Ocotea leucoxylon*	N	41	51.3	0.1	6.0	7.4	0.3	4.6
Casearia arborea	N	34	30.9	0.4	3.5	3.2	1.6	2.8	*Casearia arborea*	N	39	48.8	0.4	5.7	7.1	0.9	4.6
Schefflera morototonii	N	31	28.2	0.3	3.2	2.9	1.3	2.5	*Schefflera morototonii*	N	31	38.8	0.2	4.5	5.6	0.5	3.5
Tabebuia heterophylla	N	31	28.2	0.7	3.2	2.9	2.7	2.9	*Myrcia deflexa*	N	23	28.8	0.1	3.3	4.2	0.3	2.6
Inga laurina	N	28	25.5	0.5	2.9	2.6	2.2	2.6	*Myrcia splendens*	N	18	22.5	0.1	2.6	3.3	0.4	2.1

which best approximated the average rainfall of subtropical moist and wet forest in the LEF as reported by Murphy et al. (2017).

Carbon storage and sequestration – The Eco model was parameterized to use carbon storage and sequestration equations for tropical moist areas from Chave et al. (2005) for moist tropical climates (1500–3500 mm precipitation yr^{-1}, as defined by the Köppen-Geiger climate classification system (Peel et al., 2007)). Eco multiplies tree AGB by 0.5 to estimate carbon storage (Chow and Rolfe, 1989). To estimate annual gross carbon sequestration, DBH is incrementally increased in the computer model according to estimated annual growth rates derived from a base growth rate, length of growing season, species specific growth rates, tree competition (determined from CLE), crown condition, and tree height (Nowak, 2021).

Air pollution – Air pollution removal estimates are based on modeling of gas exchange and hourly dry deposition of carbon monoxide (CO), nitrogen dioxide (NO_2), ozone (O_3), particulate matter<2.5 μm ($PM_{2.5}$), and sulfur dioxide (SO_2). Data about airborne contaminants were acquired from four stations in Cataño, Guaynabo, Juncos, and San Juan, PR from the years 2013 and 2016, and missing hourly pollution data were filled in using procedures described in Hirabayashi and Endreny (2016). Eco calculates canopy resistance values for O_3, NO_2 and SO_2 using a combination of big-leaf and multi-layer canopy deposition models (Baldocchi et al., 1987, Baldocchi, 1988), and estimates removal values for CO and $PM_{2.5}$ based on average measured values from the literature (Bidwell and Fraser, 1972, Lovett, 1994) that are adjusted depending on leaf phenology and leaf area.

Oxygen production - Eco estimated the amount of oxygen produced from carbon sequestration based on atomic weights, where net O_2 release (kg yr^{-1}) = gross C sequestration (kg yr^{-1}) × 32/12, which does not account for losses resulting from tree mortality and decomposition (Nowak, 2021).

2.5. Statistical analyses

Descriptive statistics were calculated for plot and tree compositional, structural, and ecosystem services data, and organized by plot group and species origin (native or non-native). Analyses were then conducted to assess differences among groups due to the combination of historical canopy cover and regeneration pathway (passive vs assisted + passive natural regeneration). To compare biodiversity among plot groups, Shannon and Simpson diversity indices were calculated. Species rarefaction curves were generated using the R package "*iNEXT*" (Hsieh et al., 2016) to assess the expected number of species per area sampled. This allows for valid standardization and comparison of data among variable sampling areas without the confounding effect of tree density on species richness (Gotelli and Colwell, 2001). Tree density, basal area, leaf area, leaf biomass, and total AG biomass was calculated for each plot group, and stems were binned into five DBH and height classes to evaluate the distribution of sizes across plot groups. Importance values (IV) were calculated for the ten most common species in each plot group based on relative frequency, relative density, and relative dominance. For each ecosystem service, we calculated total ecological value per species and averages across all individuals and size classes for species represented by at least 5 individuals. Outputs for the five airborne contaminants assessed were summed to provide a combined total quantity and economic value for air pollution removal. One-way ANOVAs followed by post-hoc Tukey Kramer tests were used to test for significant differences in mean plot canopy cover, understory density, species richness, structural traits, biomass, and ecosystem services among plot groups (>50 P, <50 P, <50 A+P). Data were checked for normality and homogeneity of variance and when needed variables were transformed to meet model assumptions.

Randomization tests were used to evaluate whether native and non-native species differ in the ecosystem services they provide. Because i-Tree calculations of ecological functions and services depend on structural traits, we first grouped native and non-native trees into five DBH size classes to ensure comparison with trees of similar size. For each of these size classes, we generated random groups of natives and non-natives and used simple randomizations to test whether there were differences in the medians of each ecosystem service between the two groups ($p < 0.05$). In each random draw ($n = 10{,}000$), we randomly shuffled the values of each ecosystem service between the two groups. The observed median was compared to the expected median value of the random draws. When significant differences were observed at $p < 0.05$, post-hoc analyses were run with all trees with DBH measurement ≥ 10 cm, to examine if the observed effect was limited to the presence of smaller diameter trees. All analyses were performed using *R* (version 4.1.2; R Core Team, 2021).

3. Results

3.1. Plot characteristics and species composition

A summary of all the variables evaluated at the plot level is presented in Table 1. No significant differences were observed among plot groups with respect to plot canopy cover or understory density ($p > 0.05$) (Table 2).

The final dataset contained a total of 4,242 trees corresponding to 109 species, of which 93 species (represented by 3,605 individual trees) are native, and 16 species (represented by 637 trees) are non-native (Table 3). Six of the 16 non-native species (5% of the total) have been previously reported as invasive species in Puerto Rico (Supplementary Table 1). Regardless of the origin, five species accounted for 50% of the total IV across plots. The native palm *Prestoea acuminata* var. *montana*

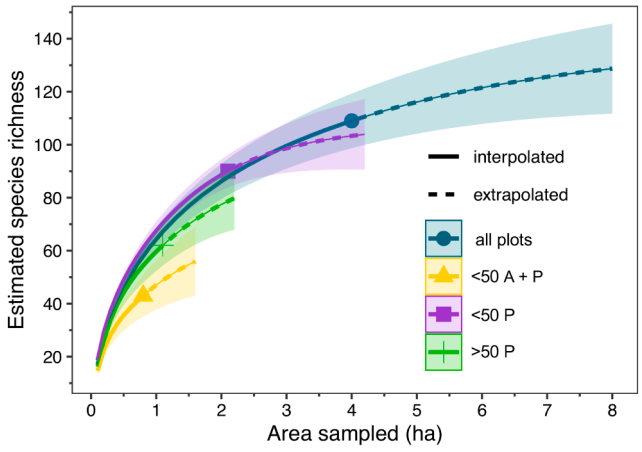

Fig. 2. Species rarefaction curves for plot groups and for all plots together. < 50 and > 50 refer to historical canopy cover in 1936. A = assisted natural regeneration, P = passive natural regeneration. Solid lines represent interpolated data and dash lines represent extrapolated data. Shaded regions represent 95% confidence interval.

Table 5
Structural and biomass metrics for all plots together and per plot group. < 50 and > 50 refer to historical canopy cover in 1936. A = assisted natural regeneration, P = passive natural regeneration. Leaf area, leaf biomass, and total aboveground (AG) biomass were estimated using i-Tree Eco.

Structural feature	All plots	>50 P	<50 P	<50 A+P
# Trees	4,242	971	2,582	689
Density (trees ha^{-1})	1,060	883	1,230	861
Tree height range (m)	1.4–33.6	1.4–25.5	1.6–32.0	2.3–33.6
Tree height mean & SE (m)	9.2 ± 0.1	8.8 ± 0.3	8.9 ± 0.2	11.0 ± 0.2
DBH range (cm)	5–145	5–145	5–130	5–124
DBH mean & SE (cm)	14.5 ± 0.2	14.6 ± 0.5	13.6 ± 0.3	17.9 ± 0.6
Basal area (m^2 ha^{-1})	29.3	24.0	27.9	40.0
Leaf area (m^2 ha^{-1})	61,455.6	45,260.4	61,153.8	84,516.1
Leaf biomass (kg ha^{-1})	5,406.7	4,213.7	5,465.6	6,892.6
Total AG biomass (kg ha^{-1})	167,159.9	115,460.9	138,789.5	312,718.6

was the most abundant species overall, representing 15% of all the trees and dominating in terms of frequency and density across the < 50 P and > 50 P plots (Table 4). In the < 50 A+P plots, the non-native tree *Swietenia macrophylla* had the greatest IV and was by far the dominant species (irrespective of origin) in terms of frequency and density. Other species with relatively greater IV across all plot groups were *Ocotea leucoxylon, Cecropia schreberiana*, and *Casearia arborea* (Table 3), all of them native species.

Among plot groups, the < 50 P plots were more diverse according to the ANOVA outputs (Table 2) and the Shannon and Simpson diversity indices (Table 3). Rarefaction curves showed that the estimated numbers of species rose similarly at first, with all plot groups registering close to 25 species at 0.25 ha of sampling effort (Fig. 2). After this point, the < 50 A+P plots began to lag, with roughly 30–50% more area needed than in the < 50 P and > 50 P plots to achieve a comparable number of species. Beyond 0.5 ha of sampling effort, the number of species in the < 50 P plots continued to rise more rapidly than the other two groups.

3.2. Structure and biomass

Stand structure varied across all plot groups (Table 5). Overall density was 1,060 trees ha^{-1}. Density was significantly greater in the < 50 P plots, but this difference did not persist when tests were run using trees with DBH ≥ 10 cm (Table 2). The average DBH for all trees measured was 14.5 cm (*SE* = 0.2), and the 5–15 cm class was dominant for all groups, representing > 60% of trees across all plots. A smaller fraction of trees occurred in larger size classes (Fig. 3a). However, many of the trees measured in < 50 A+P plots had large diameters, resulting in a significantly greater DBH for that group (Table 2). A similar pattern was observed for total height, which averaged 9.2 m across all trees measured (Table 5). Approximately 50% of all plots had trees in the 5–10 m class, yet < 50 A+P plots had taller trees (Fig. 3b) and their average height was significantly greater (Table 2).

The greater DBH of trees in < 50 A+P plots translated directly to significantly greater basal area and AG biomass as well (Tables 2 and 5; Fig. 4a). The non-native tree *S. macrophylla* was the most important contributor to basal area and total AG biomass in the < 50 A+P plots and the basal area of this species was greater than the sum of the next nine most frequently observed species (Table 4). The native palm, *P. acuminata* was another main contributor to basal area across all plot groups. In both the < 50 P and > 50 P plots, the native tree *T. heterophylla* ranked in the top three species for basal area, while in the > 50 P plots, two primary forest specialists, *Dacryodes excelsa* and *Manilkara bidentata*, were among the top five species. Average values for

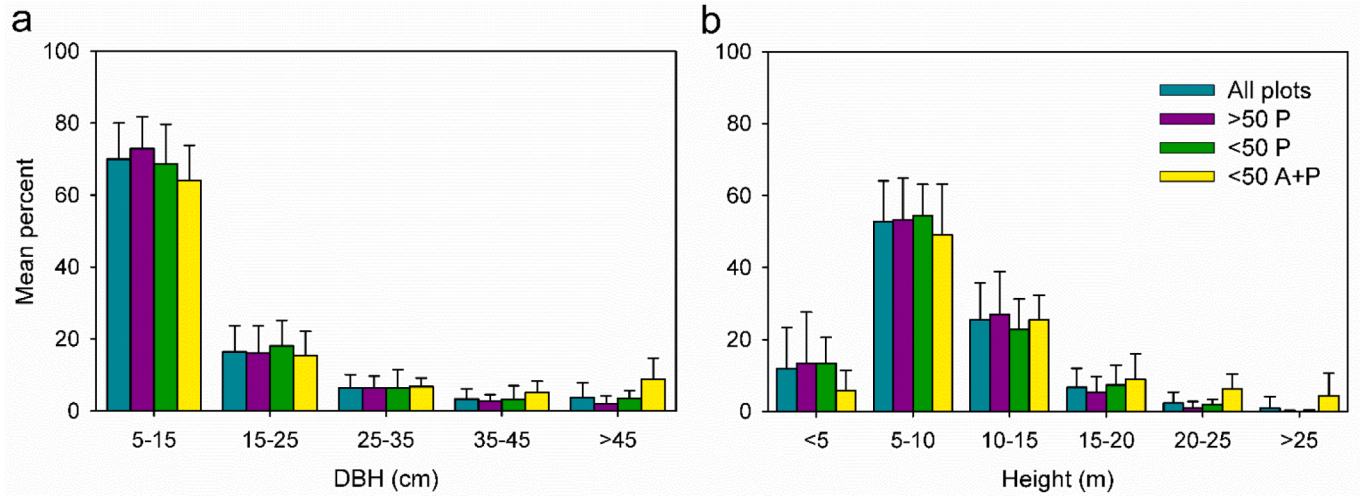

Fig. 3. Distribution of size classes for (a) DBH and (b) total height for plot groups and all plots together. < 50 and > 50 refer to historical canopy cover in 1936. A = assisted natural regeneration, P = passive natural regeneration.

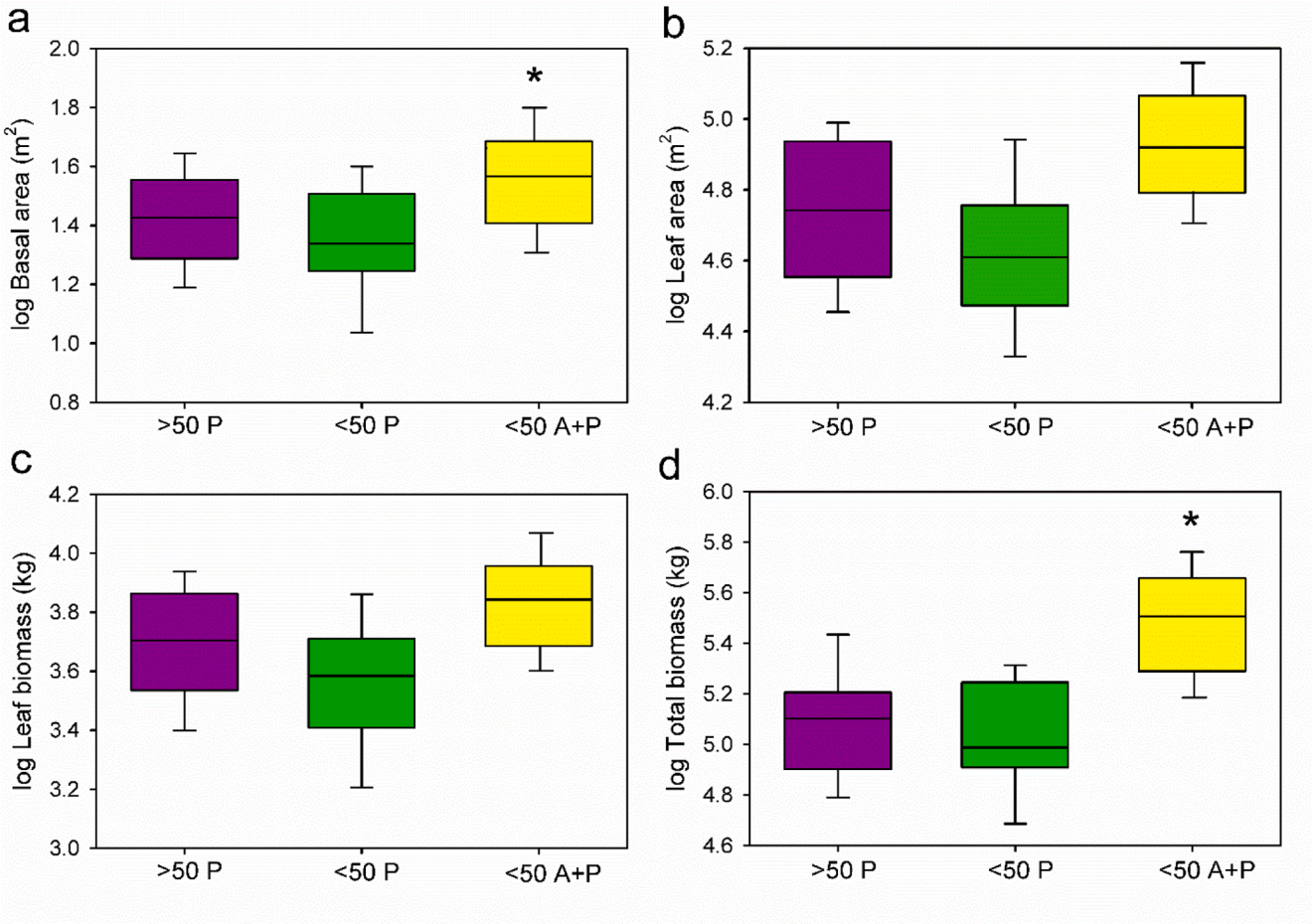

Fig. 4. Box plots of log transformed biomass data as estimated using i-Tree Eco: (a) basal area, (b) leaf area, (c) leaf biomass, and (d) total aboveground biomass for plot groups and all plots together. < 50 and > 50 refer to historical canopy cover in 1936. A = assisted natural regeneration, P = passive natural regeneration. Asterisk (*) indicates a significant difference ($p < 0.05$).

Table 6
Summary of the (a) total cumulative hydrologic functions (evaporation, transpiration) and ecosystem services (carbon storage and sequestration, pollution removal, oxygen production) as estimated using i-Tree Eco for all species, native species, and non-native species, and (b) the top 10 species, arranged in rank descending order based on carbon storage. Asterisk (*) indicates non-native species.

(a) Total cumulative	Basal area (m^2 ha^{-1})	Leaf area (ha)	Evaporation (m^3 yr^{-1})	Transpiration (m^3 yr^{-1})	Carbon storage (metric ton)	Carbon sequestration (metric ton yr^{-1})	Pollution removal (metric ton yr^{-1})	Oxygen production (kg yr^{-1})
all species	29.3	24.58	21,770.4	5,336.8	345.55	21.54	479.50	57,449.8
native species	18.8	17.34	15,358.3	3,764.9	197.51	16.72	338.27	44608.9
non-native species	10.5	7.24	6,412.1	1,571.9	148.04	4.82	141.23	12840.9
(b) Top 10 species								
*Swietenia macrophylla**	6.8	3.98	3,246.32	1,381.44	97.58	2.42	77.64	6,460.5
Prestoea acuminata	2.6	1.71	1,396.04	594.07	31.79	4.30	33.39	11,477.3
Tabebuia heterophylla	2.9	1.81	1,475.33	627.81	25.16	3.27	35.28	8,732.8
Guarea guidonia	1.7	0.88	719.80	306.31	20.07	0.02	17.21	55.6
Manilkara bidentata	0.6	0.74	604.15	257.09	13.10	0.67	14.45	1,790.2
*Pinus caribaea**	0.7	0.35	283.24	120.53	12.21	0.70	6.77	1,879.5
*Hibiscus elatus**	0.7	0.86	702.96	299.14	10.83	0.45	16.81	1,206.7
*Swietenia mahagoni**	0.6	0.27	223.26	95.01	10.72	0.27	5.34	711.6
Schefflera morototoni	0.5	0.61	494.90	210.60	7.98	1.34	11.84	3,572.1
Inga laurina	0.7	0.69	564.63	240.27	8.01	0.05	13.50	124.3

leaf area and leaf biomass were not significantly different among plot groups, although the p values were close to the $\alpha < 0.05$ level (Tables 2 and 5; Fig. 4b, c). However, total AG biomass of < 50 A+P plots was significantly greater than for the < 50 P and > 50 P plots (Tables 2 and 5; Fig. 4d). Across all plot groups, non-native species accounted for 36% of basal area, and 40% of total AG biomass.

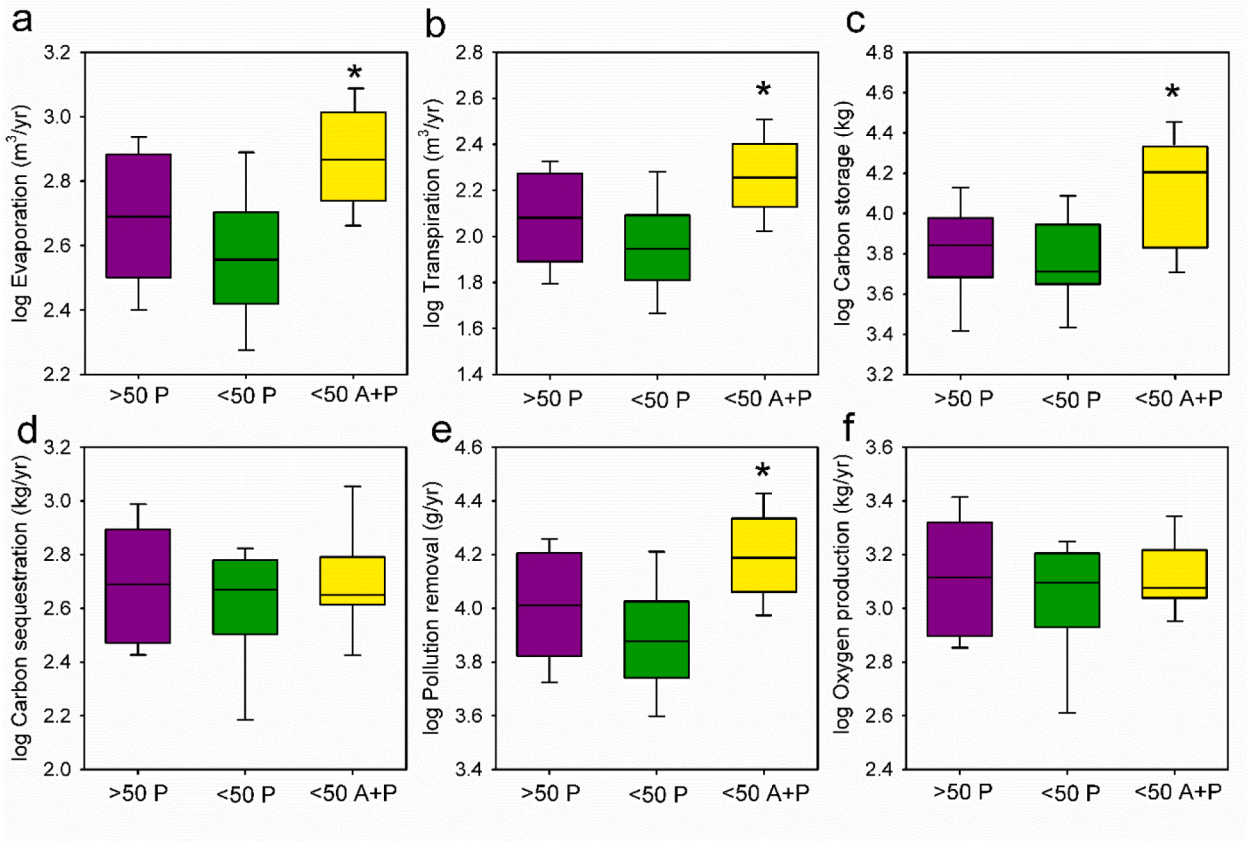

Fig. 5. Box plots of log transformed hydrologic functions (a – evaporation, b – transpiration) and ecosystem services (c – carbon storage, d – carbon sequestration, e – pollution removal (all contaminants combined), and f – oxygen production) as estimated using i-Tree Eco for plot groups and for all plots together. < 50 and > 50 refer to historical canopy cover in 1936. A = assisted natural regeneration, P = passive natural regeneration. Asterisk (*) indicates a significant difference ($p < 0.05$).

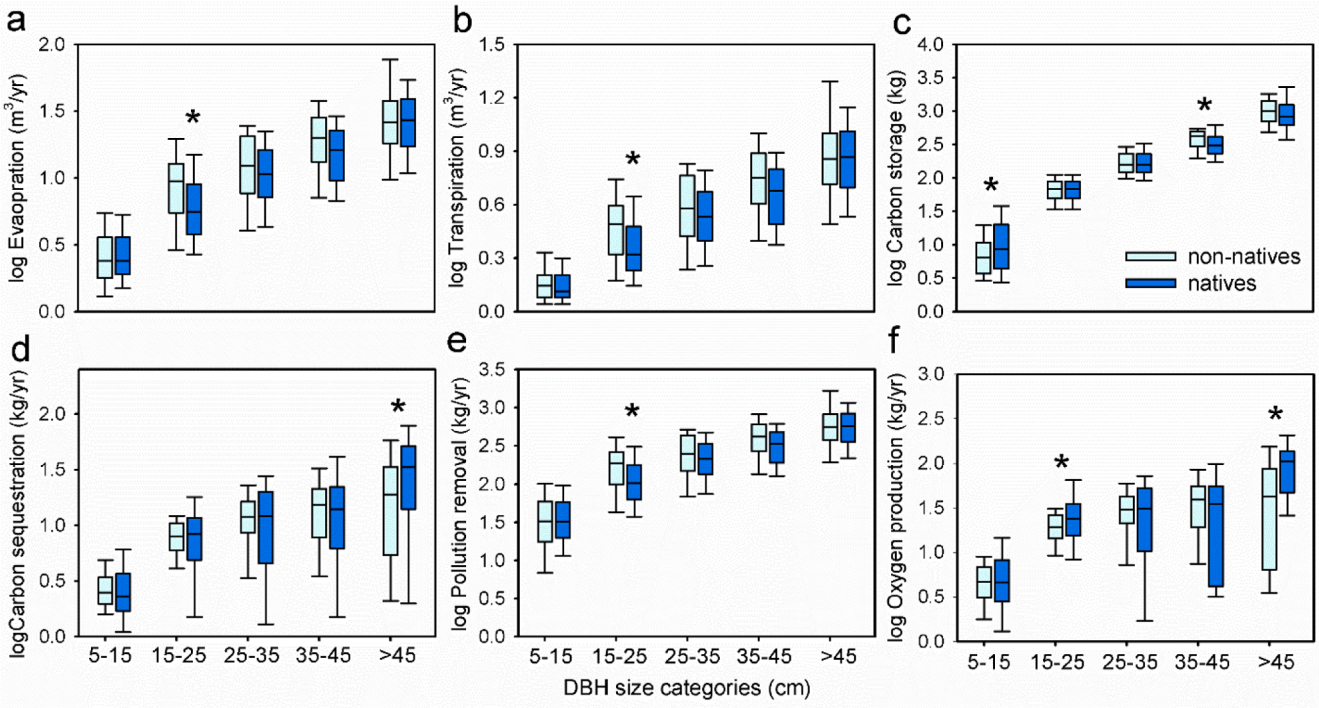

Fig. 6. Box plots per species origin of log transformed hydrologic functions (a – evaporation, b – transpiration) and ecosystem services (c – carbon storage, d – carbon sequestration, e – pollution removal (all contaminants combined), and f – oxygen production) as estimated using i-Tree Eco per DBH size class. Asterisk (*) indicates significant differences ($p < 0.05$).

Table 7
Results of randomization test for the hydrologic functions (evaporation, transpiration) and ecosystem services (carbon storage and sequestration, pollution removal, oxygen production) as estimated using i-Tree Eco, presented by DBH size class according to species origin across all plot groups for native and non-natives. Values in bold denote groups with significant differences ($\alpha = 0.05$) between native and non-native species.

Hydrologic function or Ecosystem service	*DBH size class (cm)*	*Natives (mean ± SD)*	*Non-natives (mean ± SD)*	*p value*	*Relative contribution*
Evaporation (m^3 yr^{-1})	5–15	2.14 ± 1.12	2.10 ± 1.05	$p =$ 0.38	
	15–25	**6.42 ± 3.01**	**8.87 ± 2.96**	***p* = 0.03***	Non-native > native
	25–35	11.43 ± 3.75	13.8 ± 5.82	$p =$ 0.17	
	35–45	18.57 ± 8.52	21.69 ± 8.51	$p =$ 0.17	
	>45	29.55 ± 9.55	32.87 ± 13.43	$p =$ 0.23	
Transpiration (m^3 yr^{-1})	5–15	0.52 ± 0.28	0.51 ± 0.25	$p =$ 0.43	
	15–25	**1.57 ± 0.74**	**2.18 ± 0.72**	***p* = 0.02***	Non-native > native
	25–35	2.81 ± 0.92	3.38 ± 1.43	$p =$ 0.17	
	35–45	4.55 ± 2.08	5.32 ± 2.09	$p =$ 0.17	
	>45	7.24 ± 2.34	8.06 ± 3.29	$p =$ 0.24	
Carbon storage (kg)	**5–15**	**12.85 ± 6.93**	**8.59 ± 4.05**	***p* = 0.001***	Native > non-native
	15–25	70.25 ± 16.67	63.62 ± 16.90	$p =$ 0.15	
	25–35	183.56 ± 46.94	174.83 ± 37.27	$p =$ 0.25	
	35–45	**337.88 ± 79.99**	**401.88 ± 69.71**	***p* = 0.01***	Non-native > native
	>45	1063.45 ± 456.68	1229.86 ± 484.56	$p =$ 0.18	
Carbon sequestration (kg yr^{-1})	5–15	2.07 ± 1.12	1.95 ± 0.68	$p =$ 0.17	
	15–25	8.32 ± 3.32	7.19 ± 1.83	$p =$ 0.13	
	25–35	12.65 ± 5.47	11.94 ± 3.51	$p =$ 0.32	
	35–45	14.75 ± 7.60	16.36 ± 6.44	$p =$ 0.27	
	>45	**33.95 ± 15.93**	**21.72 ± 11.68**	***p* = 0.007***	Native > non-native
Pollution removal (g yr^{-1})	5–15	47.10 ± 25.16	46.18 ± 23.05	$p =$ 0.38	
	15–25	**141.53 ± 66.47**	**195.28 ± 65.35**	***p* = 0.001***	Non-native > native
	25–35	251.66 ± 82.44	303.92 ± 128.25	$p =$ 0.18	
	35–45	409.05 ± 187.75	478.08 ± 187.39	$p =$ 0.17	
	>45	650.12 ± 210.39	723.93 ± 295.79	$p =$ 0.24	
Oxygen production (kg yr^{-1})	5–15	5.53 ± 3.01	5.19 ± 1.82	$p =$ 0.17	
	15–25	**22.19 ± 8.85**	**19.15 ± 4.88**	***p* = 0.03***	Native > non-native
	25–35	33.75 ± 14.59	31.83 ± 9.35	$p =$ 0.32	
	35–45	39.35 ± 20.28	43.60 ± 17.19	$p =$ 0.28	
	>45	**90.57 ± 42.43**	**57.90 ± 31.16**	***p* = 0.007***	Native > non-native

3.3. Ecological functions and ecosystem services

We estimated that the 4,000 + trees assessed in this study store approximately 346 metric tons of carbon, sequestering more than 21 tons and removing almost 480 metric tons of air pollution annually (Table 6). Both native and non-native species contributed to hydrologic functions and services. For the trees analyzed, functions and services were 1.3 to 3.5 times greater for native species compared to non-native species, yet non-native species were important contributors to all the functions and services we evaluated (Table 6, Supplementary Table 2). At the species level, the non-native tree *S. macrophylla* had the highest functional values for evaporation and transpiration, and service values for stored carbon and pollution removal. The native trees *P. acuminata, T. heterophylla, G. guidonia,* and *M. bidentata* were also important for carbon storage, pollution removal, evaporation and transpiration, and *P. acuminata* and *T. heterophylla* were the top two species for annual carbon sequestration and oxygen production. Three other non-native trees, *Pinus caribaea, Hibiscus elatus,* and *Swietenia mahagoni* made smaller but important contributions to the functions and services evaluated as well (Supplementary Table 2).

When averages of calculated functions and services per tree across all individuals and size classes were examined, many of the same species persisted as important for hydrologic functions and regulating services, and several other species emerged as well. For native species, the trees *Homalium racemosum* and *D. excelsa* were among the top three species with the highest average values for evaporation, transpiration, and pollution removal, while *Buchenavia tetraphylla, Hymenaea courbaril,* and the palm *Roystonea borinquena* were among top five species that contributed to carbon storage, annual sequestration, and oxygen production (Supplementary Table 2). Regarding non-natives, the tree *P. caribaea* had the highest average carbon storage, sequestration, and oxygen production, and *Pterocarpus macrocarpus* had the second highest amount of evaporation, transpiration, and pollution removal (Supplementary Table 2).

When comparing across plot groups, we detected significantly higher average values in the calculated amounts of evaporation and transpiration as well as the carbon stored, and pollution removed by < 50 A+P plots compared to < 50 P and > 50 P plots (Table 2, Fig. 5a-e). No significant differences were observed among plot groups for carbon sequestration, or oxygen production (Table 2, Fig. 5d, f). The results of the randomization tests showed significant differences between native and non-native species regarding the contributions of different DBH size classes to hydrologic functioning and the provision of ecosystem services (Fig. 6, Table 7). We found that non-native species in the size class with DBH = 15–25 cm had significantly higher rates of evaporation, transpiration, and pollution removal than natives in the same size category (Fig. 6a, b, e). For carbon storage, we found that native species in the smallest size class (DBH = 5–15 cm) had significantly higher rates than non-native species, but the opposite relationship was detected for trees with DBH = 35–45 cm for which the rates calculated for non-natives were significantly higher compared to natives (Fig. 6c). Finally, native species in the largest size class (DBH > 45 cm) had higher rates of carbon sequestration and oxygen production than non-natives (Fig. 6e). No significant differences between native and non-native species were detected for the contribution of any other size categories to the hydrologic functions or ecosystem services analyzed (Table 7).

4. Discussion

This study aimed to assess the influence of historical land use and passive vs assisted natural regeneration in a tropical montane secondary forest with a complex management history. The plot groups we studied do not represent three forest stands of distinct ages. Rather, there is temporal overlap in the maximum regeneration time for trees in < 50 P and < 50 A+P plots, as they were both identified as having < 50% forest cover in 1936. However, whereas the < 50 P plots have regenerated

passively since that time, the < 50 A+P plots continued to receive land use management activities for several more decades in the form of assisted natural regeneration including both native and non-native species; it was not until the early 1980s that passive regeneration fully ensued in those plots. The signal of this management comes through clearly in terms of some of the results we observed. In this section we discuss our findings in terms of differences among plot groups regarding species composition, structure and biomass, and ecological functions and services, as well as patterns observed for the overall study area.

4.1. Species composition

The results revealed that species composition is not uniform across plot groups, and the < 50 P plots have higher species diversity compared to the other plot groups, including the highest diversity of both native and non-native species (Tables 2 and 3, Fig. 2). Differences in species composition do not appear to be due to native species dominating plots that only experienced passive regeneration (i.e., the < 50 P and > 50 P plots) and non-natives dominating plots that experienced both assisted and passive regeneration (i.e., the < 50 A+P plots). Rather, the difference can be attributed to the presence of both more native and non-native species that were unique to the < 50 P plot group than those found in the > 50 P and < 50 A+P groups (Supplementary Table 1). One possible explanation could be related to anthropogenic disturbance and the historical introduction of non-native tree species to the LEF's secondary forest areas. Non-native tree species were intentionally and repeatedly introduced to the LEF over several decades during the mid-20th century for silvicultural enhancements, fuelwood production, and watershed restoration (Foster et al., 1999, Weaver, 2012). Between 1919 and 1953 the USDA Forest Service also supported a few hundred temporary residents in the LEF, where they were allowed to engage in agroforestry practices that helped contribute to restoring degraded lands (Weaver, 2012). These activities would likely have affected both the < 50 P and < 50 A+P plot groups. However, in areas where the < 50 A+P plots are located the Forest Service also conducted limited thinning and culling of smaller diameter stems to promote the growth of desirable timber species (Weaver, 2012). Thus, the greater number of introduction events and individuals could potentially result in a higher rate of propagule pressure for non-native species (Lockwood et al., 2009), while the lack of active management in the < 50 P group may have helped maintain this diversity. Furthermore, previous studies of natural succession on abandoned pastures in the Luquillo Mountains and other areas of Puerto Rico have revealed that after several decades, regenerated forest communities often include both native and non-native species and the number of native species tends to increase with time after disturbance (Aide et al., 1995, but see Rojas-Sandoval et al., 2022), in some cases contributing to the majority of the importance value (Silver et al., 2004). Additional investigation regarding differences in stand age is needed to explore the effects of recovery time on successional trajectories in the secondary forests of the LEF.

Regarding forest composition more generally throughout the study area, we observed a dominance of native species (Tables 3 and 4 and Supplementary Table 1), including trees previously associated with both primary and secondary forest assemblages across the Luquillo Mountains (Thompson et al., 2002, Weaver, 2010). The abundance of *P. acuminata,* which represented 15% of the trees monitored, is typical of subtropical wet forest in the LEF, where it can achieve stem densities of up to 20% (Weaver and Gould, 2013). In recovering secondary forests, *P. acuminata* tends to be absent during early stages of succession and then appears in later stages (Aide et al., 2000). Similarly, *T. heterophylla* is a species characteristic of lower elevation secondary moist forests recovering from past agricultural activities (Weaver and Gould, 2013). It produces wind-dispersed seeds that grow well on degraded soils (Silver et al., 2004), and is frequently found in abandoned pasture lands (Aide et al., 2000). In contrast, *C. schreberiana* is a pioneer species uncommon in pastures that dominates only following canopy disturbances (e.g., related to forest gaps or hurricane), taking advantage of high light to grow rapidly and reach the canopy (Brokaw, 1998).

Non-native tree species were present as well, although the proportion of non-native species in the plots we monitored (15%) is relatively lower than for Puerto Rico as a whole (22%) (Lugo et al., 2022). The most abundant non-native tree was *S. macrophylla*, which occurred across all plot groups. Its dominance across can be attributed directly to management activities conducted between 1934 and 1945 when more than two million seedlings of *S. macrophylla and S. mahagoni* were planted in the LEF for reforestation purposes, and then between 1960 and the early 1980s when *S. macrophylla* × *S. mahogoni* hybrids were sown as line plantings for enrichment purposes on degraded secondary forest (Weaver and Bauer, 1986, Weaver, 2012). One species that was conspicuously uncommon in our plots is the non-native tree *Spathodea campanulata,* which is one of the most abundant species found on secondary forests following agricultural abandonment across Puerto Rico (Aide et al., 2000, Marcano-Vega, 2017). In our study site, however, *S. campanulata* was quite rare (0.24% of the trees monitored) and such differences may be partly attributable to the age of the forest we monitored. It has been shown that *S. campanulata* is highly dependent on disturbance to recruit, and therefore becomes less dominant in late secondary forests (Aide et al., 2000). Other plausible factors include the availability of seed sources and dispersal vectors, as well as environmental conditions that affect establishment, such as soil conditions and light availability.

4.2. Structure and biomass

We observed a dominance of smaller diameter trees and relatively shorter tree heights across plot groups (Fig. 3), two characteristics frequently associated with tropical secondary forests (Brown and Lugo, 1990). The inverse J-shaped curve of the diameter distribution is consistent with island-wide data from previous USDA Forest Inventory and Analysis (FIA) surveys conducted in Puerto Rico (Brandeis and Turner, 2013, Marcano-Vega, 2017), and more generally with the decrease in numbers of individuals with size typical of uneven-aged tropical forests where natural regeneration is sufficient (Poorter et al., 1996). Still, the < 50 A+P plots had more trees in the larger size classes above 25 cm DBH and 15 m height, which resulted in significantly greater basal area and total AGB compared to the other plot groups (Fig. 4, Table 2). As with the compositional differences, the larger structure and greater biomass of the < 50 A+P plots (Tables 2 and 5, Fig. 4) is likely due to the assisted natural regeneration that augmented recruitment and growth of select timber species during the mid-20th century (Weaver, 2012), and which persists today despite approximately four decades of passive regeneration. Fu et al. (1996) also found that plantation trees ≥4 cm DBH in a 64-year-old stand of *S. macrophylla* had a greater total height than trees of similar age in a paired secondary forest that regenerated without assistance. The fact that significant differences were not observed for LA and LB may reflect the post-hurricane conditions during which the monitoring was done. LiDAR analysis of forest structural damage from Hurricane María in the LEF showed that 2.5 years after the storm there was still a net loss of vegetative material and canopy height from crown damage or treefall events, resulting in a shorter, more open forest canopy (Leitold et al., 2022). Furthermore, the dominance of a palm species in the <50 A+P plots (and among all plot groups) may help explain the lack of observed differences in LA and LB, owing to the difference in structural attributes as compared with tropical hardwood canopies.

Regarding the influence of species origin on structural attributes, non-native species comprised 15% of the trees we monitored yet accounted for approximately one-third of the basal area and two-fifths of the total AGB. A similar pattern has also been observed to hold true more broadly at the scale of the entire island, and indicates that some non-native species play an outsized role, relative to their abundance, on ecosystem functional processes in the secondary forest (Lugo et al.,

2022). This influence has direct implications for ecological functions and ecosystem services and will be discussed further in the following section.

4.3. Ecological functions and ecosystem services

In general, the LEF is an important forest landscape that provides numerous ecosystem services to nearby human communities, including services related to carbon, water, and air (López-Marrero and Hermansen-Báez, 2011). In our study of the LEF's secondary forests, regulating services (as estimated from the structural parameters measured) such as carbon storage and annual carbon sequestration stood out as the dominant benefits provided by the trees monitored (Table 6). Previous work has also documented functional processes related to carbon cycling in the LEF's secondary forests and other nearby areas in subtropical wet forest. Silver et al. (2004), working in a 60-year tropical reforestation project on abandoned pastures in the LEF, found greater rates of carbon sequestration and combined accumulation of below and aboveground biomass than in an adjacent pastureland. Similarly, Marín-Spiotta et al. (2007) found greater biomass in 80-year-old secondary forests than in remnant fragments of primary forest in the nearby Sierra de Cayey. Our analysis also suggests that secondary forest in the LEF contributes to removing airborne contaminants, including sulfates and $PM_{2.5}$ associated with African dust and anthropogenic aerosols that have been reported to affect climate, weather, human and ecosystem health in Puerto Rico (Prospero and Mayol-Bracero, 2013, Subramanian et al., 2018). Prior research about land–atmosphere interactions and aerosol dust deposition in the LEF has been focused on higher elevation cloud forest vegetation (Royer et al., 2018).

Composition and structure are among the key forest attributes that can serve as good predictors of ecosystem services (Felipe-Lucia et al., 2018), and tree size is an especially important physical attribute that shapes aboveground biomass stocks and carbon dynamics (Piponiot et al., 2022). The contribution of large diameter trees to aboveground biomass and carbon storage has been documented both globally (Lutz et al., 2018) and for neotropical forests (Clark and Clark, 1996). Ecosystem services analysis from numerous urban settings have also confirmed the greater carbon storage and sequestration, air pollution removal, and hydrologic benefits afforded by a few large trees relative to many small ones (Nowak, 1994, Davies et al., 2011). In our study, the <50 A+P plots, which experienced assisted regeneration for several decades, have a greater average DBH and the tallest trees. When these structural attributes were extrapolated to the estimation of hydrologic functions and ecosystem services using i-Tree Eco, the model outputs suggested that trees in the <50 A+Ps group provide significantly greater rates of evaporation and transpiration, and greater benefits associated with carbon storage, and pollution removal than the other plot groups. Importantly, the greater rates of service provision by the <50 A+P plots occurred despite having fewer numbers of species and a lower stem density than the > 50 P plots (Table 2). Hence, species diversity and stem density alone do not necessarily translate into greater ecosystem services for a given forest stand. At the species level, several non-native species planted for timber and enrichment purposes were all observed to have estimated ecosystem services (average value per individual) that fell among the top twelve species, even with relatively low abundances (Supplementary Tables 1 and 2). While the present study did not examine whether the structural differences observed and associated services estimated are due to specific species traits, our findings signal the general importance of historical management legacies – and specifically the role of assisted natural generation – as a factor that can influence the composition and structure of individual trees and the services they cumulatively provide at the landscape scale for several decades following cessation of land use.

We also observed greater total cumulative values of individual regulating services rendered by native compared to non-native species, which is indicative of the local dominance and importance of natives as service providers in the secondary forest community we monitored. Island-wide data from the 2014 FIA assessment in Puerto Rico show that native species represent 70% of trees and contribute 62% of live aboveground tree carbon (Lugo et al., 2022). Yet, when we compared random equal-sized groups of natives and non-natives, our results indicated that trees provide different services among distinct size classes. This underscores the relevance of structural parameters such as DBH for estimating ecosystem services using models like i-Tree Eco. Smaller diameter native trees outperformed non-natives in terms of carbon storage, yet for larger diameter trees non-natives were more efficient. In contrast, for annual rates of carbon sequestered, the largest native trees had values significantly greater than the non-native ones. Regarding hydrologic functions, our results showed that the non-native trees monitored had significantly higher rates of evaporation and transpiration as compared to natives, but only for the 15–25 cm size class.

Other studies have described differences in carbon and water cycling between native and non-native species in tropical forests, but they frequently aggregate DBH data from trees across a broad range of diameter classes. For example, using trees $\geq$ 2 cm DBH Mascaro et al. (2012) found greater aboveground biomass and belowground carbon storage in novel forests dominated by non-native species in lowland Hawaiian forests. Sohel (2022) examined the relation between water use and DBH for 162 tropical trees and found that native species use more water than non-natives, with tree size and leaf area among several functional traits positively correlated with increased water use. In general, these results as well as our work suggest that it is too simplistic to consider only the origin of the species (natives vs. non-natives) when evaluating the overall performance and contribution of tree species to a given ecological function or ecosystem service. The functions and services of both native and non-native species can vary in accordance with dynamic structural attributes of individuals. Accounting for this heterogeneity of ecological functions and services is essential for scaling up from individual trees to catchment and landscape scales in managed forest systems (Seidl et al., 2013). This conclusion is particularly relevant in diverse landscape contexts like the LEF, where land use history, management activities, and regeneration pathways of secondary forests can be highly variable. Additional research is required to assess tradeoffs associated with different types and degrees of historical and ongoing land use.

Our findings also align with broader ecological theory and literature on global-scale secondary forest dynamics, restoration, and ecosystem service provision. Regrowth of tropical secondary forests like those in Puerto Rico and other post-agricultural societies can deliver multiple ecosystem services pertaining to ecological, social, and economic dimensions that both directly improve human well-being (Chazdon and Guariguata, 2016). These include storing large amounts of carbon in their above- and belowground biomass (Schwartz et al., 2020), which can help mitigate climate change, regulating water flow through evapotranspiration and soil infiltration processes (Benayas et al., 2009), which can protect water supplies and buffer the effects of flooding and drought, and tree canopies intercepting airborne particulate matter (Rosenfield et al., 2023), which can improve air quality and human health. Both natural regeneration and assisted natural generation have notable potential as underutilized and cost-effective strategies for large-scale landscape restoration of degraded tropical lands (Chazdon and Guariguata, 2016). These practices can likewise contribute to long-term global goals related to carbon sequestration, protection of soil and water resources, biodiversity conservation, and supporting local livelihoods through sustainable harvesting of forest-based resources (Chazdon and Uriarte, 2016). Importantly, the element of time is critical for recovery of these ecological functions and the provision of ecosystem services in secondary tropical forests (Poorter et al., 2021a, Poorter et al., 2021b). In the case of the LEF, the secondary forest we assessed has been regenerating for >70 years, which has facilitated the return of key structural and functional attributes. Future research is necessary to examine the secondary forest against old-growth stands in the LEF and

compare the level of recovery.

5. Conclusions

Research on tropical secondary forests is important for understanding the long-term effects of land use on forest composition and structure, the implications for ecosystem functioning, and the generation of goods and services. We examined a secondary forested landscape in Puerto Rico that has experienced variable degrees of historical clearing and both passive and assisted natural regeneration in the process of recovery since agricultural abandonment many decades ago. Our results suggest differences among plots with distinct historical canopy cover and post-agricultural recovery pathways in the LEF's late secondary forest with respect to species composition, forest structure, evapotranspiration processes, and the provision of some ecosystem services, including carbon sequestration and storage, and removal of airborne contaminants. The differences can be attributed to historical management actions (i.e., planting, thinning, culling) in concert with successional trajectories characteristic of novel secondary forests (Lugo and Heartsill-Scalley, 2014, Lugo et al., 2020). Both passive and assisted regeneration of secondary forests can result in the provision of multiple ecosystem services over the long-term, with considerable variability among tree species and size classes. Our conclusions are limited by a lack of fine-scale detail regarding the historical management interventions. There is documentation about the total number and origin of species planted and estimations of seedling density within the LEF as a whole (see Marrero, 1947, Francis, 1995, Weaver, 2012) including areas classified as secondary forest (EYNF, 2018), yet we did not have data specific to our monitoring plot locations concerning the tree species planted, planting density, and exact timing of interventions. We address other limitations regarding sampling design, and analysis of biomass and ecosystem services in the Supplementary material.

This study marks the first assessment of its kind that explores relationships between structural attributes, ecological functions, and the ecosystem services provided by montane secondary forest trees in Puerto Rico and is one of only a handful of such studies from the Caribbean. Our findings illuminate the dynamic complexity of ecosystem functions and the need for individual and stand level data when examining compositional and structural influences of trees to draw landscape-scale conclusions about forest ecological functions and ecosystem service provision. Additional investigation is needed to compare the results with old-growth forest stands, examine the long-term effects of repeated large-scale disturbances, such as hurricanes, on the provision of goods and services in tropical secondary forests, and determine how active management may reduce ecosystem vulnerability and moderate functional tradeoffs. Considering increasing environmental pressures on forest ecosystems globally, including clearing of primary forest for agriculture and development purposes and climate change stressors (Curtis et al., 2018), this research could provide a useful point of comparison for future analysis, and help inform management decisions in other recovering tropical landscapes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

A link to the research data used is shared in the manuscript.

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Appendix A. Supplementary data

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