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ARTICLE

ISLAND EFFECT ON THE TAXONOMIC, FUNCTIONAL AND PHYLOGENETIC MEASURES OF BIODIVERSITY IN BAHÍA MÁLAGA, COLOMBIA

Martín Llano Almario, Angelica Guzmán Guzmán, Edier Alberto Soto Medina*, Alba Marina Torres González
Grupo de Investigación Ecología y Diversidad Vegetal, Universidad del Valle, Cali, Colombia

*** Corresponding Author:** *Edier Soto Medina, ediersot@gmail.com, https://orcid.org/0000-0002-1518-4805*

Abstract. Tropical rainforests harbour at least 50% of the world's biodiversity and such richness can be measured as the number of species per area unit. The present study seeks to assess the effect of geographic isolation on the vegetation structure and taxonomic, functional and phylogenetic measures of diversity of the woody vegetation in the Parque Nacional Natural (PNN) Uramba, Colombia. For this purpose, a 1 ha plot (100x100 m) was established in Isla Palma within which individuals with DBH ≥10 cm were recorded. The following functional traits were evaluated: leaf area (mm^2), specific leaf area (mm^2/mg), leaf dry-matter content (mg), leaf type (simple or compound), basal area (m^2), wood density (g/cm^3), fruit length (cm), seed length (cm) and type of dispersal (biotic or abiotic). The structural and functional aspects were compared with data from the permanent plot in La Plata, which is in the continental area of the PNN Uramba. Diversity, richness and taxonomic composition were lower in Isla Palma. The species composition suggests a good degree of conservation in the forest since no families typical of disturbed zones were found amongst those with high abundance. In Isla Palma, higher specific leaf area and lower wood density values were observed. Differences in the functional and phylogenetic biodiversity were not observed between the insular and continental areas which suggests that an ecological filter prevents the colonization of some species in Isla Palma. Rather, an exchange of species occurs, and they fill the different functional niches with a similar phylogenetic representation.
Keywords: *Tropical rain forest, permanent plot, functional traits, Rao, Tumbes-Chocó-Magdalena.*

INTRODUCTION

Tropical rain forests harbour at least 50% of the world's biodiversity, and such richness can be observed as the total number of species and their number per area unit. Few studies, however, have addressed the richness, abundance and structural patterns of vegetation on islands and the potential controlling factors. These factors have not been addressed, for example, in the Tumbes-Chocó-Magdalena region, an area known as one of the 35 biodiversity hotspots in the world and designated as such because of its great biodiversity and degree of endemism (Myers et al. 2000, Poveda et al. 2004). Furthermore, most areas that prioritize the conservation of biodiversity frequently lack a plan of action to mitigate the current rate of environmental degradation (Jantz et al. 2015). Within tropical rain forests, certain factors promote changes in the composition of plant communities and lead to a greater degree of richness compared with other ecosystems; accordingly, the identification of such factors is of paramount importance (Baldeck et al. 2016).

Recent studies have indicated that the knowledge of functional traits and their implications could resolve effectively several ecological issues such as assembly rules and responses to disturbance (Salgado et al. 2016). The functional traits of plants are defined as any morphological, physiological or phenological characteristic that can be ≈measured individually and which influences the performance of the plant (Chain et al. 2017). Furthermore, functional traits provide essential information that reflects the strategies and environmental functions of the species and, taken across species, indicates how plant communities respond to environmental factors and the consequences for other trophic levels (Pérez et al. 2013, Cornelissen et al. 2003). Several research programmes in the last few years have focused primarily on creating dynamic models of the world's vegetation with the aim of predicting vegetation changes using physical gradients in addition to evaluating the effect that plants have on the function and resilience of ecosystems (Pérez et al. 2013).

One of the aims of functional ecology is to understand how functional traits vary among and within species and to determine their ecological and adaptive value (Chain et al. 2017). In this regard, accurately scaling the patterns of functional variation in individuals or species within a community is key to understanding the structure of the community as well as ecosystem processes and the co-existence of species (Salgado et al. 2016). Furthermore, functional ecology seeks to recognize the variation in patterns of functional traits in communities with abundant species caused by the exchange of species rather than by inter-specific variation. In this sense, sufficient knowledge of the community's structure is necessary for an accurate interpretation of functional diversity.

In addition, to attempt to understand the assemblage mechanisms of these communities, different studies have compared the diversity of taxonomic, phylogenetic and functional traits, testing the influence of environmental filters and the competitive exclusion of functionally similar species (Purschke et al. 2013, Baraloto et al. 2012). In general terms, if the species co-existing in a community are functionally more similar than expected (i.e., have greater functional evenness) given a certain species abundance, then an environmental filter is likely present, whereas a lower than expected functional similarity is likely to be a direct consequence of the competitive exclusion of functionally similar species (i.e., functional dispersion) (Purschke et al. 2013).

Determining the taxonomic diversity of islands is of great importance from a biogeographic point of view since there is a direct correlation between the area of an island, its proximity to a continental mass, and the number of plant and animal species on the island (MacArthur & Wilson 1967). The major goal of island biogeography is to understand the processes responsible for the heterogeneous biodiversity among islands (Bunnefeld et al. 2012). Island biogeographic models have focused on the effect of area and isolation on the richness of species, with particular attention paid to extinction and immigration events and a lack of focus on other factors, such as fragmentation or edge effects, among others (Lawrence 2008). Despite the advances made in the theory of island biogeography, many questions remain unanswered, such as the role of functional biodiversity in the assembly patterns of island species (Patiño et al. 2017). Few studies have focused on the island effect on functional and phylogenetic diversity. The present study seeks to compare vegetation structure, and taxonomic, functional and phylogenetic measures of diversity of the woody vegetation between island and continent in the PNN Uramba, in Bahía Málaga, Colombia. The hypothesis to be evaluated is that Isla Palma, being smaller and isolated, will have a lower species richness as established by the island biogeography's, which would favor a lower vegetation structure, functional and phylogenetic diversity.

MATERIAL AND METHODS.

Study site

The PNN Uramba was established in 2010 and is located in the municipality of Buenaventura, Valle del Cauca, Colombia. It has a total area of 47,094 hectares (Parques Nacionales Naturales de Colombia 2010). The PNN Uramba is located within tropical wet forest and has two rainy seasons, with one occurring from September to November and the other occurring from March to April. The area has an average annual precipitation greater than 6,000 mm, the temperature ranges from 25-27°C, and the relative humidity is 90% (Rangel & Arellano 2004). The PNN Uramba includes several islets, with Isla Palma being the most distant from the continent at a distance of 1.5 km; moreover, it is also the largest with an area of 125 ha. Its geographic coordinates are 3.912494 N, 77.356984 W.

Vegetation sampling

A permanent plot was designed and established on Isla Palma in October 2017. The plot has an area of 1 ha (100 m x 100 m), which was divided into 25 sub-plots (20 m x 20 m) using ropes. All woody individuals within the plot with a diameter at breast height (DBH) ≥10 cm were tagged with an aluminium tag bearing sequential numbering. Each individual was recorded by its assigned number, circumference at breast height (CBH), total height and species' identity. Herbarium specimens of each species were collected and stored in the CUVC Herbarium of the Universidad del Valle, where their identification was confirmed. In addition, those morphospecies from Isla Palma that were only determined to genus were examined (to allow adequate estimation of their functional and phylogenetic diversity indices), and compared with the specimens collected from La Plata. In general, it was possible to determine to species a substantial proportion of the material (65%), with the exception of some genera that are little known in the Chocó biogeographic region. Information for the permanent plot "La Plata" (25 subplots), which is located in the continental area of the PNN Uramba was also downloaded (González & Quintana 2017a). Since both plots were evaluated using the same methodology, their taxonomic, functional and phylogenetic diversity can be compared to determine the island effect on these components.

Functional traits

All the recorded species in the permanent plot in Isla Palma were selected. For all woody species that represent 80% of the importance value index (IVI) in the plot, five individuals were sampled and considered as 'dominant'. For the non-dominant species, only one or two individuals were sampled. The following functional traits were measured for each individual following the methods and recommendations proposed by Garnier (2001), Cornelissen et al. (2003) and Chave et al. (2005): leaf area (mm^2) (continuous), specific leaf area (mm^2/mg) (continuous), leaf dry-matter content (mg) (continuous), leaf type (simple or compound) (categorical), wood density (g/cm^3), fruit length (cm) (continuous), seed length (cm) (continuous) and type of dispersal (abiotic or biotic) (categorical). Leaf type, fruit length, seed length and dispersal type were obtained from the available literature (Kubitzki 2013, Lakshmi 2009, and Carrasquilla 2006). The traits that were considered in this study were selected following Lohbeck et al. (2015), who proposed that these traits are related to the states of succession and degrees of disturbance.

Data analysis

The basal area, relative frequency and relative density were estimated for each species based on the parameters evaluated in Isla Palma and those recorded in La Plata. Additionally, the IVI was estimated for the species and families found in each site (Alvarez-Dávila *et al*. 2016).

The taxonomic diversity was estimated as species richness (S), the Shannondiversity index (H) and the Simpson diversity index (D). Hill numbers were used to compare the effective number of species between the continent and the island (Magurran 2004). The taxonomic diversity was calculated for each sub-plot using a rarefaction curve to determine species richness and the Shannon diversity index (Colwell et al. 2012). The composition of species in each locality was evaluated through non-metric multidimensional scaling (NMS) based on Sørensen's index (McCune et al. 2002).

Initially, we evaluated whether or not there was a different phylogenetic signal with respect to the continent and the island, to determine if it was necessary to make a phylogenetic correction to our estimates of functional diversity; however, such a difference was not observed, thus no correction was required. The functional traits chosen for Isla Palma and recorded in La Plata were averaged for each sub-plot using the community-weighted mean (CWM) of each or, where appropriate, of the plot in each locality. This value was obtained from the sum of the product of relative abundance for each species. The functional traits observed in Isla Palma and La Plata were compared using T- or Mann Whitney U-tests (Vallejo et al. 2005: Casanoves et al. 2011: Álvarez *et al.* 2016). The functional diversity was estimated for both the insular and continental localities through the indices rRao (Relative Rao), FEve (Functional evenness), FDiv (Functional divergence) and FDis (Functional dispersion). The calculation of each index was based on a dendrogram constructed with all the traits using the Gower index, which is adequate when using both categorical and continuous traits. These indices were used because they consider the abundances of each species and are not sensitive to the effect of differences in taxonomic richness (Casanoves et al. 2011). These parameters were compared across both localities (insular and continental) using T- or Mann Whitney U-tests (Casanoves et al. 2011: Colwell et al. 2012).

The Phylogenetic Measures of Biodiversity were estimated using the indexes PSV (phylogenetic species variability), PSR (phylogenetic species richness), PSE (phylogenetic species evenness) and PSC (phylogenetic species clustering) (Helmus et al. 2007). Initially, a phylogenetic tree was built in Phylomatic (an online tool to assemble species lists into phylogenies), which uses an APG3 (Angiosperm Phylogeny Group) derived megatree (Webb and Donoghue 2005). The tree obtained became ultrametric (rooted) in order to calculate the phylogenetic distances among the species that make up each community (i.e., each plot) (Casanoves et al. 2011). The indices of phylogenetic and functional diversity were obtained using the software FDiversity (Casanoves et al. 2011). Furthermore, a principal component analysis (PCA) was performed based on the functional traits observed in each sub-plot to compare the composition of these traits between the island and the continent. These analyses were performed using the software PAST 4.0. (Hammer et al. 2001).

RESULTS

Vegetation structure and composition

In the plot of Isla Palma, 505 individuals belonging to 49 species representing 26 families were recorded. In contrast, in the plot of La Plata, 621 individuals belonging to 111 species representing 33 families were recorded. Between these localities, only 21 families and 19 species were shared. The most abundant species in Isla Palma were *Eschweilera sclerophylla*, *Guapira costaricana*, *Pentaclethra macroloba*, *Nectandra* sp., *Lacistema aggregatum*, *Simarouba* sp. and *Guatteria cargadero* (Table 1); whereas the most abundant species in La Plata were *Oenocarpus mapora*, *Pouteria* sp., *Welfia regia*, *Croton crenatus*, *Iryanthera ulei* and *Brosimum utile* (Table 1).

Among the 10 most abundant species, *E. sclerophylla* was the only one shared in both localities. Moreover, although the species pairs *P. macroloba* and *Simarouba amara* and *W. regia* and *B. utile* were present in both

Table 1. Most abundant plant species in Isla Palma and La Plata, PNN Uramba, Bahía Málaga, Buenaventura, Colombia (* data obtained from González & Quintana 2017a).

Isla Palma	Number of Individuals	%	La Plata *	Number of Individuals	%
Eschweilera sclerophylla	78	15.4	*Oenocarpus mapora*	43	6.75
Guapira costaricana	33	6.5	*Pouteria* sp.	37	5.81
Pentaclethra macroloba	33	6.5	*Welfia regia*	30	4.71
Nectandra sp.	32	6.3	*Croton crenatus*	29	4.55
Lacistema aggregatum	31	6.1	*Iryanthera ulei*	27	4.24
Simarouba amara	30	5.9	*Brosimum utile*	25	3.92
Guatteria cargadero	20	4.0	*Otoba latialata*	24	3.77
Alchorneopsis floribunda	19	3.8	*Eschweilera sclerophylla*	20	3.14
Ficus sp.	17	3.4	*Eschweilera* sp.	15	2.35
Hernandia didymantha	17	3.4	*Dacryodes peruviana*	14	2.20

localities, they were only among the top ten species in Isla Palma and La Plata, respectively (Table 1).

According to the IVI, the most important species present a different arrangement compared with the most abundant species. In Isla Palma, the species *P. macroloba* was the most important, at an estimated value of 10.9%, followed by *E. sclerophylla* (10.0%) and *Alchorneopsis floribunda* (8.6%) (Fig. 1A). However, in La Plata, the most important species were *Pouteria* sp. (6%), *C. crenatus* (4.7%) and *W. regia* (4.5%) (Fig. 1C).

The observed IVI values at the family level showed that Fabaceae was the most important family in Isla Palma, followed by Lecythidaceae and Euphorbiaceae (Fig. 1B), and this result is consistent with the three most important species since they belong to each of these three families. In La Plata, however, Sapotaceae was the most important family followed by Arecaceae and Myristicaceae (Fig. 1D), and these families are not represented among the five most important species in Isla Palma according to the IVI (Fig. 1A).

The DBH class analysis described similar inverted “J” shaped curves between the two localities (Fig. 2). In Isla Palma, most individuals (69.0%) are found in class I, and then the value rapidly decreases to 18.1% in class II, 4.6% in class III and less than 3% in the remaining diametric classes. In La Plata, this decrease was less drastic at 64.7% individuals in class I to 20.3% in II, 7.1% in III and values lower than 5% in the remaining diametric classes. In both locations, a slight increase between diametric classes IV and V was observed.

Taxonomic diversity and abundance of vegetation.

The abundance and richness of woody plant species was higher for La Plata (621 individuals, 111 species) than for Isla Palma (505 individuals, 49 species). Furthermore, the richness estimators indicated that the number of species in La Plata was significantly higher than that in Isla Palma ($p<0.001$), suggesting that the species richness in the continental zone was double the number of species observed in Isla Palma as shown by the rarefaction curves (Fig. 3).

Shannon’s index showed a higher diversity of species in La Plata than in Isla Palma ($p<0.001$) (Table 2), whereas Simpson’s index suggested a greater dominance in Isla Palma than in La Plata. Furthermore, the species abundance per sub-plot was higher in the continental area than in the insular area ($p<0.001$), and the species richness presented a similar trend ($p<0.001$). Furthermore, the Hill numbers showed that La Plata presented a higher effective diversity of species than did Isla Palma

According to the NMS results, the composition of plant species in La Plata was different from that in Isla Palma (Fig. 4). Thus, although 19 species were shared between the two localities, the composition of species per sampling unit was very different between the two locations.

Functional traits

Significant differences were found between the island and the continent regarding several of the evaluated functional traits (Table 3), e.g., the specific leaf area and leaf dry-matter content showed significantly higher values in Isla Palma than La Plata. Furthermore, the average fruit length and number of species with simple leaves, abiotic dispersal and occurrence of achene and legume fruits were significantly higher in Isla Palma. La Plata showed higher values regarding the wood density and number of species with compound leaves, biotic dispersal and berry fruits.

The PCA showed that for traits per sampling unit, the trait composition of woody plants was different between Isla Palma and La Plata despite some overlapping components (Fig. 5).

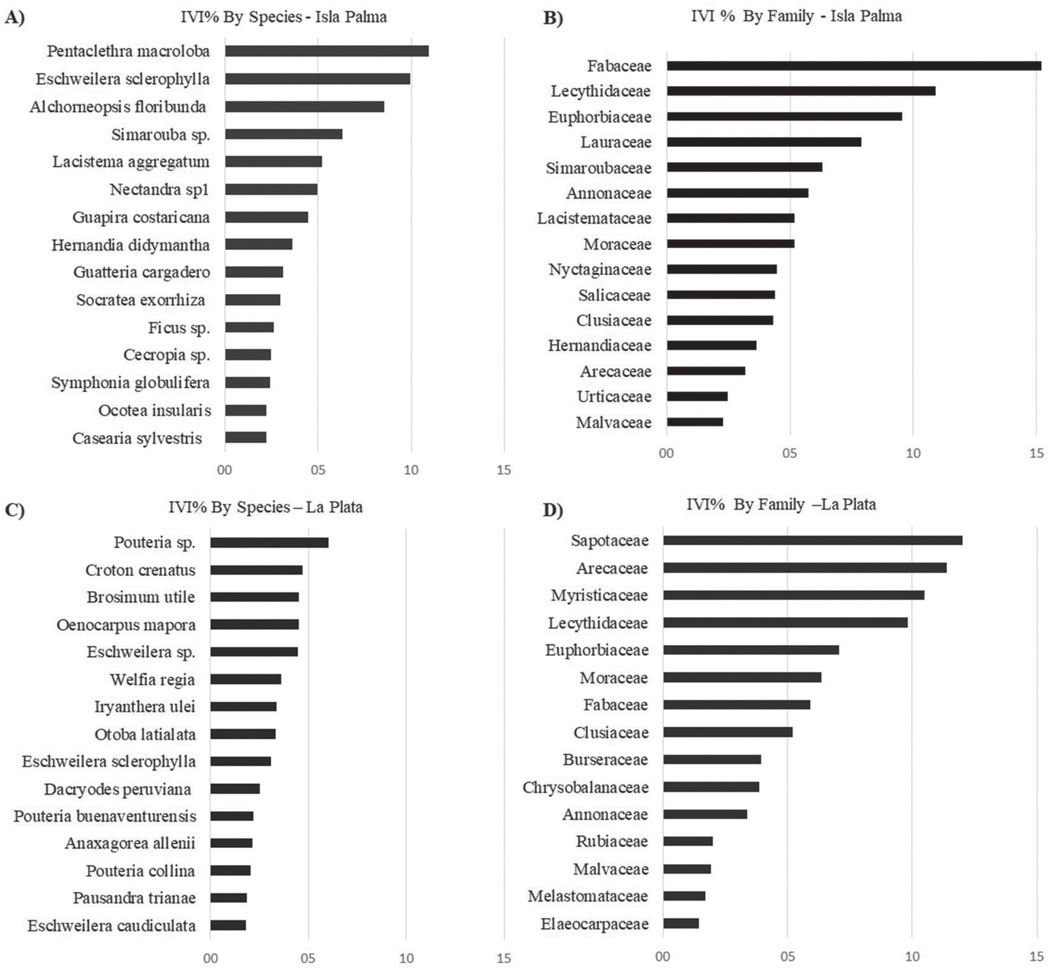

Figure 1. Most important species according to the importance value index (IVI) in Isla Palma and La Plata, PNN Uramba, Bahía Málaga, Buenaventura, Colombia. A) Most important species in Isla Palma; B) most important families in Isla Palma; C) most important species in La Plata; and D) most important families in La Plata.

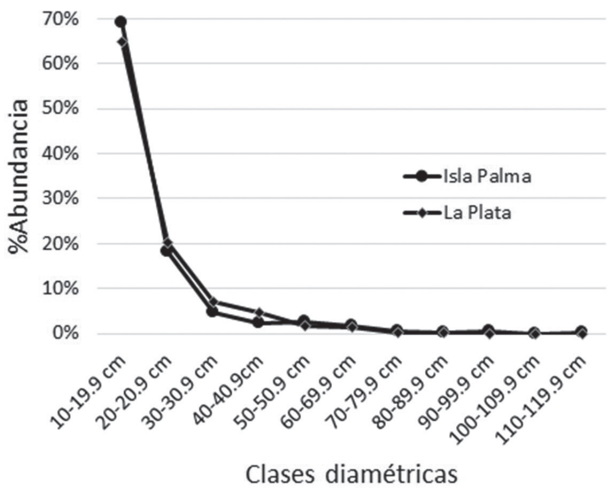

Figure 2. Diameter class distribution of woody vegetation in Isla Palma (black line) and La Plata (grey line), PNN Uramba, Bahía Málaga, Buenaventura, Colombia.

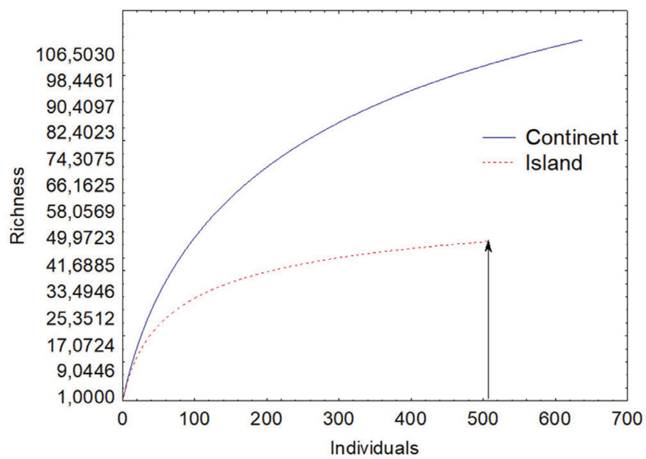

Figure 3. Rarefaction curves of woody plant species from Isla Palma (dotted line) and La Plata (solid line), PNN Uramba, Bahía Málaga, Buenaventura, Colombia.

Table 2. Indices of taxonomic, functional and phylogenetic measures of diversity in Isla Palma and La Plata, PNN Uramba, Bahía Málaga, Buenaventura, Colombia.

		La Plata	Isla Palma	*t*-value	P
Taxonomic diversity	Taxa_S	18.00	11.24	8.40	0.00
	Individuals	25.48	20.20	3.35	0.00
	Dominance_D	0.08	0.13	-6.51	0.00
	Simpson_1-D	0.92	0.87	6.51	0.00
	Shannon_H	2.75	2.21	8.60	0.00
	Evenness_e^H/S	0.88	0.84	2.43	0.02
	q0	18.00	11.24		
	q1	15.61	9.13		
	q2	13.04	7.41		
Functional diversity	FDiv	0.69	0.68	0.71	0.48
	FDis (log)*	6.25	6.60	-1.99	0.05
	rRao	0.70	0.75	-1.92	0.06
	FRic (log)*	13.91	13.59	0.74	0.46
	FEve	0.13	0.25	-2.33	0.02
Phylogenetic diversity	PSV	0.72	0.72	0.31	0.76
	PSR	12.92	8.04	7.64	0.00
	PSE	0.71	0.68	1.79	0.08
	PSC	0.75	0.67	4.99	0.00

* Logarithmic transformation to meet the assumptions of homogeneity of variances

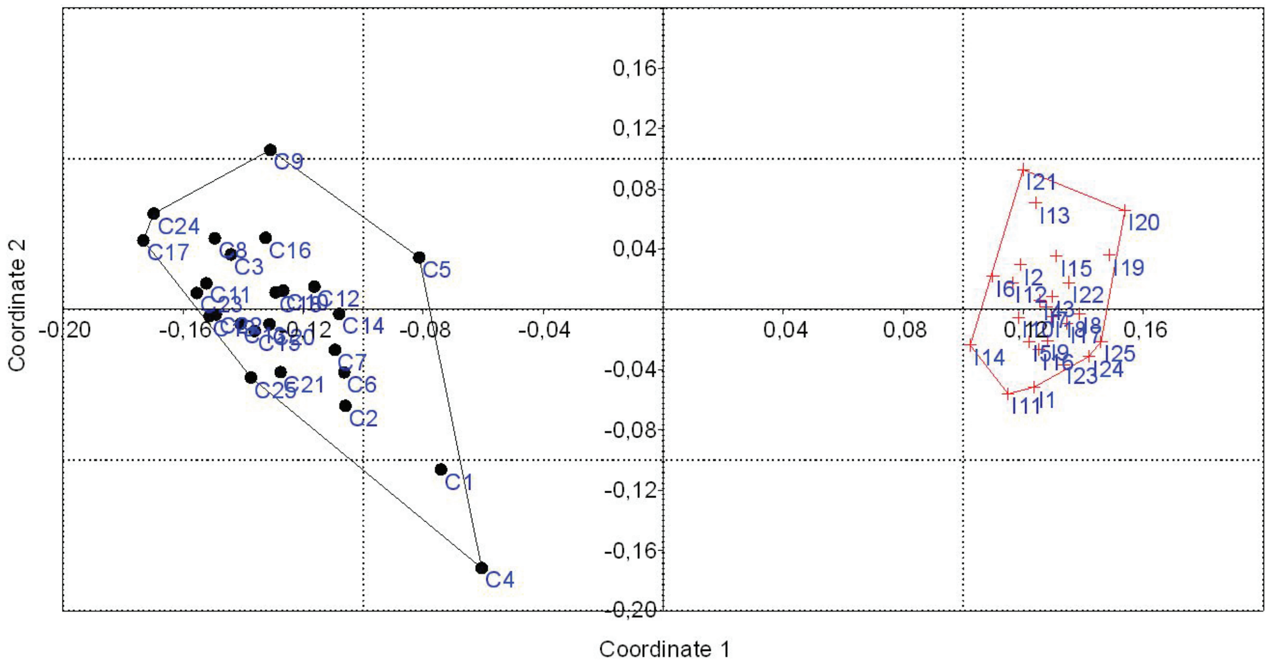

Figure 4. Non-metric multidimensional scaling of woody plant species in Isla Palma (crosses) and La Plata (points), PNN Uramba, Bahía Málaga, Buenaventura, Colombia.

Table 3. Functional traits of woody plants from Isla Palma and La Plata, PNN Uramba, Bahía Málaga, Buenaventura, Colombia.

Trait	Mean La Plata	MeanIsla Palma	t-value	P	SD La Plata	SD Isla Palma	F-ratio Variances	p
AB (m^2)	427.50	464.31	-0.89	0.38	84.33	188.09	4.97	0.00
Leaf area (mm^2)	1029943.80	2268080.31	-1.96	0.06	1580766.92	2726379.68	2.97	0.01
Specific leaf area (mm^2/g)	12.46	90.29	-18.71	0.00	3.73	20.46	30.05	0.00*
Leaf dry-matter content (mg)	563.86	2092.90	-9.91	0.00	207.10	743.01	12.87	0.00*
Wood density (g/cm^3)	0.52	0.47	3.93	0.00	0.04	0.04	1.03	0.95
Fruit length (cm)	4.31	5.18	-1.99	0.05	0.87	1.98	5.19	0.00
Simple leaf	0.73	0.81	-2.34	0.02	0.12	0.11	1.20	0.66
Compound leaf	0.27	0.20	2.09	0.04	0.12	0.12	1.09	0.83
Achene	0.00	0.03	-3.18	0.00	0.01	0.04	29.36	0.00*
Berry	0.24	0.17	2.01	0.05	0.12	0.10	1.38	0.44
Capsule	0.34	0.31	0.81	0.42	0.13	0.16	1.42	0.40
Drupe	0.36	0.35	0.07	0.95	0.12	0.17	1.80	0.16
Follicle	0.00	0.00	1.00	0.32	0.01	0.00	0.00	1.00
Legume	0.06	0.10	-2.00	0.05	0.06	0.08	1.83	0.14
Zoochory	0.95	0.79	6.15	0.00	0.05	0.12	7.21	0.00*
Abiotic dispersal	0.04	0.17	-5.10	0.00	0.04	0.12	7.09	0.00*
Seed length (mm)	17.04	8.80	1.13	0.27	29.59	21.45	1.90	0.12

* t-test on log-transformed variables

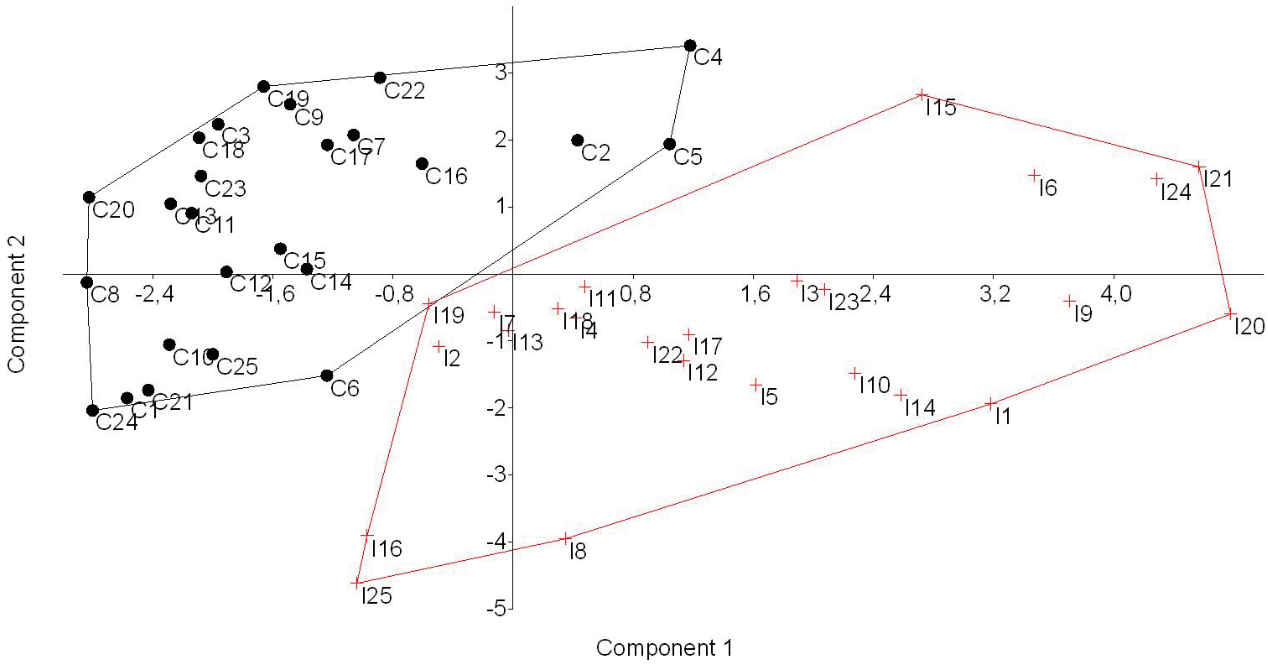

Figure 5. Principal component analysis of the functional traits of woody plants from Isla Palma (red) and La Plata (black), PNN Uramba, Bahía Málaga, Buenaventura, Colombia.

Functional and Phylogenetic Measures of Diversity

The functional diversity showed a different pattern compared with the taxonomic diversity. The FEve index was higher in Isla Palma, whereas the rRao, FRic, FDiv and FDis indexes did not show significant differences between the two localities. We conclude that both localities showed similar functional diversity regarding functional dispersion and divergence; however, functional evenness was higher in Isla Palma.

Phylogenetic variability and evenness did not show significant differences between Isla Palma and La Plata, whereas phylogenetic clustering and richness was higher in La Plata. Therefore, although taxonomic diversity was lower in Isla Palma, the functional and phylogenetic measures of diversity did not change between the two areas evaluated.

DISCUSSION

The proximity of Isla Palma to La Plata (~1.5 km) would suggest, *a priori*, high similarity in the characteristics of the vegetation between these localities since it is widely accepted that the proximity of islands to the continent results in a higher exchange of species (Bisconti et al. 2001, MacArthur & Wilson 1967). However, the composition of species in Isla Palma is different from that on the continent at La Plata, with a defined group of species observed for each locality based on the NMS analyses. Moreover, only 19 tree species are shared between the two localities. Furthermore, although the structure of the vegetation based on the diametric classes is very similar between Isla Palma and La Plata, there are more trees with smaller diameter in Isla Palma, suggesting higher environmental disturbance. The present study, however, could not determine the factors that drive this higher disturbance effect in Isla Palma compared with La Plata. The differences in the composition and structure of the vegetation show that isolation has important implications for plant communities, even over short distances.

The concepts of island biogeography have been applied to fragmented habitats (Haila 2002), regardless of the ongoing debate on this subject (Wiens 1995). Such debate, however, has highlighted the importance of understanding other factors in addition to isolation *per se* and has led to the design and execution of more complete studies, although these studies have focused on fragmented habitats rather than not islands (Lawrence 2008).

The composition of plant species from Isla Palma and La Plata suggests that both localities are well conserved, which is supported by the presence of species in the families Lauraceae, Lecythidaceae, Chrysobalanaceae and Myristicaceae, which are associated with the mature forests of the Tumbes-Chocó-Magdalena region (Rangel 2004). Other woody species typical of a mature forest may also be present in early successional stages of tropical forests. These will only be detected if seedlings and saplings are surveyed and may take up to 40 years to reach the DBH ≥10 cm cut-off used in the current survey (Guariguata & Ostertag 2001). Accordingly, the composition of a mature forest differs from the typical forest composition encountered in these areas, which present greatly degraded cover and are commonly dominated by arboreal species of the family Urticaceae (i.e., *Cecropia, Pourouma*) and *Ochroma pyramidale* (Malvaceae) (Rangel 2004). In the present study, we did not find *O. pyramidale* and report only a single species each of *Cecropia* and *Pourouma* in the continental area. However, the presence of these pioneer species does not necessarily imply habitat deterioration since some individuals can be normally found in natural clearings of mature forests (Knight 1975).

The present study confirms that the richness of woody plant species in Isla Palma is less than half of that reported for the continent. This low plant species richness in Isla Palma was also reported by Soto et al. (2015), who compared it with the continental locality of Playa Chucheros on the Pacific Coast. In a comparable study, Yockteng & Cavelier (1998) reported that Isla Gorgona possessed half the richness of woody species compared with the continental forest of Bajo Calima in the Tumbes-Chocó-Magdalena region. Nevertheless, the biological diversity (*i.e.,* Simpson's and Shannon's indices) and evenness were lower and the dominance was higher in Isla Palma than in our continental site at La Plata.

Regarding functional traits, some differences were observed between the insular and continental areas, suggesting the presence of two opposing evolutionary strategies. In Isla Palma, leaf area, specific leaf area and leaf dry-matter content were higher while the basal area and wood density traits were lower in comparison with La Plata on the continent. These observations suggest that the vegetation of Isla Palma leans towards acquisitive strategies whereas the vegetation in the continental zone favours conservative strategies. Acquisitive strategies, such as high values of specific leaf area, leaf nutrients, nitrogen and phosphorus, result in increased respiration, assimilation and photosynthesis rates (Wright et al. 2004) as well as low structural investment related to physical defence against herbivores (*i.e.,* high leaf dry-matter content) (Coley 1983). Furthermore, low wood density, which is a by-product of high vessel density, results in increased hydraulic efficiency, thereby improving primary production (Méndez et al.

2012). Functional acquisitive characteristics are common to early-succession forests, where plants need to acquire nutrients rapidly so that growth can also occur rapidly (Lohbeck et al. 2015, Derroire et al. 2018). These observations point towards the characteristics of an early-succession forest in Isla Palma, which could be further explained by its small area and vulnerability to strong storms as evidenced in the present study by the constant treefall in the area.

Conservative species, however, are the other end of the spectrum, which was the case of the vegetation in the continental area in La Plata. The species found in this area presented low specific leaf area values, suggesting a low concentration of leaf nutrients, low metabolic rate, and high investment of carbon into physically resistant structures. This latter characteristic diminishes their attractiveness to herbivores and increases leaf longevity (Reich et al. 1999). Furthermore, long-lived species with a low specific leaf area are highly persistent and known to invest their resources against a slow but sure return (Sterk 2006). Moreover, the investment of resources into resistant leaves with low nutrient content could also decrease the physical risk of foraging by herbivores (Coley 1983) thereby increasing the useful life-span of leaves and the plant's persistence. In addition, conservative species also tend to have greater basal areas and higher wood densities as was observed in the functional traits of the vegetation in the continental area of La Plata.

The forest in the continental area is dominated by timber species that are commonly used in construction and the manufacture of long-lasting objects (Camacho & López 2002). Furthermore, basal area increases rapidly with the age of the site since establishment (Chazdon et al. 2007), indicating that the species found in the continental area have been present longer than those in the island area. On the other hand, the low wood density of the tree species in Isla Palma indicates faster growth due to the low volumetric construction cost and greater hydraulic capacity; regardless, a high wood density, such as that observed in the continental area of La Plata, leads instead to increased survival due to the biomechanical action that makes them more resilient to storms, pathogens, herbivores or physical damage (Pérez et al. 2013).

Several studies have reported the relationship between the spectra of the leaf and trunk economies, meaning that the leaf area tends to diminish as the wood density increases (Baraloto et al. 2010). This pattern is consistent with that observed in the present study, where it was considered a compensation strategy before the application of environmental filters (Freschet et al. 2010, Méndez et al. 2012, Kursar et al. 2009).

The continental zone of La Plata has a higher number of individuals with compound leaves, whereas the island zone of Isla Palma has more trees with simple leaves, and this difference could influence the leaf area results since simple leaves occupy a larger space than compound leaves. Moreover, light intensity could also influence individual selection since the species with compound leaves often have photonastic leaves (Roller & Shak 1990) that prevent high insolation and enable them to resist high temperatures and excessive evaporation by folding their leaflets at noon or during the dry season. Compound leaves also have a faster cooling rate and better water loss management, thus increasing the leaf area for efficient light capture (Lohbeck *et al.* 2015).

Seed dispersal was higher in Isla Palma than in La Plata, which could be explained by the lower amount of fauna and higher wind influence in Isla Palma (Giraldo et al. 2014 and Cantera et al. 1998). In general, insular locations have lower richness of fauna compared with continental environments of the same area. This low richness is attributed to the decreased probability of immigration as the distance to the continent becomes greater. Similarly, the probability of extinction increases as the size of the island decreases (MacArthur & Wilson 1967, Losos, & Ricklefs, R 2009 and Wright 1980). Regardless, Lohbeck et al. (2015) demonstrated that differences in the seed volume of humid forests may be more closely related to the different taxa of dispersing animals than the biotic-abiotic dichotomy. These authors also claim that biotic dispersal increases the possibility of seed dispersal to safe locations, whereas a larger seed size increases the success rate of establishment, which is very important in shaded environments.

The incidence of biotic factors becomes evident in the seeds of Sapotaceae, which are primarily dispersed by primates. Sapotaceae, moreover, is the most important family in the continental area according to the IVI. This family, however, is not even among the ten most important species in Isla Palma, which implies the absence of potential seed dispersers since Isla Palma is free of primates and only hosts frugivorous bats (Giraldo et al. 2014, Velandia et al. 2012).

Regarding functional measures of diversity, a pattern different from the taxonomic diversity pattern was observed since the indices rRao, FRic, FDiv and FDis did not show significant differences between the two localities although the FEve index was higher in Isla Palma. On the other hand, Karadimou et al. (2016) showed that distinct aspects of functional diversity respond differently to the species richness of an area. The indexes rRao and FDis measure the similarity of individuals in a functional volume, suggesting that Isla Palma and La Plata have similar functional diversity despite the notable differences in richness, diversity and composition of species. The index FDiv measures the divergence of individuals in a functional space, and it indicated that the distribution of abundance of dominant species is similar in Isla Palma and La Plata. Last, the index FEve was higher in Isla Palma, which is probably because of the higher richness of the continental locality and its potential to contain more rare species as well as a greater abundance of common individuals, thus causing a biased distribution of species abundance and diminishing the functional evenness (Karadimou et al. 2016).

Despite the perception that Isla Palma has not undergone extensive habitat deterioration by anthropic actions, the characteristics of its more acquisitive functional traits and the high frequency of some species associated with processes of selective extraction instead of clear cutting, such as *L. agregatum* (Rangel 2004), shows a similarity with successional forests. Furthermore, despite the difference in taxonomic diversity, which is lower in Isla Palma, some similarities can be observed in the indices of functional and phylogenetic diversity between the insular and continental localities. As a result, both localities display a similar successional status, which is mainly because a lower functional and phylogenetic diversity would be expected due to the dominance of similar pioneering species (Purschke et al. 2013, Lohbeck et al. 2015). However, the higher FEve index value and incidence of acquisitive strategies in Isla Palma suggests higher seasonal dynamics, which is possibly due to the greater impact of strong wind and rain events (Laurence 1991, 2008; Lohbeck et al. 2015).

In conclusion, the results from the present study indicate that Isla Palma has lower species richness than the continental area due to its smaller size. The indices of functional and phylogenetic diversity, however, suggest that both the continental and insular localities possess similar successional statuses despite the reduced richness in the latter. Moreover, we found that the species in Isla Palma tended to be exhibit more acquisitive strategies whereas those in La Plata were more conservative. This implies that the higher seasonal dynamics, i.e., rain and wind, have a potentially stronger effect upon the vegetation of Isla Palma due its smaller size. Understanding the processes which structure the plant communities on both island and mainland requires an integration of taxonomic, functional and phylogenetic components .

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