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Abstract

A challenge in community ecology is the development of ecosystem baselines, allowing the assessment of the variation in the ecological dynamics through different temporal and spatial scales. To our best knowledge, no studies have been carried out in seasonal evergreen forests of Belize to establish a baseline for future monitoring. Hence, a floristic study of the woody plant species diversity and composition was carried out at the Billy Barquedier National Park (BBNP) to develop an ecosystemic baseline for the assessment of the originally implemented conservation strategies. A thorough floristic survey was performed from May to August 2015 in 42 rectangular plots (500 m²) randomly allocated along the 100 to 500 m elevation gradient of the BBNP. Species richness, diversity, composition, and aboveground biomass were assessed. Likewise, information of a series of indicators on protection and risk situation (e.g., IUCN Red List of threatened species, CITES categories), and restoration for each relevant species are also provided. The BBNP is an important forest with 67 woody species distributed in 30 plant families. *Terminalia amazona* and *Corozo palm Attalea cohune* are the most important species in the reserve, in terms of abundance, frequency, and biomass. A clear trend between biodiversity metrics, elevation, and aboveground biomass was noted. This study contributes to understand relevant ecological topics as well as provides key elements for the management and conservation of the BBNP area and Belize.

Keywords

forest inventory, vascular plants, species richness, National Park, Belize

Tropical forests are one of the main terrestrial carbon reserves (Whittaker & Likens, 1975). Moreover, Mesoamerica is one of the most important biodiversity hotspots in the world (Myers et al., 2000; Robertson & Chan, 2011), and its forests provide a wide variety of ecosystem services (Aide & Grau, 2004; Wright & Muller-Landau, 2006). Despite the importance of the region, deforestation due to land-use change is high of these ecosystems (Aide et al., 2012; Geist & Lambin, 2002; Lambin et al., 2003). Belize, which comprises large forested areas (about 1,393,000 ha; Forest Resources Assessment, 2015) and more than 3,400 vascular plant species (Balick et al., 2000), is not the exception. Although historically it has been the Central American country with the lowest deforestation rates (0.2% per year), the deforestation processes have been accelerated between 1990 and 2010. About 12.2%

(193,000 ha) of its forests were deforested due to the economic development policy (Young, 2008). Belize lowlands and tropical forests are under pressure for conversion to agricultural land use, and if this deforestation rate continues, the forest cover could be reduced

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significantly in the next decade (Herrera et al., 2018). In addition, the selective extraction of the main commercial forest species has important effects on composition and structure due to collateral damage to plant communities (Gadow et al., 2004; González-Castillo et al., 2007; Montenegro et al., 2006).

The understanding of the factors influencing the spatial variation patterns of composition, diversity, and structure of woody species is a challenge in community ecology (Lomolino, 2001). It has been widely demonstrated that altitude is one of the main drivers on the emergent properties of the communities (Gaston, 2000; Grytnes & Beaman, 2006; Guo et al., 2013; Pianka, 1966). For example, changes in forest structure of temperate forests—such as the decrease of living biomass in the soil; the increase of stem density with the altitude (Grubb, 1977); and a tendency of leaves to become smaller, thicker, and harder—have been observed. There are several abiotic factors that change forest structure and species composition with elevation. For example, Körner (2007) observed a reduction of the number of species as well as of productivity (Luo et al., 2004). Such changes were influenced by abiotic factors such as temperature, decreasing atmospheric pressure, and solar radiation (increases with elevation; Christy & Jonh-Arvid, 2010).

It has been proposed that biodiversity plays an important role in ecosystem function, particularly in productivity (Cadotte, 2013). Several studies have found positive relationships between biodiversity and productivity, measured through biomass (Coelho de Souza et al., 2019), and this relationship has been explained as a function of the complementarity between plant life strategies and use of resources (Gross et al., 2007; Loreau & Hector, 2001). On the other hand, negative relationships between biodiversity and productivity (biomass) have been reported as a result of the selection effect, that is, the caused effect when a set of dominant species excludes those less productive species (Turnbull et al., 2013). However, because most of the studies have been carried out in grasslands, in which fast-growing species dominate and the structure of the community is less complex (Warren et al., 2009), both types of relationships remain controversial in tropical forest ecosystems (Adler et al., 2011; Fraser et al., 2015).

Biomass is one of the most used predictors of productivity because it represents the stocks of organic matter in forests, and its quantification and monitoring are relevant to establish strategies against global warming (Cifuentes, 2010). There are two methods to estimate biomass, direct and indirect. Direct methods involve the tree felling and the drying of each tree component, whereas in indirect methods, the biomass is estimated using allometric equations, which incorporate one or more tree (e.g., breast height diameter or wood density)

or stand variables (mean diameter, dominant height, basal area or stems per ha; Chave et al., 2005).

Belize is one of the countries with the lowest deforestation rates in Latin America. However, agricultural activities have steadily increased. At present, the Stann Creek district is one of the major agricultural regions of Belize. The soils along the North Stann Creek, Sittee, and South Stann Creek rivers support a flourishing citrus and banana industry, and there are plans for exponential growth in areas for citrus and agricultural activities to boost the country's economy (Ministry of Agriculture of Belize, 2017). Likewise, some of the areas have historically been used for the extraction of nontimber forest products, hunting and logging, which is threatening biodiversity (Association of Protected Areas Management Organizations, 2011). To reduce the imminent increase of deforestation by agricultural activities in Stann Creek, and to protect the watersheds and its associated biodiversity, a natural reserve was established in 2001. An evergreen forest area with abundant watersheds was selected, and named the *Billy Barquedier National Park* (BBNP).

The objectives of this study were (a) to describe the species diversity, composition, and structure; (b) to evaluate the altitude–biodiversity of woody species relationships; and (c) to analyze the woody species diversity–productivity relationship in the tropical forest of the BBNP reserve.

Materials and Methods

Study Site

The sampling sites are located within the BBNP (663.3 ha; Figure 1), District of Stann Creek Valley in southeast Belize (17°02'24.3"–88°27'32.0"N, 17°01'50.0"–88°26'20.6"W; Association of Protected Areas Management Organizations, 2011; Figure 1). The BBNP is crossed by the Emerald Valley Mountain and surrounded in the North by the Manatee Forest reserve, in the South by the private farmland of the Steadfast Community Village, and in the East and West by state lands. The BBNP is part of a mountainous system with a short elevation gradient that ranges from 100 to 500 m above sea level (m.a.s.l.) at its highest point. The climate is classified as seasonal tropical wet, with the rainy season running from June to December and the dry season from February to April (Walsh, 1996). The mean annual temperature ranges between 27°C and 30°C, with the highest temperatures in April, and mean annual precipitation between 2,500 and 3,048 mm (Pither & Kellman, 2002). The vegetation is classified as evergreen seasonal broad-leaved lowland forest, and dominant genera in the forest are *Simarouba*

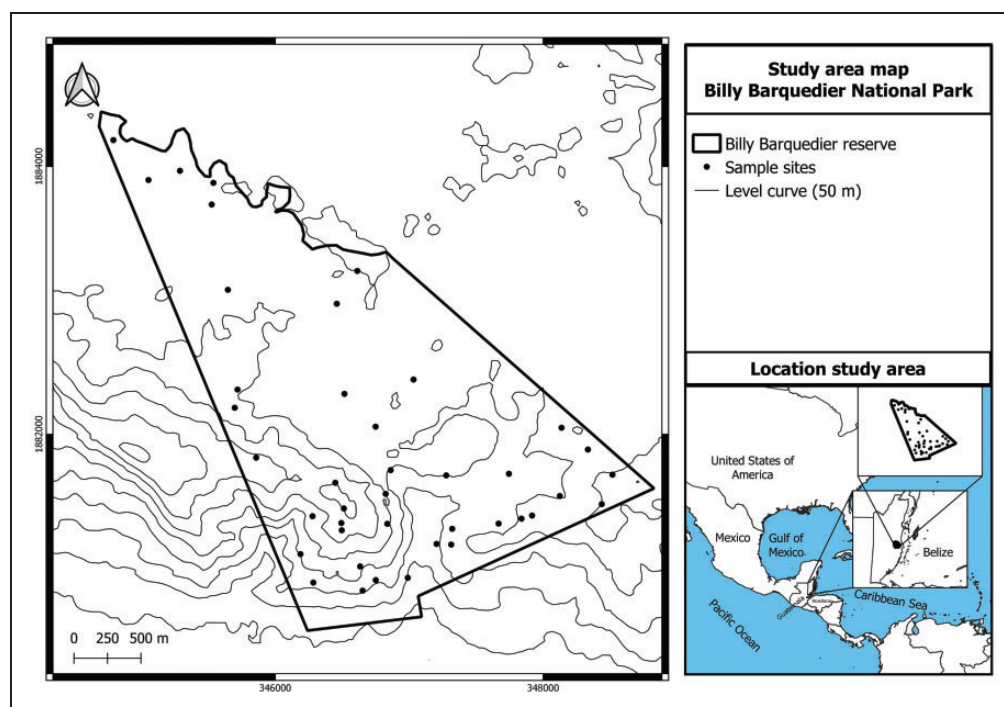


Figure 1. Location and Samples Sites at the Billy Barquedier National Park, Stann Creek Valley District, Southeast Belize (17°02′24.3″–88°27′32.0″ N, 17°01′50.0″–88°26′20.6″ W).

and *Terminalia* (code: IA2a (1) (a) – ST), with upper canopy height ranging from 15 to 25 m (Meerman & Sabido, 2001). This ecosystem is a secondary forest of 40 years age average. Soils in the National Park are derived from metamorphic and limestone igneous materials and red soils, or deep brown lateritic soils derived from alluvial or igneous materials, as well as in deep clay soils derived from limestone loams in slightly undulating terrain. Outcrops of basaltic rocks with shallow soils can also be found.

Field Sampling

A survey at the BBNP during the first half of the rainy season (May–August) in 2015 was conducted. A total of 42 plots of 500 m² (25 × 20 m) were randomly located throughout the reserve (Figure 1), comprising a total area of 2.1 ha. Each sample plot was located with GPS (Garmin 64s) and the following variables were recorded: diameter at breast height (DBH, cm) of all woody species ≥10 cm, the taxonomic identity of all species, and the above sea level height of the plot center (m). Species were identified in the field by expert botanical taxonomists; in those cases, where individuals could not be recognized to species level, they were treated at the genus or family level. Scientific names were reviewed using online catalogs (IPNI, 2019; Missouri Botanical Garden, 2019) and reassessed to eliminate synonyms.

Analyses of Diversity and Species Composition

To analyze the species diversity of woody plants in the BBNP, the species richness was estimated (*S*) using the rarefaction and extrapolation (R/E) approach (Chao et al., 2014; Colwell et al., 2012; Hsieh et al., 2016). The analyses were carried out using iNEXT library in R software (Hsieh et al., 2016). In addition, the Shannon-Wiener (*H'*) index was calculated. To determine the relative importance of the species composition, the importance value index (IVI) was computed. The IVI values were calculated by summing the relative basal area, the relative abundance, and the relative frequency each species (Mueller-Dombois & Ellenberg, 1974). Finally, the newly recorded and endemic species of Belize present at the BBNP were also pointed out following the approach by Balick et al. (2000).

Biomass Estimation

Allometric equations are commonly used to estimate aboveground biomass (AGB) of plant communities (Anaya et al., 2009; Barrachina et al., 2015; Bortolot & Wynne, 2005). For all species, except for palms, the equation developed for moist tropical forests at a pan-tropical level was used (Chave et al., 2005).

$$\ln(\text{AGB}) = a + b \ln(\text{D}) + \ln(\rho),$$

where D is the DBH (cm), ρ is the average wood density of the species, and a and b are the model parameters to be estimated. This equation has been widely used to calculate biomass in neotropical secondary forests around the world (Poorter et al., 2016), in Mexico (Návar, 2009; Ramírez Ramírez et al., 2017), and in the Amazon (Asner, 2009), with acceptable results and uncertainty levels below 5%.

The equation proposed by Goodman et al. (2013), developed for palm species in the Amazon, was used in this study for estimating the biomass of palm species:

$$\ln(\text{AGB}) = a + b \ln(D),$$

where D is the DBH (cm) and a and b are the model parameters to be estimated. This equation has also shown high levels of certainty when used in individuals of the Areaceae family (Avalos & Sylvester, 2010; Goodman et al., 2013). Because no studies reporting the wood density for the tree species sampled in Belize was found, we used wood density values reported of studies in Central America (Chudnoff, 1984; Reyes et al., 1992; Zhu & Waller, 2003) and south of Mexico (Urias, 1996).

Data Analysis

To determine the relationship between species richness (S) and the Shannon-Wiener (H') diversity indices with altitude and productivity, regression analyses using the `glm2` package (Marschner, 2011) in the R software (R Development Core Team, 2012) were performed.

Status Indicators of the Species

Protection and risk status indicators were obtained from available online databases: (a) Forest Protection of Trees Regulations, Belize (Belize Government, 2003); (b) IUCN Red List of Threatened Species (IUCN, 2019); (c) IUCN Species for Restoration in Mexico, Central America, and the Caribbean (IUCN-ORMACC, 2015); (d) Convention on International Trade in Endangered Species of Wild Fauna and Flora (United Nations Environment World Conservation Monitoring Centre, 2019); (e) Global Invasive Species Database (Invasive Species Specialist Group, 2015); and (f) Ethnobotanical Use of the Species. These data were sorted in two classes depending on the region based on use: local use (reported for Belize) and regional use (reported for Central America; Balick et al., 2000; Missouri Botanical Garden, 2019).

Results

Species Diversity

A total of 937 individuals were recorded, of which 792 were identified at species level. The identified individuals

belong to 30 families and 44 genera; 46 species were identified, although some individuals were only identified to genus (11) and family (10) levels. Hence, the total species richness was 67 (Table 1). Estimated species richness was 76.4 (95% CI = 66.6–86.1), with a high sample coverage estimator ($C_{\text{hat}} = 0.982$), while the Shannon-Wiener diversity index was 1.8 (CI = 0.34–2.51).

The distribution of species among families was uneven. Five families with four or more species encompass the greatest number of species (28 species, 41% of the total species richness). By contrast, the remaining 25 families were represented from one to three species, accounting 39 species (59% of the total species richness). The five most species-rich families were Fabaceae with 10 species, followed by Sapotaceae and Malvaceae with 5 species, and Sapindaceae and Moraceae with 4 species. Likewise, the five families with the highest number of individuals were Clusiaceae (82), Annonaceae (59), Sapotaceae (53), Celastraceae (52), and Lauraceae (52). Finally, *Xylopia frutescens* (55, Annonaceae), *Clusia massoniana* (54, Clusiaceae), and *Zinowiewia pallida* (52, Celastraceae) were the most abundant species.

Species Composition

According to the IVI, *Attalea cohune* had the maximum value (22.74%), representing the most dominant species, followed by *Terminalia amazonia* (18.77%) and *Pouteria sp* (14.74%). Only eight other species had an IVI > 10%, namely, *Vochysia guatemalensis* (13.71%), *Calophyllum brasiliense* (13.09%), unidentified Lauraceae (13.07%), *Zinowiewia pallida* (12.77%), *Xylopia frutescens* (12.70%), *Spondias mombin* (12.13%), *Cojoba arborea* (11.00%), and *Clusia massoniana* (10.74%); see Figure 2A. These 11 species together covered >50% of the total community IVI. Two families had the maximum IVI value: Fabaceae (25.63%) and Arecaceae (25.50%); and other four families had an IVI > 15%: Clusiaceae (23.79%), Combretaceae (19.55%), Sapotaceae (19.43%), and Lauraceae (15.97%); see Figure 2B. These six families represent >40% of the total community IVI. The vegetation structure presented a j -inverted shape (licourt type) diametric distribution, which is characteristic of secondary succession forest, given the tree density decreases with diameter increase.

Biomass of Woody Plants

Average of basal area, AGB and DBH calculated for the BBNP were 17.30 m²/ha (minimum to maximum range 14.12–21.33 m²/ha), 160.84 Mg ha⁻¹ (88.52–220 Mg ha⁻¹), and 22.36 cm (20.31–24.41 cm), respectively. The top five tree species that contributed most to AGB were *Terminalia amazonia* (25.33 Mg ha⁻¹, 15.75%), *Pouteria sp* (18.74 Mg ha⁻¹, 11.65%), *Attalea cohune*

Table 1. Names of Woody Species and Plant Families in the Billy Barquedier National Park, Belize.

Species	Family	No. Ind (ha)	Av. DBH	AGB (ha)	Mg ha ⁻¹	RDL	RST	FLB
<i>Terminalia amazonia</i> (TerAma)	Combretaceae	720	62.86	19,389.13	25.34	—	*	*
<i>Pouteria</i> sp. (MorPou)	Sapotaceae	760	24.93	17,965.48	18.74	—	—	—
<i>Attalea cohune</i> (AttCoh)	Arecaceae	880	31.61	632.16	18.65	—	—	—
<i>Vochysia guatemalensis</i> (VocGua)	Vochysiaceae	320	58.46	44,132.70	15.34	—	*	*
<i>Calophyllum brasiliense</i> (CalBra)	Clusiaceae	560	16.55	331.04	9.77	LC	*	*
<i>Zinowiewia pallida</i> (ZinPal)	Celastraceae	1,040	23.56	7,139.57	8.03	—	—	—
<i>Virola koschnyi</i> (VirKos)	Myristicaceae	320	35.89	16,793.52	4.47	—	*	—
<i>Spondias mombin</i> (SpoMom)	Anacardiaceae	660	36.53	9,054.16	3.92	—	*	—
<i>Psychotria</i> sp. (PsyI)	Rubiaceae	400	29.51	8,783.64	3.79	—	—	—
<i>Lonchocarpus</i> sp. (MorLon)	Fabaceae	100	13.80	22,464.78	3.73	—	—	—
<i>Simarouba amara</i> (SimGla)	Simaroubaceae	460	14.99	9,934.23	3.66	—	*	*
<i>Xylopia frutescens</i> (XypFru)	Annonaceae	1,100	21.47	3,832.33	3.57	—	—	—
<i>Clusia massoniana</i> (CluMas)	Clusiaceae	1,080	16.74	334.86	3.4	—	—	—
<i>Tabernaemontana donnell-smithii</i> (TabDon)	Apocynaceae	360	31.34	7,481.96	2.81	—	*	—
<i>Schizolobium parahyba</i> (SchPar)	Fabaceae	60	47.36	48,850.01	2.63	—	*	—
<i>Ficus</i> sp. 1 (Fic1)	Moraceae	20	9.62	98,281.97	2.11	—	—	—
<i>Matayba apetala</i> (MatApe)	Sapindaceae	300	54.62	6,777.56	1.69	—	—	—
<i>Bursera simaruba</i> (BurSim)	Burseraceae	120	50.61	1,012.23	1.67	—	*	—
<i>Cochlospermum vitifolium</i> (CocVit)	Bixaceae	340	21.14	422.87	1.65	—	*	—
<i>Zanthoxylum setulosum</i> (ZanSet)	Rutaceae	140	38.90	11,466.76	1.54	—	—	*
<i>Cajoba arborea</i> (CajArb)	Fabaceae	300	38.32	766.49	1.49	—	*	—
<i>Cecropia peltata</i> (CecPel)	Urticaceae	520	65.73	1,314.62	1.2	—	*	—
<i>Hampea stipitata</i> (HamSti)	Malvaceae	280	25.35	7,487.12	1.11	—	—	—
<i>Miconia argentea</i> (MicArg)	Melastomataceae	340	59.09	4,476.58	0.84	—	*	—
<i>Schefflera morototoni</i> (SchMor)	Araliaceae	100	36.86	9,416.04	0.84	—	*	—
<i>Dialium guianense</i> (DiaGui)	Fabaceae	40	21.36	13,662.91	0.8	—	*	*
<i>Cupania belizensis</i> (CupBel)	Sapindaceae	480	21.71	434.17	0.78	—	—	—
<i>Lonchocarpus castilloi</i> (LonCas)	Fabaceae	140	14.32	4,961.26	0.66	—	—	*
<i>Byrsonima crassifolia</i> (ByrCra)	Malpighiaceae	200	20.50	409.98	0.61	—	*	—
<i>Krugiodendron ferreum</i> (KruFer)	Rhamnaceae	40	28.58	6,368.58	0.5	—	—	—
<i>Pouteria sapota</i> (PouSap)	Sapotaceae	40	14.96	8,679.33	0.49	—	*	*
<i>Damburneya salicifolia</i> (DamSal)	Lauraceae	160	14.48	289.66	0.45	—	—	—
<i>Aspidosperma spruceanum</i> (AspSpr)	Apocynaceae	20	12.13	242.55	0.43	—	—	—
<i>Coccoloba belizensis</i> (CocBel)	Polygonaceae	80	16.54	330.83	0.39	—	—	—
<i>Miconia impetionalis</i> (MicImp)	Melastomataceae	30	15.36	9,029.08	0.39	—	*	—
<i>Pouteria campechiana</i> (PouCam)	Sapotaceae	80	31.70	4,576.35	0.37	—	—	—
<i>Eugenia</i> sp. (MorEug)	Myrtaceae	140	21.87	4,677.33	0.35	—	—	—
<i>Protium copal</i> (ProCop)	Burseraceae	160	14.01	2,462.29	0.31	—	—	—
<i>Vismia camparagwey</i> (VisCam)	Hypericaceae	120	21.10	3,819.65	0.24	—	—	—
<i>Byrsonima bucidifolia</i> (BirBuc)	Malpighiaceae	60	27.71	554.18	0.23	—	—	—
<i>Inga vera</i> (IngVer)	Fabaceae	40	15.69	6,530.34	0.23	—	*	—
<i>Lonchocarpus guatemalensis</i> (LonGua)	Fabaceae	80	17.13	2,432.86	0.18	LC	—	—
<i>Inga</i> sp. (Ing1)	Fabaceae	20	30.88	7,165.82	0.13	—	—	—
<i>Cupania</i> sp. (MorCup)	Sapindaceae	80	11.18	223.67	0.1	—	—	—
<i>Erythrina standleyana</i> (ErySta)	Fabaceae	40	22.28	5,266.11	0.1	—	—	—
<i>Annona</i> sp. (MorAnn)	Annonaceae	60	29.92	598.42	0.09	—	—	—
<i>Ceiba pentandra</i> (CeiPen)	Malvaceae	20	31.79	635.86	0.09	LC	*	—
<i>Hampea trilobata</i> (HamTri)	Malvaceae	20	24.14	9,000.30	0.09	—	—	—
<i>Chrysophyllum cainito</i> (ChrCai)	Sapotaceae	20	23.94	478.74	0.08	—	*	—
<i>Cryosophila</i> sp. (MorCry)	Arecaceae	120	169.98	3,399.55	0.08	—	—	—
<i>Hampea nutricia</i> (HamNut)	Malvaceae	60	14.07	2,815.65	0.08	—	—	—
<i>Ficus</i> sp. 2 (Fic2)	Moraceae	20	24.64	5,243.79	0.05	—	—	—
<i>Swietenia macrophylla</i> (SwiMac)	Meliaceae	20	13.43	2,834.30	0.04	VU	*	*
<i>Ficus</i> sp. 3 (Fic3)	Moraceae	20	29.84	3,109.32	0.02	—	—	—
<i>Licaria peckii</i> (LicPec)	Lauraceae	20	16.62	2,945.09	0.02	—	—	—

(continued)

Table 1. Continued.

Species	Family	No. Ind (ha)	Av. DBH	AGB (ha)	Mg ha ⁻¹	RDL	RST	FLB
<i>Ochroma pyramidale</i> (OchPyr)	Malvaceae	20	7.99	4,353.36	0.02	—	*	—
<i>Thrinax radiata</i> (ThrRad)	Arecaceae	20	10.92	1,872.45	0.01	—	—	—
Unidentified (Ann)	Annonaceae	20	23.09	14,062.96	10.34	—	—	—
Unidentified (Apo)	Apocynaceae	20	31.00	2,310.31		—	—	—
Unidentified (Com)	Combretaceae	20	23.71	7,402.70		—	—	—
Unidentified (Fab)	Fabaceae	2,880	63.03	6,483.12		—	—	—
Unidentified (Fla)	Flacourtiaceae	140	14.07	16,656.96		—	—	—
Unidentified (Lau)	Lauraceae	200	18.27	3,852.94		—	—	—
Unidentified (Mor)	Moraceae	140	17.36	3,792.14		—	—	—
Unidentified (Myr)	Myrtaceae	400	15.41	4,789.23		—	—	—
Unidentified (Sap)	Sapindaceae	80	36.45	5,209.26		—	—	—
Unidentified (Spo)	Sapotaceae	160	23.94	2,224.08		—	—	—

Note. The table include the individual number (N) and conservation status in RDL, International Union for Conservation of Nature Red List categories (LC, least concern species; VU, vulnerable species); RST, IUCN Recovery Species; and FLB, protected trees by Forest Law of Belize. DBH = diameter at breast height; AGB = aboveground biomass.

(18.64 Mg ha⁻¹, 11.59%), *Vochysia guatemalensis* (15.34 Mg ha⁻¹, 9.53%), and *Calophyllum brasiliense* (9.76 Mg ha⁻¹, 6.07%), whereas the families with the higher AGB were Combretaceae (25.49 Mg ha⁻¹, 18.8%), Sapotaceae (19.94 Mg ha⁻¹, 14.73%), Arecaceae (18.73 Mg ha⁻¹, 13.84%), Vochysiaceae (15.34 Mg ha⁻¹, 11.33%), and Clusiaceae (13.16 Mg ha⁻¹, 9.27%); see Table 1. AGB biomass of woody species did not vary with respect to elevation gradient ($R^2 = .028$, $p = .2885$).

Elevation–Biodiversity and Biodiversity–Biomass Relationships

It has been observed that elevation has implications for species richness and biodiversity (Guo et al., 2013). However, few studies have investigated this relationship in a short altitudinal gradient. In this study, species richness decreased between the 130 and 400 m.a.s.l. There was a significant negative relationship between species richness and the Shannon-Wiener index with the elevation, but with low R^2 values ($R^2 = .239$ $p < .001$, and $R^2 = .3941$ $p < .001$, respectively; Figure 3A and B). For the entire data set, we found a slight trend in the species richness–productivity (AGB) and diversity–productivity relationships (Figure 3C and D). Both diversity indices showed a unimodal trend respect to AGB, with R^2 values of .1668 and .1725 for species richness and Shannon-Wiener index, respectively. The highest values of the diversity indices tested in this study were found between 200 and 300 Mg ha⁻¹ of AGB.

Current Species Status Indicators

Protected and Risk Species. Nine of the woody plant species under protection by the subsidiary laws of the Belize Government were found in the BBNP: *Calophyllum brasiliense*, *Dialium guianense*, *Lonchocarpus castilloi*,

Pouteria sapota, *Simarouba amara*, *Swietenia macrophylla*, *Terminalia amazonia*, *Vochysia guatemalensis*, and *Zanthoxylum setulosum*. *Swietenia macrophylla* is the only IUCN Red List vulnerable species recorded at the BBNP. Otherwise, three vascular plant species present in the study are considered as Least Concern (LC), that is, they were evaluated by the IUCN Red List as not being a focus of species conservation: *Calophyllum brasiliense*, *Ceiba pentandra*, and *Lonchocarpus guatemalensis* (Table 1). *Swietenia macrophylla* is a species protected by CITES (Appendix II) against overexploitation through international trade. No invasive woody plants species were detected in the BBNP.

Restoration and Recovery. Landscape restoration aids in solving environmental problems and recovering the production capacity of ecosystem goods and services in degraded areas. The IUCN-ORMACC has proposed many species for restoration and recovery of degraded landscapes in Mexico, Central America, and the Caribbean; 23 of those species were found in the BBNP (Table 1), and at least 4 are among the 10-most species with the highest aboveground biomass estimated in this study: *Terminalia amazonia* (15.75 Mg ha⁻¹), *Spondias mombin* (2.43 Mg ha⁻¹), *Calophyllum brasiliense* (6.07 Mg ha⁻¹), and *Simarouba amara* (2.77 Mg ha⁻¹).

Discussion

This study identified the ecological properties of the woody species community, such as species richness, composition, and biomass, as well as conservation status to offer elements for its conservation (Hu et al., 2012). Likewise, it is of a practical floristic monitoring with

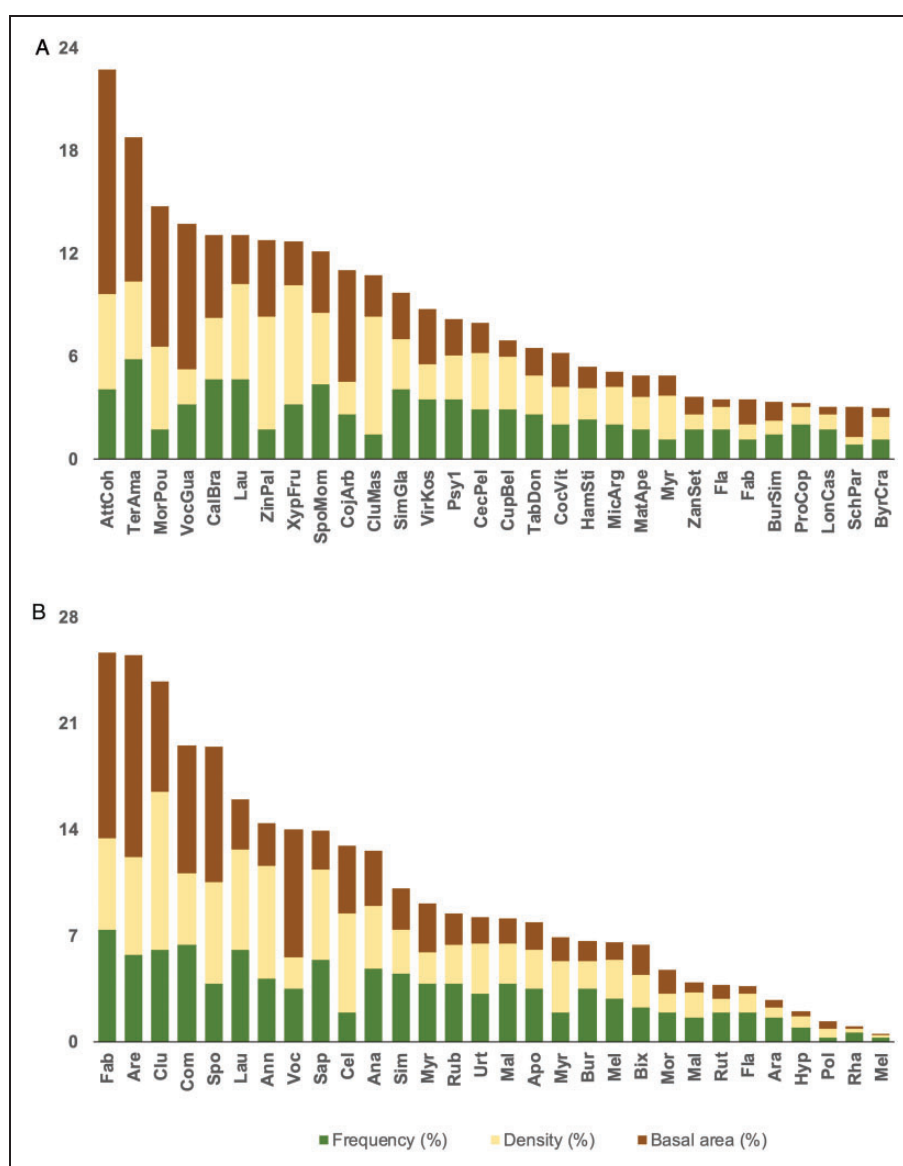


Figure 2. Importance Value Index (IVI) of Woody Species (A) and Families (B) in the Billy Barquedier National Park, Belize. IVI is presented for all the families, although only the species listed with $>3\%$ IVI values are displayed.

implications for conservation and sustainable management of biodiversity (Miles et al., 2006).

A total of 67 tree species were found in 42 plots distributed throughout the BBNP in Belize. The species composition revealed families and predominant genera that are typical of the humid regions of tropical forests (Gentry, 1992), including Central America (Coates, 1987), and widely reported for the Neotropical region (Trejo, 1998). According to Hartshorn et al. (1984), the forests of Belize contain about 700 woody species. The observed and estimated number of species (67 and 76, respectively) found in this study at the BBNP represents about the 10% of the total woody plants present in the country. The observed species richness is different to

that reported in other areas of Belize with different vegetation types. For instance, using online databases, Bridgewater et al. (2006) recorded about 320 tree species in 106,800 ha of the Chiquibul Forest (Belize), which includes several variants of lowland and submontane tropical evergreen broadleaf forests. Likewise, Meave et al. (1991) reported 187 woody species and Goodwin et al. (2013) found 362 in 234,200 ha forests and savannas of Belize. This variation in recorded species number is best explained, by the sampled area, the presence of fragmentation conditions and the presence of communities of plants associated with different stages of secondary succession (e.g., pioneer species). The estimator of the coverage of the sample in the BBNP was remarkably

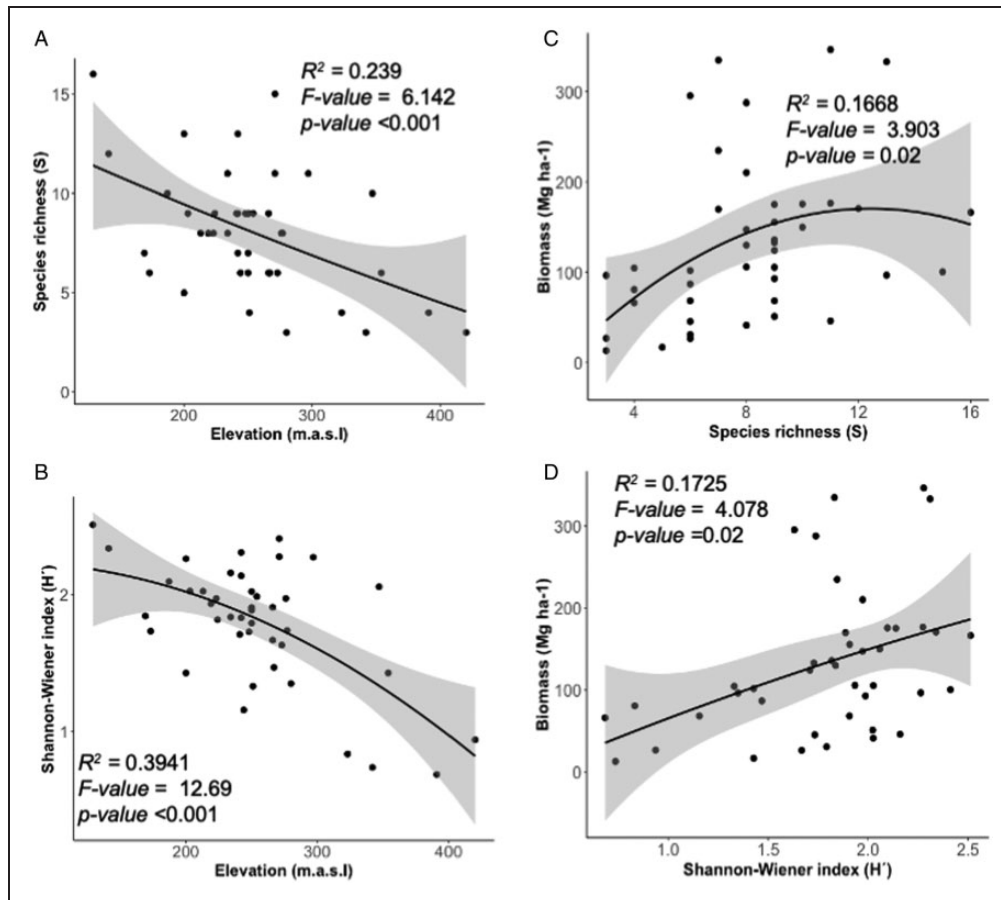


Figure 3. Change in Species Richness and Shannon-Wiener Index Along an Elevational Gradient (A and B), and Biomass-Diversity Indices Relationships (C and D). The lines were fitted by using square polynomial regression models. The R^2 values of the regression models are listed in each graphic.

high ($C_{\text{hat}} = 0.982$), which suggests that the late stages of secondary succession show a decrease in species richness (Bonger et al., 2009). Hence, a comprehensive sampling effort was carried out, although the species richness in the BBNP is lower when comparing with the above-mentioned studies.

Since the need of forest conservation is an important aspect of the BBNP goals, a general knowledge about the ecosystemic and socioeconomic relevance of plants present at the national park should be stated. Therefore, several indicators were traced for the woody plant species at the BBNP.

Nowadays, the Government of Belize (2003) regulates several woody plant species in order to control the forest management practices as well as to promote the sustainable development and conservation of the forests. Among the nine protected species found in the BBNP, the big-leaf mahogany *Swietenia macrophylla* is of particular interest because it has been for centuries the most commercially valuable timber species in the Neotropics (Snook, 1998; Weaver & Sabido, 1997). Since both deforestation and wood extraction have significantly

reduced the abundance of mahogany in natural forests during the past 300 years, this species is now included at the IUCN Red List as a vulnerable species to extinction and at the Appendix II of the CITES to prevent over-exploitation due to international trade (Lamb, 1966; Navarro-Martínez et al., 2018; Shono & Snook, 2006). Protected areas are suitable refuge for native species by locally preventing habitat degradation attributable to human activities and acting as a natural filter against invasions (Gallardo et al., 2017; Pyšek et al., 2003). In consequence, BBNP could be considered as an efficient conservation effort, although further studies would be necessary in order to address the detection of smaller invasive plants.

The IVI is a reliable measure to assess the relative importance of a species since it takes into account several properties of the species in the vegetation (Curtis & McIntosh, 1950). The highest IVI species value was recorded for *Attalea cohune* Mart., 1844, which belongs to Arecaceae (palms), the family with the highest IVI value. In consequence they are the most relevant species and family founded in the BBNP, not only in terms of

abundance, frequency, and basal area but also in implications for conservation.

Many tropical species are threatened by the reduction in forest cover, fragmentation, and degradation. However, some are resilient to disturbance like *Attalea cohune*. This species is one of the most representative native trees in Central America. It can be found up to 600 m.a.s.l. and reaches up to 20 m height (Furley, 1976). palm is common in the country's lowland forests and in the anthropogenic settings becoming a dominant species in regrowth forests (McSweeney, 1995). This species has adapted well-drained but moist soils supplied with high nutrient concentrations.

It is not surprising that forest owners have sought to start performing agricultural activities within the current BBNP borders before the natural park establishment in 2001. In fact, the cropland trend seemed to continue invading further within the reserve. However, nowadays the forest landscape at the BBNP has recovered about 24.2 ha of previously degraded forest lands. The regrowth forests are of paramount importance in conservation and restoration of tropical ecosystems, since they can present a similar species richness as that of an old-growth forest and serving as biodiversity repositories (Chazdon et al., 2009). Also, they might serve as buffer zones around the old-growth forests, ameliorate edge effects, and reduce anthropogenic disturbances (Yirdaw et al., 2019). Hence, the recovery of the vegetation at the BBNP by regrowth forests may increase the conservation value of the reserve, and particularly because 23 of the species proposed for restoration and recovery of degraded landscapes in Mexico, Central America, and the Caribbean (IUCN-ORMACC, 2015) are present within the borders of the natural reserve (Table 1).

It has often been claimed that simply using stem diameter as a predictive variable of AGB is an effective approach (Wirth et al., 2004). However, this situation is more complex for the tropical forests, where regression models including mixed-species should be used. In this study, one of the simplest models to estimate AGB for tropical forests around the world (Chave et al., 2005) was chosen in order to consider the principle of parsimony based on their mathematical simplicity. Previous studies have already shown that species specific equations are unnecessary in estimating forest biomass (Gibbs et al., 2007). The two equations used in this study are general for all woody species and palms and are reported as alternative equations to estimate AGB in tropical countries with similar ecosystems, climate, and soils (Chave, 2005). The AGB estimations for BBNP ($131.53 \text{ Mg ha}^{-1}$) are lower than those reported in studies of high-altitude tropical ecosystems by Ensslin et al. (2015) and Lewis et al. (2013), who reported AGB values of 372 and 395 Mg ha^{-1} , respectively, but higher than

those reported by Campbell (1996) in Zambia and Zimbabwe (52 Mg ha^{-1}), Girardin et al. (2010) in Peruvian Andes (129 Mg ha^{-1}), Shirima et al. (2011) in Tanzania (46.4 Mg ha^{-1}), and Zimudzi and Chapano (2016) in Zimbabwe (34 to 65 Mg ha^{-1}). As pointed out by Shirima et al., causes of these differences may be diverse; for instance, species composition used allometric biomass equations, sampling approach, or plot sizes.

No biomass and carbon stocks estimates have been previously performed for tropical forests in Belize. This study represents, therefore, the first effort to generate knowledge about these issues in the country. Due to the key role that tropical forests play in ecosystem carbon sequestration, and hence for climate change mitigation, these results are relevant to develop forest management programs. It is noteworthy to point out that the vegetation composition, diversity, and biomass herein reported were derived from a short altitudinal transect located at the BBNP. Future studies are required to obtain further vegetation assessments but at the regional and national levels.

One of the most widely used parameter to evaluate the functioning of ecosystems is productivity (De Aguiar et al., 2013), defined as the biomass production per area. Authors like Lehman and Tilman (2000) and Barrufol et al. (2013) point out that plant diversity increases when the productivity of the community also increases, whereas others have found that AGB does not vary significantly with species richness (Kenkel et al., 2000). Our findings allowed to identify a hump-shaped (or unimodal) relationship between diversity and biomass, which has been frequently observed in mature ecosystems (Mittelbach et al., 2001; Roy, 2001). We observed that when biomass is relatively low, biodiversity increases to a certain level. After this optimal point, diversity trends to be lower. Diversity values where highest at medium AGB biomass and then decreased afterwards, which is similar to that reported by Ding et al. (2019) in South China and by Shang and Chen (2015) in Canada. The optimal biomass level was found close to 200 Mg ha^{-1} for both diversity measures used, and it is related to 10 and 2.1 values of species diversity and Shannon-Wiener indices, respectively (Figure 3C and D). The mechanisms behind these relationships have been discussed in terms of species facilitation and competition (Guo, 2007); that is, when biomass is relatively low, species richness increase due to interspecific facilitation; whereas when biomass accumulates to a certain point, competition leads to lower diversity (Weiner, 2001). Nevertheless, it is important to point out that this relationship could be influenced by the historical management practices in the BBNP. Therefore, further studies are necessary to confirm this hypothesis. Despite our results, we found no clear evidence that species diversity

influences strongly forest productivity (forest biomass production), which coincides with the conclusions reported by Kenkel et al. (2000), that increasing plant diversity does not influence productivity.

Along the elevational gradient, species richness and Shannon-Wiener diversity indices showed a negative pattern, that is, diversity decreased with increasing elevation, where mid-elevation points were found to have maximum values (15 and 2.4, respectively). These results agree with Ding et al. (2019) who point out that in tropical forest, mid-elevation transects have the highest species richness and the largest biomass, as well as the maximum height, which consequently provides more species for coexisting species with varied light requirements and results in higher species richness in mid-elevation habitats. Ding et al. (2019) report R^2 values for the elevation–species richness and functional richness–elevation relationships of .39 and .22, respectively. These values are similar to those obtained in this study for species richness and Shannon-Wiener indices (.239 and .375, respectively).

Implications for Conservation

International commitments, as well as the possibilities to obtain financing for communities that develop orderly conservation projects, have led to the development of monitoring strategies that range from the population to communities levels and even ecosystems. In addition, there has been a considerable increase in the development of voluntary community conservation schemes, with emphasis on the development of monitoring projects that affect the sharing of information for decision-making (Stoll-Kleemann, 2010). In particular, the case of the BBNP community reserve is an interesting case, because it is an initiative promoted by local people in collaboration with the Belizean government, which offers recognition, but not funds, for its operation. The BBNP is proposed as a strategy to contain the advancement of the agricultural frontier, specifically the establishment of citrus plantations, as well as to maintain water collection in the basin in which it is located. Consequently, the present study has important edges for conservation; on one hand, it establishes a baseline of ecological attributes and characteristics such as species richness and composition, biomass, IVI, as well as the rarity of the woody species that make up the plant community. On the other hand, from the reserve recovery has been observed in certain areas that were degraded due to anthropic activities. At the moment, the reserve is a counterweight with a landscape function as a reserve of flora and fauna in the region. Additional studies are required of tree species which could be used for restoration and recovery of degraded areas of Belize in order to warrant future ecosystem services.

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