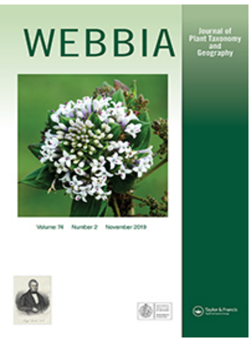

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ARTICLE

Diversity and distributional patterns of aroids (Alismatales: Araceae) along an elevational gradient in Darién, Panama

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ABSTRACT
The family Araceae (aroids) represents an ecologically important and diverse group of plants in Panama, represented by 25 genera, 615 species, of which 277 (45%) are considered endemic. The aim of this study is to analyse the diversity and distributional patterns of aroids along an elevation gradient in the species-rich forests of Darién, Panama. We confined our study to three study sites, selected across gradients of elevation (ranges): 100–300, 500–700 and 1100–1300 m. We recorded 3187 specimens, of which 397 were terrestrials, 637 epiphytes and 2153 nomadic vines, distributed in 10 genera and 61 species. Our study shows that the most diverse areas were those between 500 and 700 m and the highest abundance were measured at 1100–1300 m. The epiphytic aroids displayed greater species richness and abundance at 1100–1300 m; the nomadic vines had greater richness between 500 and 700 m and greater abundance from 100 to 300 m. Similarly, terrestrial aroids showed greater richness at 500–700 m, and exhibited abundance values similar to that of the epiphytes. We measured a high degree of aroid species turnover along the elevation gradient and some genera and species (many being endemic) appeared strongly associated with sites at specific elevations.

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KEYWORDS
Cerro Pirre; endemism; species turnover; World Heritage Site; multivariate analysis; epiphytes; nomadic vines

Introduction

The Darién province contains one of the most important and most biodiverse natural forests of Panama, characterised by the great number of species reported and a high degree of endemism (Dinerstein et al. 1995). This region is home to one of the largest natural reserves in Central America: the Darién National Park. This protected area comprises 401,000 ha of continuous natural vegetation and is currently considered a Biosphere Reserve and a World Heritage Site established by UNESCO (Gradstein and Salazar 1992). Within the limits of the park there are several isolated mountain ranges that comprise large areas of pristine forests, important contributors to its biological diversity and for the high degree of endemism (Bermúdez and Sánchez 2000). The higher peaks of the Serranía de San Blas, Darién, Majé and Pirre are covered in tropical cloud forest. Both the flora and fauna of these relatively isolated ranges comprise an assemblage of species with South American and Central American affinities (Dinerstein et al. 1995).

The family Araceae (aroids) is characterised by having calcium oxalate crystals, inflorescences with fleshy axes, bearing small flowers usually arranged in spirals and subtended by a conspicuous leaf-like or petal-like bract (Mayo et al. 1997). The family has world-wide distribution and contains an estimate of about 3645 species, grouped in 144 genera. These plants occur in habitats ranging from open freshwater to deserts, occurring on all continents except Antarctica (Mayo et al. 1997; Boyce and Croat 2018). Among the most outstanding features that distinguish the Araceae is the great diversity of life forms, including aquatic, terrestrial, epilithic, epiphytic and hemi-epiphytic species (Croat 1988) and, probably, each one of them has different ecological requirements. The growth of aroids depends mainly on the availability of water and atmospheric humidity. Structurally and physiologically, they are not adapted for growth in arid or cold conditions and, therefore, most species fail to thrive in extreme environments (Mayo et al. 1997). The presence of aroid species is equally dependent on warm temperatures and high humidity (Croat 1995; Mayo et al. 1997). The diversity and abundance of aroids is affected mainly by factors such as temperature, atmospheric humidity, precipitation (Mayo et al. 1997; Leimbeck et al. 2004), elevation and topographic variables (Wolf and Flamenco 2003; Leimbeck et al. 2004; Krömer et al. 2005; Acebey and Krömer 2008; Sungkajanttranon et al. 2018), soil properties (Leimbeck and Balslev 2001; Sungkajanttranon et al. 2018), the availability of phorophytes (Leimbeck and

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Balslev 2001), solar light intensity (Sungkajanttranon et al. 2018) and the structure of the vegetation (Simmonds 1950).

Aroids represent a very important herbaceous group of plants in Panama, being represented by 26 genera and 615 species, with 277 (45%) being endemic (Ortiz et al. 2018; Croat unpublished data). Along this line, Panama is considered a centre of endemism for several genera of aroids such as *Anthurium*, *Dieffenbachia*, *Spathiphyllum*, *Philodendron*, *Monstera* and *Stenospermation* (Croat 1986a, 1991, 1994; Ortiz et al. 2018). In the particular case of *Anthurium* and *Philodendron*, both genera contain 63% of the aroid species registered in Panama (Ortiz et al. 2018; Croat unpublished data). As was shown for *Anthurium* (Croat 1986b), endemism of *Philodendron* (subgenus *Philodendron*) is concentrated mainly in the isolated mountain ranges distributed along the Panamanian territory (Croat 1991).

Field work carried out in recent years in remote mountainous areas of Panama has uncovered the existence of many aroids with restricted distribution ranges (Ortiz et al. 2018), strongly supporting the hypothesis that Panama is a major centre of diversification of aroids in the Central American region. Because aroids constitute a major group of plants in the Panamanian flora, this study aims to analyse its diversity and distributional patterns along an elevation gradient in a biologically important area, the Darien forest, which is considered a hotspot of biodiversity and endemism (Myers et al. 2000). Our study provides a baseline for understanding the alpha and beta diversity patterns of aroids in Panama, which could be use to better inform the identification and protection of specific areas of endemism in the Darién National Park.

Materials and methods

Site description

The study area is located within the Serranía de Pirre, a mountainous formation 50 km long and 25 km wide, located in the Panamanian Pacific south-eastern part of the Darién province (Figure 1(a)). The ridge that forms the mountain range of Pirre extends to the north about 35 km from the border with Colombia and is composed of igneous rocks from the Cretaceous (Myers 1969; Robbins et al. 1985; Dalfelt and Morales 1988). The highest point of the Serranía is Cerro Pirre, with an elevation gradient that goes from 90 to 1550 m (Robbins et al. 1985). The region has a humid tropical climate with average annual temperatures of 20–25°C. The average annual rainfall is 3000–3500 mm, with a pronounced dry season during January to April (Gradstein and Salazar 1992). The study was carried out in the vicinity of Cerro Pirre (near the biological station of Rancho Frío) mountain located north of the Serranía de Pirre (Figure 1(a)), within the geographical coordinates 8°1′8.80″N, 77°44′5.30″W.

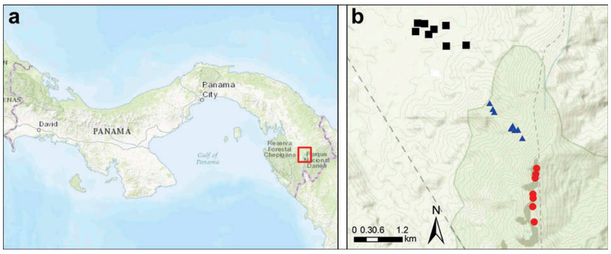

Figure 1. Map with the (a) study area (Cerro Pirre) and (b) the locations of the plots in the elevation gradient: mountain base plots (MB: black squares), mid-elevation slope plots (MS: blue triangles) and mountain ridge plots (MR: red circles).

Along the elevation gradient of Cerro Pirre we observed clear changes in the structure and composition of the forest (Figure 2). At the base of the mountain, between 100 and 300 m, the forest presents three well-defined strata with emerging trees of *Ceiba pentandra* and *Cavanillesia platanifolia* that can reach up to 45 m; the understorey is open, heavy on the amount of leaf litter and dominated by individuals of the family Arecaceae, Piperaceae and Rubiaceae. The remaining strata often consist of trees of the family Lecythidaceae (*Lecythis ampla*), Rubiaceae and palms such as *Socratea exorrhiza*, *Wettinia radiata* and *Attalea* sp. On mid-elevation slopes (500–700 m), the forest has three defined strata with trees usually less than 25 m. The understorey usually is open between c. 500–650 m and above these elevations it becomes closed, with Piperaceae, Rubiaceae and Melastomataceae being the

Figure 2. Sampling sites on Cerro Pirre. (a) Mountain base (MB: 100–300 m). (b) Mid-elevation slope (MS: 500–700 m). (c) Mountain ridge (MR: 1100–1300 m). (d) Partial view of Cerro Pirre. Photo credits: © Orlando O. Ortiz.

most common families. Above 700 m, we noticed a radical change in the structure of the vegetation, accentuating the transition between the evergreen forest and the submontane forest. In this transition area, the topography is characterised by extremely steep slopes, and it is common to see shrubs and trees of *Conchocarpus nicaraguensis*, *Eugenia sanjuanensis*, *Phyllanthus gentryi* and *Weinmannia pinnata*. Along the mountain ridge (1100–1300 m), the vegetation forms a dwarf forest (usually less than 12 m) with two defined strata. It is characterised by its abundant humidity and persistent fog, which intensifies in the afternoon (around 3 pm). It is rich in mosses and epiphytes, individuals of the families Bromeliaceae, Dryopteridaceae, Araceae, Gesneriaceae and Ericaceae (Myers 1969). The undergrowth is slightly closed, characterised by shrubs of the family Rubiaceae and arborescent ferns of the genus *Cyathea*. The tree vegetation is mainly composed of individuals of the families Chloranthaceae (*Hedyosmum* sp.), Rubiaceae (*Amphidasya spathulata* and *Pogonopus exsertus*), Magnoliaceae (*Magnolia* sp.), Lecythidaceae (*Eschweilera* sp.), emergent trees of *Cecropia* sp. (Urticaceae) and palms of *Dictyocaryum lamarckianum* (Arecaceae).

Sampling methods

Three study sites were established in different types of vegetation located along an elevation gradient of Cerro Pirre: mountain base (MB: 100–300 m), mid-elevation slope (MS: 500–700 m) and mountain ridge (MR: 1100–1300 m) (Table 1; Figures 1(b) and 2). For the samplings, 24 plots of 20 × 20 m (400 m^2) were established, eight (0.32 ha) in each study site (defined above as MB, MS and MR). Sampling was designed based on the methodologies proposed by Krömer and Gradstein (2016) and Gradstein et al. (2003), but with modifications. These methodologies mention that at least eight plots of 20 × 20 m (400 m^2) must be used for each study site or vegetation type, accompanied by a vertical sampling of the most predominant tree for its height, which must be located inside the plot. Several studies support the notion that the epiphytic and hemiepiphytic Araceae usually grow in the lower strata of host trees (Gradstein et al. 2003; Jácome et al. 2004; Arévalo and Betancur 2006; Krömer et al. 2007). The modification made to this methodology consisted of eliminating the vertical sampling of the highest tree of the plot and sampling from the ground with the help of binoculars and telescopic pruners.

We identified all aroid species present on each plot, quantifying the total number of individuals (abundance) and their life form. In order to cross-check previously registered species of the study site, all aroid specimens from Cerro Pirre were reviewed at the herbaria of the University of Panama (PMA) and Missouri Botanical Garden (MO). To be able to recognise the morphological variation in each identified species (especially in nomadic vines), field observations on different growth phases (seedling, juvenile and adult) were carried out. Voucher specimens for all species recorded in this study were collected (stored in 70% ethanol). Specimens were subsequently processed and deposited in PMA and MO herbaria (see supplemental online material).

The determination of terrestrial and epiphytic life forms was made using the classifications proposed by Croat (1988) and Schimper (1903), respectively. We use the term nomadic vine explained by Zotz (2013), which includes all climbing plants that germinate on the ground and may lose the older parts of their stem in the process of ascending. This term includes many species that were previously described as secondary hemi-epiphytes (*sensu* Croat 1988). The concept of an individual as defined by Sanford (1968) was used. This defines an individual as a group of rhizomes and leaves belonging to a specific species that is clearly separated from another group of this species by uninhabited space or by another species. Data on species distribution were obtained from TROPICOS (2019).

Data analysis

To evaluate the sampling efficiency and inventory integrity, the non-parametric estimators Jackknife 2 and Chao 2 were used (Gotelli and Colwell 2011). Additionally, we computed individual-based rarefaction curves and their 95% confidence intervals (Moreno 2001; Gotelli and Colwell 2011). Abundance (number of individuals) and

Table 1. Study sites along the Cerro Pirre elevation gradient.

	Mountain base (MB)	Mid-elevation slope (MS)	Mountain ridge (MR)
Coordinates	08°01 15″ N, 077°44 03″ W	07°59 49″ N, 077°42 42″ W	07°59 18″ N, 077°42 27″ W
Elevation (m)	100–300	500–700	1100–1300
Rainfall (mm)	3000	3500	3500
Temperature (°C)	25–26	24	20–21
Evapotranspiration (mm)	1300	1200–1300	1000
Slope degree	≤10	16–30	≥30
Vegetation type	Lowland semi-deciduous	Submontane evergreen	Lower montane evergreen
Life zone	Premontane wet forest	Tropical wet forest	Premontane rain forest

All the data were obtained from ANAM (2010). The data of temperature, rainfall and evapotranspiration correspond to annual means. The life zones are according to the Holdridge et al. (1971) system.

species richness (for all species and life forms separately) were determined for each of the study sites. In addition, specific species richness was calculated using the Margalef and Menhinick indexes; to measure heterogeneity, we used the Simpson's reciprocal index (1/*D*) and the Shannon entropy index (*H*) for each study site (Moreno et al. 2011). The values obtained from Shannon entropy were converted to Shannon diversity (effective number of species) which was calculated according to the formula $^1D = \exp(H)$, described in Jost (2006).

To determine statistical differences in species richness and abundance (including analysis of life forms separately), Simpson's reciprocal index, Shannon diversity, Margalef index and Menhinick index values between the study sites, we used analysis of variance (one-way ANOVA, $\alpha = 0.05$) followed by Tukey's test to determine specific differences between means. When necessary, we square-root transformed our data to comply with parametric assumptions. Data failing to meet the homogeneity of variance were analysed using a Welch ANOVA.

The associations of the aroid genera, species and life forms between the study sites were tested using simple Correspondence Analysis (CA), where the statistical independence between rows and columns is evaluated by means of a χ^2 test (Addinsoft 2017). To analyse aroid composition between sites, a nonmetric multidimensional scaling (NMDS) and cluster analysis (UPGMA method) was implemented using the Bray–Curtis similarity index (Bray and Curtis 1957; Kruskal and Wish 1978; Krebs 1999). The results of the cluster analysis and NMDS were evaluated through a Permutational Multivariate Analysis of Variance (one-way PERMANOVA) and analysis of similarities (one-way ANOSIM) (including posterior paired tests), using 9999 permutations and the Bray–Curtis similarity index as a measure of distance (Clarke 1993; Anderson and Walsh 2013). Also, we performed a Hierarchical Clustering Algorithm (HCA) and Euclidean distance measurements with Ward´s method (without a second data standardisation) for all plots and aroid species.

The construction of the rarefaction curves and the calculations of diversity indexes, ANOVA, Welch ANOVA, CA, cluster analysis (UPGMA), NMDS, PERMANOVA and ANOSIM, were performed using PAST v.3.0 software (Hammer et al. 2001). CA for aroid species was done using the XL-STAT software (Addinsoft 2017) and the Euclidean HCA was performed using JMP Pro v.14 software.

Results

General patterns of aroid diversity and abundance

In total, we registered 3187 individuals, distributed in 10 genera and 61 species, of which 12 were endemic to Panama (Table 2; supplemental online material). Of these, 18 species and 637 individuals were epiphytes, 32 species and 2153 individuals were nomadic vines, and 11 species and 397 individuals were terrestrials (Table 2). In terms of species richness and abundance, the genera *Anthurium* and *Philodendron* contained 68.7% of the listed species and 84.7% of the individuals registered in all plots.

Table 2. Aroid abundance, endemism and diversity parameters for the study sites.

Parameters		Sites			
		MB	MS	MR	All sites
Species richness	All life forms pooled	29	40	25	61
	Epiphytes	5	9	11	18
	Nomadic vines	20	22	12	32
	Terrestrials	4	9	2	11
Abundance	All life forms pooled	1150	611	1426	3187
	Epiphytes	30	53	554	637
	Nomadic vines	1043	516	594	2153
	Terrestrials	77	42	278	397
Endemic species		1	2	10	12
Jackknife 2		33	56	29	77
Chao 2		30	50	26	70
Percentage collected		92	75	91	83
Simpson's reciprocal index		5.65	8.09	5.86	–
Shannon diversity		9.70	16.54	8.37	–
Menhinick index		0.85	1.62	0.66	–
Margalef index		3.97	6.08	3.30	–

Percentage collected values were computed as (total species/mean of Jackknife 2 and Chao 2) × 100.

According to our calculations, the percentages of representativeness in all sites are higher or equal to 75% (Table 2). The rarefaction curves between sites indicated that the MS had the highest species richness, followed by MB and MR (Figure 3), which were in agreement with calculated values for the Margalef and Menhinick indexes (Table 2). No significant differences in aroid species richness for all life forms pooled were detected ($F = 0.7$, $p = 0.503$). However, calculated values of the Menhinick index ($F = 5.7$, $p = 0.010$) and Margalef index ($F = 6.1$, $p = 0.008$) showed statistical differences (see Figure 4).

Of the total registered individuals, close to 45% were accounted for in MR, followed by MB with 36% and MS with 19% (Table 2). The statistical analysis showed significant differences in the abundance of all life forms pooled among sites ($F = 7.8$, $p = 0.003$) (Figure 4). Regarding species diversity, we did not find any statistical differences between sites according to the calculated values of the Shannon diversity (Welch ANOVA: $F = 3.7$, $p = 0.056$) and Simpson's reciprocal index (Welch ANOVA: $F = 2.0$, $p = 0.175$).

Diversity and distributional patterns of aroid life forms

Taking into account the life forms, the epiphytes present the highest values of richness ($F = 11.2$, $p < 0.0001$) and abundance ($F = 42.6$, $p < 0.001$) in the MR, showing the lowest values in the MB (Figure 4;

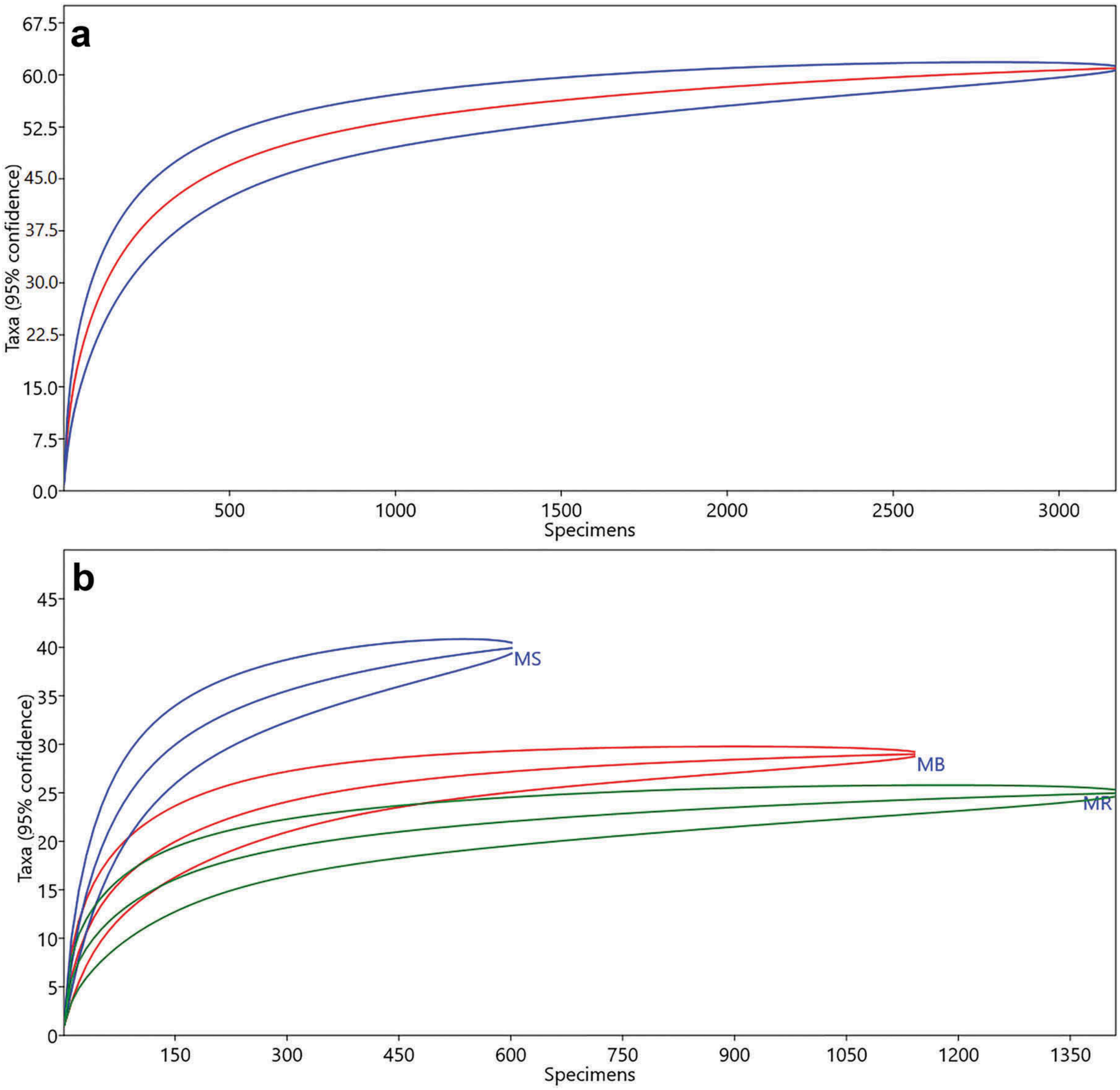

Figure 3. Rarefaction curves for individuals of aroid species. (a) Pooled rarefaction curve for all aroid species recorded at any of three sites (MB, MS and MR). (b) Rarefaction curves for recorded aroid species for each study site.

Table 2). In the case of nomadic vines, the highest values for species richness were found in the MS and the lowest values in the MR ($F = 6.8$, $p = 0.006$), whereas the highest abundance was obtained in the MB ($F = 6.1$, $p = 0.008$), and decreased at upper elevations (MS and MR sites) (Figure 4; Table 2). The highest richness for terrestrial aroids was measured in the mid-elevation sites (MS) and abundance values were markedly higher in the MR. Although no significant differences were found in the richness of terrestrial aroids between sites (Welch ANOVA: $F = 0.8$, $p = 0.487$), however, differences in the abundance of terrestrial individuals were significantly different ($F = 7.5$, $p = 0.003$) (Figure 4).

Our results on the abundance and distribution of life forms across the three elevation gradients are in agreement with our CA, which indicated a significant association between life forms and study sites ($\chi^2 = 827.9$, $p = 0.0001$, inertia = 0.25). The CA allows us to separate the three study sites visually based on the abundance of aroids according to their life forms, the strongest associations being those located at the ends of the ordering graph. The CA biplot for aroid life forms vs study sites suggests that nomadic vine individuals are strongly associated with low- and mid-elevation sites (MB and MS) (Figure 5(a)). Additionally, it shows associations between terrestrial and epiphytic individuals and high-elevation sites (MR). Given the position of epiphytes at the end of the graph with a smaller angle, it seems that MR is even more strongly associated with epiphytic individuals than with terrestrial individuals (Figure 5(a)).

Aroid community composition and endemism along the elevation gradient

The CA indicated a significant association between the genera of Araceae and the study sites ($\chi^2 = 2355.1$, $p = 0.0001$, inertia = 0.74), suggesting that aroid genera can show specificity to certain sites along the elevation

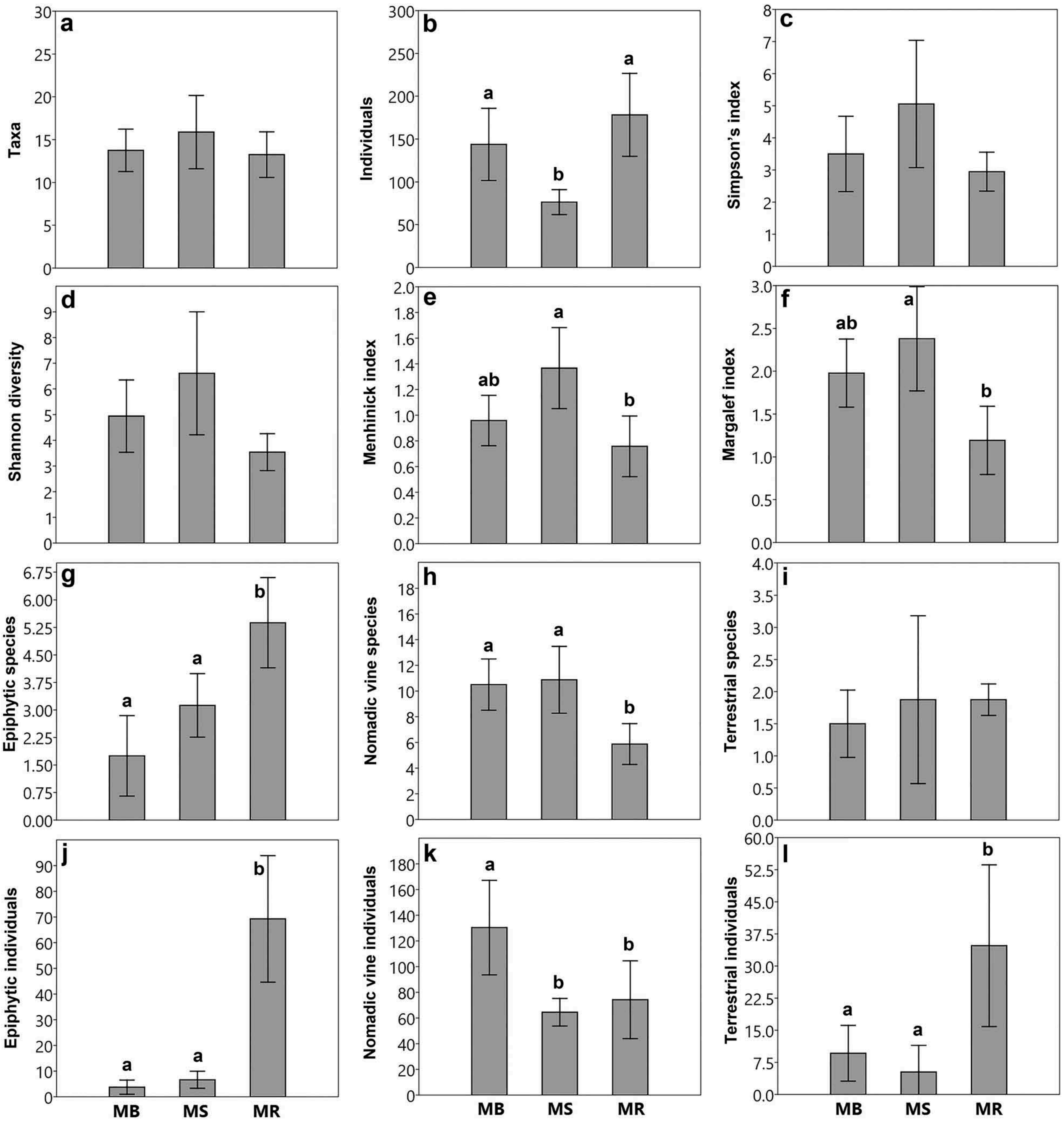

Figure 4. Average abundance and diversity parameters among study sites. (a) Species richness (all life forms pooled). (b) Abundance (all life forms pooled). (c) Simpson's reciprocal index (1/*D*). (d) Shannon diversity. (e) Menhinick index. (f) Margalef index. (g) Epiphytic aroid richness. (h) Nomadic vine aroid richness. (i) Terrestrial aroid richness. (j) Epiphytic aroid abundance. (k) Nomadic vine aroid abundance. (l) Terrestrial aroid abundance. Bars are presented with 95% confidence intervals. Different letters above the bars indicate significant differences (Tukey's test: $p < 0.05$).

gradient of the Cerro Pirre (Figure 5(b)). *Anthurium* and *Stenospermation* are strongly associated with high-elevation sites (MR), whereas *Monstera*, *Syngonium* and *Philodendron* are with low- and mid-elevation sites (MB and MS). Only two species, *Philodendron wilburii* and *Syngonium* sp. 1, were distributed along the elevation gradient of Cerro Pirre and most of the endemic species (83%) were reported in MR plots (Table 2; supplemental online material). In this same sense, the CA determined the existence of a strong association between 10 endemic species (*Anthurium niqueanum*, *A. pirrense*, *A. rubrifructum*, *Anthurium* sp. nov. 1, *Anthurium* sp. nov. 2, *A. terryae*, *A. dukei*, *Philodendron clewellii*, *P. niqueanum*, *Stenospermation* sp. nov. 1) and MR plots (χ^2 = 4264.222, p < 0.0001, inertia = 1.34). In addition, we found strong associations between *Philodendron inaequilaterum* and MB plots, as well as between *Anthurium ramonense*, *Philodendron edenudatum*, *P. fragrantissimum*, *Spathiphyllum phryniifolium* and MS plots (see Figure 6).

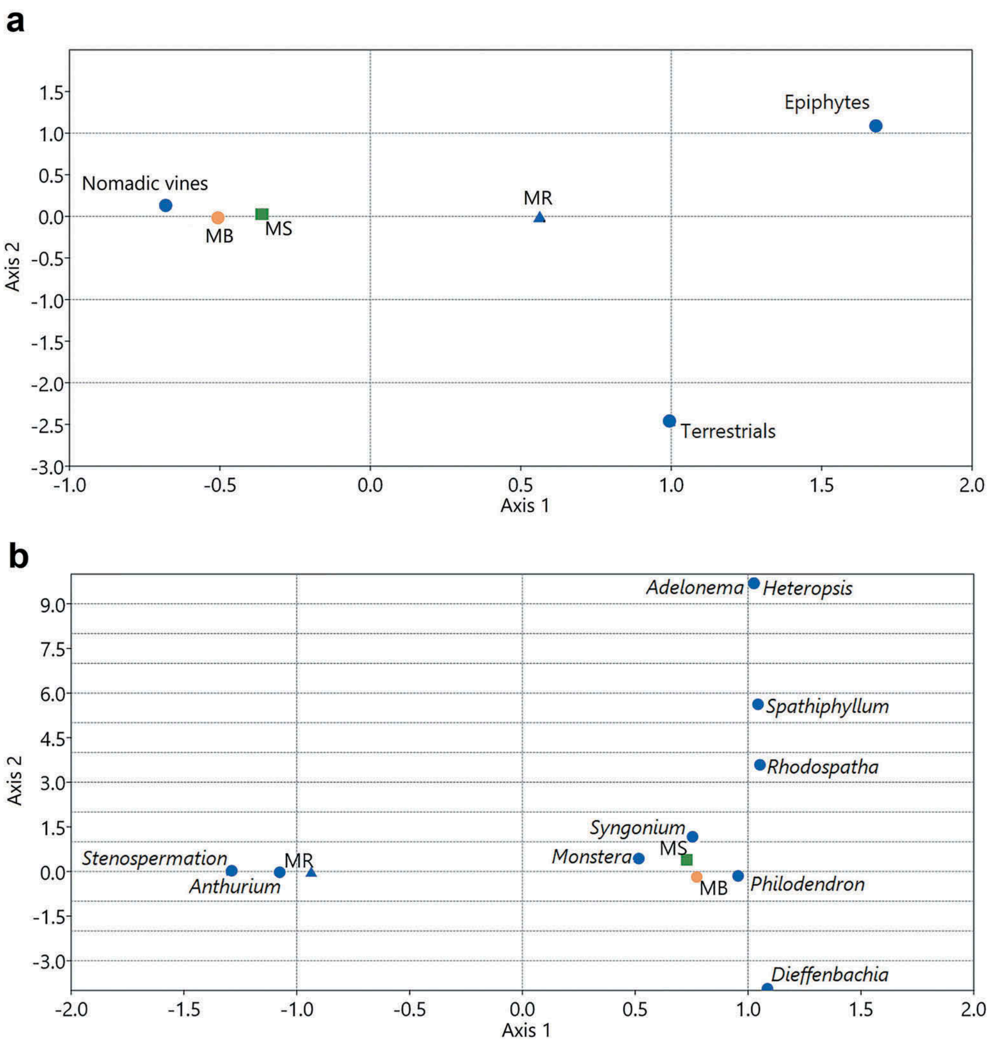

Figure 5. Plots of Correspondence analysis (CA). (a) CA biplot for aroid life forms and study sites (MB, MS and MR), the values of axis 1 (99.86%) and axis 2 (0.14%) represent a percentage of cumulative variance of 100%. (b) CA biplot for aroid genera and study sites (MB, MS and MR), the values of axis 1 (95.89%) and axis 2 (4.11%) represent a cumulative variance percentage of 100%.

Bray–Curtis cluster analysis shows that the species composition existing in MR is totally different compared to that of the MB and MS sites (Figure 7(b)). Additionally, although the Bray–Curtis cluster analysis suggests that MB and MS sites share some species, it also shows important differences, evidenced by a similarity value of 0.4, which indicates that both sites exhibit a dissimilarity of 60% of the total number of species. For its part, the NMDS analysis recognised three groups corresponding to the sites represented along the Cerro Pirre elevation gradient. Among the recognised groups, it is observed that the plots within MS are more separated from each other, indicating that the aroid community of Cerro Pirre at the MS site is very diverse (Figure 8(b)).

Both the PERMANOVA (Pseudo-F = 12.04, p = 0.0001) and the ANOSIM (R = 0.8829, p = 0.0001) determined significant differences in the aroid composition among the elements of the landscape evaluated (MB, MS and MR). Subsequent pairwise tests of PERMANOVA and ANOSIM indicated significant differences in the aroid species composition among all study sites (Table 3). The R statistic calculated in the ANOSIM test indicates that the distances between MR and MB, and MR and MS are markedly different, as their R values were 1 and 0.99, respectively; however, the value of R between MB and MS is lower (R = 0.55) (see Table 3). These results agree with those of the Euclidean HCA, which suggests that the separation between the MB and MS communities is not complete and that there is overlap. In contrast, the existing community in MR is markedly different compared to the other two sites (Figures 7(a) and 8(a)).

Discussion

General patterns of aroid diversity and abundance

Aroid species reported for all sampled sites indicate that the aroids, in general, have become accustomed to the different elevation gradients of Cerro Pirre.

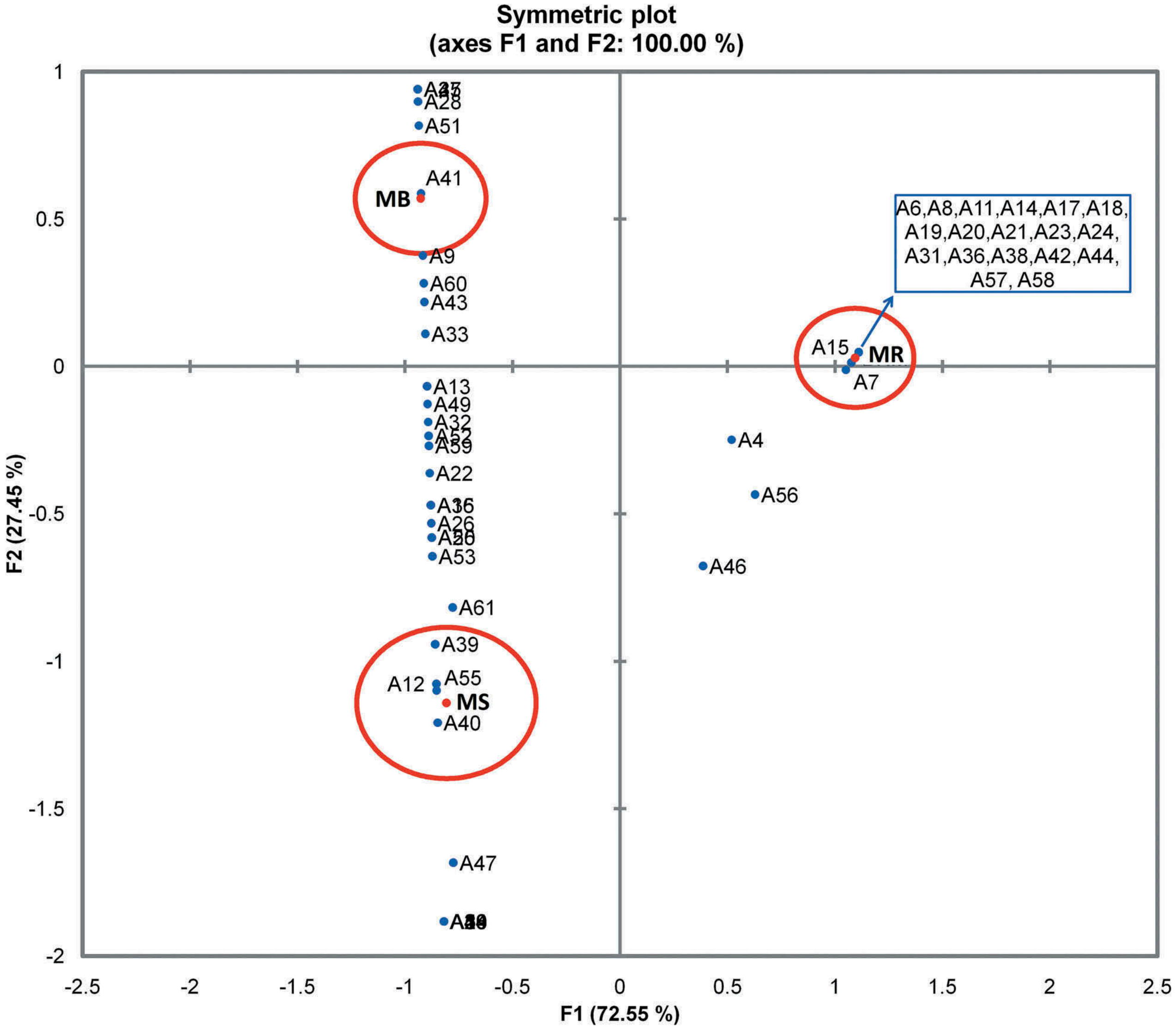

Figure 6. Correspondence Analysis (CA) biplot for aroid species (blue points with their respective codes) and study sites (MB, MS and MR). The CA explains 100% of the variance of the matrix with the first two factors. The species codes are presented in the supplemental online material.

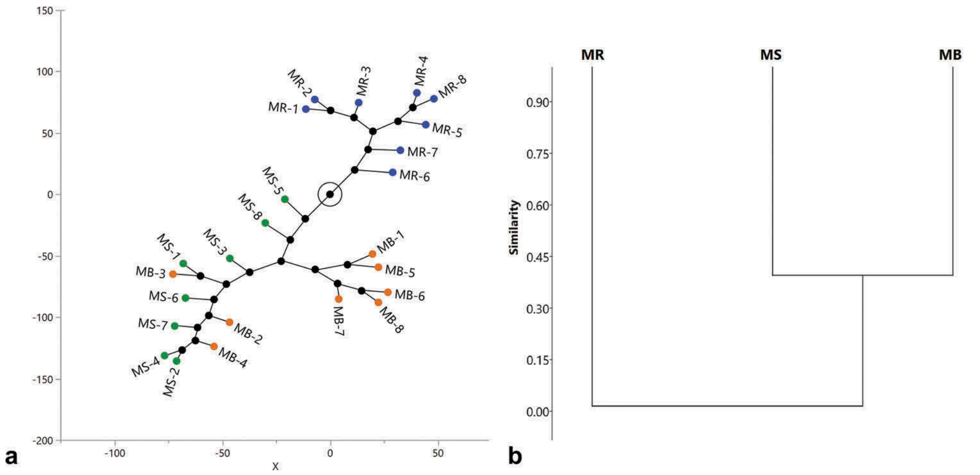

Figure 7. Clustering multivariate analysis. (a) Constellation plot from Hierarchical Cluster Analysis (HCA). (b) Bray–Curtis similarity dendrogram between the study sites (MB, MS and MR).

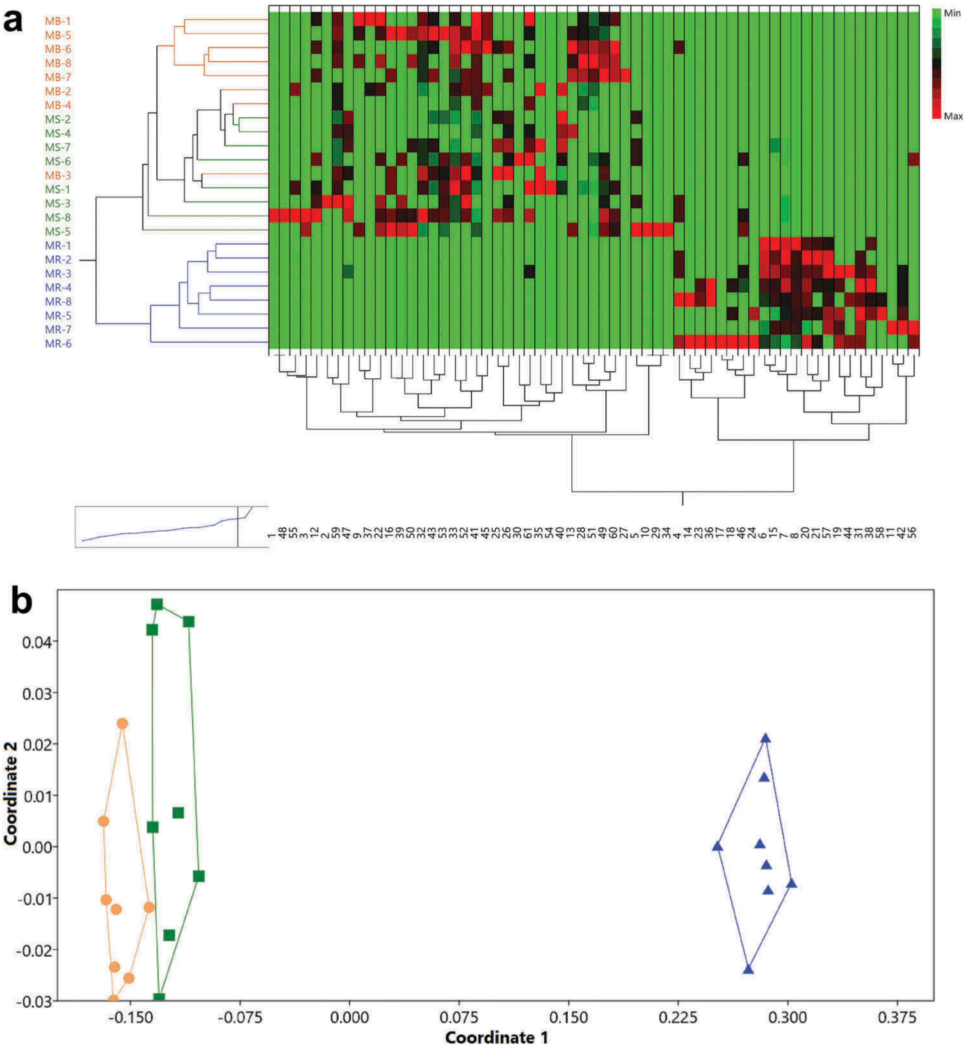

Figure 8. Ordination and clustering multivariate analysis. (a) Hierarchical Cluster Analysis (HCA) for all plots and aroid species shown as a heatmap [colours represent the abundance per species from minimum (green) to maximum (red), species codes are presented in the supplemental online material]. (b) NMDS analysis of aroid assemblages in the Cerro Pirre [axis 1 = 0.625, axis 2 = 0.06, stress = 0.17; MB (yellow circles), MS (green squares), MR (blue triangles)].

Table 3. Results of the pairwise tests of PERMANOVA and ANOSIM for the elevation factor, using the Bray–Curtis matrix with 9999 permutations.

	PERMANOVA		ANOSIM	
Sites	Pseudo-*F*	*p*	*R*	*p*
MB/MS	4.67	0.0004*	0.55	0.0006*
MB/MR	20.21	0.0003*	1.00	0.0001*
MS/MR	13.89	0.0004*	0.99	0.0002*

Asterisks indicate significant differences.

The highest aroid species richness (all life forms combined) was found in the MS site, which includes sites ranging between 500 and 700 m. These results differ from those obtained by Acebey and Krömer (2008), who reported that the highest aroid species richness is found mainly in sites at low elevations and decreases linearly at higher elevation. Comparing only the epiphytic richness pattern, our results are in complete disagreement to those obtained by Krömer et al. (2005), where richness values were constantly high from 350 m to about 1000 m and then linearly decreased. That might be due to the fact that the elevational gradient covered in our study (at Cerro Pirre) is not large at all, compared to the one covered by Krömer et al. (2005).

Zotz and Bader (2011) mentioned that in certain cases it is difficult or impossible to make comparisons between studies, because the results can be influenced by the inclusion or exclusion of hemiepiphytes (referred to here as nomadic vines). In a study conducted in Costa Rica by Cardelús et al. (2006), the authors reported that the high richness of epiphytic Araceae (including hemiepiphytes) occurs at lower-elevation sites. However, they argue that the true aroid richness is probably hidden by the incorporation of hemiepiphytes among true epiphytes. It is possible that the aroid richness pattern obtained in our study differs from the monotonic decline pattern (see Acebey and Krömer 2008) due to the incorporation of all life forms (terrestrial, epiphytes and nomadic vines). Therefore, it is crucial to analyse the richness and abundance patterns of Araceae according to the life forms and their ecological requirements.

According to the Margalef and Menhinick indexes, the species richness for both MB and MR sites is lower. Perhaps this is due to the predominant dominance of some species in these sites. The plots sampled at the MB site exhibited a high abundance of *Philodendron inaequilaterum*. This species, belonging to the subgenus *Pteromischum*, has a wide geographic distribution and is usually tolerant to low levels of precipitation and regular dry seasons (Grayum 1996). It has been documented that this species is abundant in the lowland forests of central Panama (Croat 1978), however, its distribution throughout the forest is usually irregular (Royo and Carson 2005). This irregular distribution in the forest can be linked to vegetative reproduction, by means of flagelliform shoots or flagellar leaves (Bogner 1987; Ray 1987), which are common structures in *Philodendron* subgenus *Pteromischum* (Grayum 1996).

On the other hand, *Anthurium terryae* is highly abundant in the MR site. This endemic species grows as an epiphyte and its distribution in the elevation gradient is restricted to MR (Figure 6; supplemental online material). We speculate that the mode of dispersal may play a role in its distribution and abundance. *Anthurium terryae* has pendant infructescences with white berries, suggesting a dispersal carried out by flying (bats) or arboreal mammals (rodents), which are relatively diverse and abundant in the study site (Arosemena 2000; Castillo et al. 2016). Another factor involved in its abundance could be that *A. terryae* presents apomixis or self-pollination. When pollinator frequencies are limited or absent, some aroid species may develop facultative apomixis (Hentrich et al. 2010) or they could self-pollinate (Chouteau et al. 2008).

Diversity and distributional patterns of aroid life forms

Comparing the overall pattern of all life forms pooled to that of each life form separately, it becomes obvious that epiphytes and nomadic vines follow opposing patterns in species richness and abundance (Table 2; Figure 4). This underpins the notion of Zotz and Bader (2011) that combining data of epiphytic and nomadic vine aroid species may mask patterns of species richness intrinsic to these specific life forms. In the case of the epiphytic aroids, the richness and abundance increased with the elevation. This was mainly driven by the high richness and abundance of *Anthurium* and *Stenospermation* that both showed strong associations with the MR (see Figure 5(b)). This result was expected, since both genera constitute an important percentage of the epiphytic aroids from Panama, and their species occur primarily in mid-elevation cloud forests and less frequently in dry forests (Croat 1986a, 1988).

We believe that, perhaps, the patterns obtained in the epiphytes and nomadic vines are due to the changes caused indirectly by the elevation in the forest structure, precipitation and atmospheric humidity of the studied sites (see Table 1). The lowland forests at MB have the lowest precipitation values in the elevation gradient of Cerro Pirre and are characterised by being semi-deciduous. The levels of precipitation can vary dramatically even though the sites are in close proximity to one another, particularly at the lower altitudinal limits for cloud formation (Haber 2000). During the dry season, many trees shed their leaves, promoting the presence of dry microclimates in the understorey. According to Einzmann et al. (2015), host trees that are deciduous during dry seasons promote sunny and dry microclimates, directly affecting the abundance and diversity of epiphytic communities in lowland forests. On the contrary, the cloud forests at MR are evergreen, have a high biomass of mosses (Gradstein and Salazar 1992), and have greater availability of water and humidity (Myers 1969), perhaps owing to the formation of orographic rains (Whiteman 2000) or by horizontal precipitation (Stadtmüller 1986), which generates the constant presence of atmospheric humidity in the form of fog in the highest parts of the mountain (Myers 1969). Sugden and Robins (1979) reported that the montane habitats in north-eastern Colombia have a greater diversity and abundance of vascular epiphytes than do lowland regions, mainly due to the frequency and duration of periods of cloud cover. The growth of epiphytes in particular depends heavily on the abundant and continuous supply of water (Laube and Zotz 2003; Kreft et al. 2004) and its establishment in some cases is conditioned by the presence of mosses in the host trees (Croat 1988).

Regarding nomadic vines, richness and abundance patterns are markedly different from those obtained in epiphytes (Table 2; Figure 4). These results support the notion of Zotz and Bader (2011) that the ecology of the secondary hemi-epiphytes (referred to here as nomadic vines) and epiphytes differ fundamentally. The pattern of species richness of nomadic vines shows the highest values of richness in low to mid-elevation sites (MB and MS), coinciding with the results of Küper et al. (2004). As shown in Figure 4, the richness and abundance of aroid nomadic vines decreases drastically at the highest elevation sites (MR). One explanation could be that the excessive humidity present in the highest mountain ranges may restrict the growth of some nomadic vines, similar to the case of *Philodendron* in Colombia, where apparently many species do not grow in areas with excessively high precipitation levels (Grayum 1996; Croat 1997; Leimbeck et al. 2004). Another factor that limits the richness and abundance of nomadic vines could be the nutrient composition of soils (see Woods et al. 2018). The high abundance of nomadic vines reported in MB may be related to the vegetative propagation, as mentioned by Irume et al. (2013). The associations between various genera of nomadic vines at lower and mid-elevational sites (MB and MS) may suggest that they have intrinsic eco-physiological adaptations that allow them to tolerate environments. The nomadic vine life form (referred to as secondary hemi-epiphytes) has the ability to mobilise in response to favourable growth conditions, such as higher luminosity and availability of host trees, allowing individuals to move and find suitable sites with adequate conditions for their development (Madison 1977; Lee and Richards 1991; Croat 1997).

The terrestrial aroids presented greater richness in mid-elevation sites (MS) (similar to the nomadic vines guild), however, the highest values for abundance were given to the MR (similar to the epiphytes guild). This was expected since the requirements for epiphytes and terrestrial herbs are similar, especially in soil fertility and water availability (influenced by dry seasons) (Gentry and Emmons 1987). Croat (1988) mentions that in cloud forests the conditions present in the soil and in trunks from host trees are virtually identical, due to the continuous drainage of water and the excessive accumulation of organic matter. By contrast, soils in lowland forests and montane forests can vary significantly in fertility, which can be a product of soil age, topography, and its interaction with climate and forest composition (Silver et al. 1994; Benner et al. 2010). The high richness of terrestrial species in MS is probably due to the precipitation levels in the upper slopes and the edaphic and orographic characteristics of the mid-elevation slopes. These last factors are key given that changes in edaphic conditions and topography can potentially affect both the distribution and richness of terrestrial species in general (Poulsen and Balslev 1991).

Aroid community composition and endemism along the elevation gradient

The results obtained in this study through the multivariate cluster and ordering analysis determined the existence of changes in the composition of aroids between sites. This pattern has been documented in epiphytic communities (including Araceae) from other tropical regions, where communities undergo a turnover of species as elevation increases (Gentry and Dodson 1987; Küper et al. 2004; Ding et al. 2016). According to Küper et al. (2004), changes caused by increases in the amount of epiphytic species turnover reflects ecological differences. Some studies have documented that even small micro-climatic differences can affect the composition of epiphytic aroid communities (Leimbeck and Balslev 2001) and epiphytes in general (Barthlott et al. 2001). In addition, it has been documented that elevation can modulate the distribution of plant communities according to their life forms (Vázquez and Givnish 1998; Watkins-Jr et al. 2006). Most of the aroid genera are closely related to specific life forms (Croat 1988) and in some cases may be linked to evolutionary factors (Mayo et al. 1997; Cusimano et al. 2011; Canal et al. 2019).

Mountainous ridges (MR) in general, are associated with high levels of endemism (Figures 6 and 8(a); Table 2). This agrees with similar opinions (Kessler 2002) that state that high percentages of endemism are linked to higher-elevation sites. Similar patterns have been documented in isolated mountains of Panama by Croat (1986b), where he reports some cases of restricted distributions of *Anthurium* associated with isolated cloud forests. The patterns of endemism can be influenced both by the autoecology of taxa, their specific interaction with historical processes (Kessler 2002; Leimbeck et al. 2004), and by environmental factors such as topographic fragmentation, elevation and the presence of habitats with pronounced reliefs (Gentry and Dodson 1987; Kessler 2002; Küper et al. 2004; Leimbeck et al. 2004; Köster et al. 2013; Ding et al. 2016).

As mentioned above, perhaps the changes in species turnover along elevational gradients are the result of an existing environmental gradient; however, the main explanation for the high endemism determined in MR could be linked to historical factors. Haffer (1969) proposes the possibility of the existence of isolated refuges during the dry periods of the Pleistocene having consequences on the speciation and extinction of the biota in the Neotropical forests (see Haffer 2001; Hooghiemstra and van der Hammen 2001). Some of these refuges include mountain ranges located in eastern Panama (Pirre, Sapo and Tacarcuna) (Haffer 1967a, 1967b). Perhaps because of the isolation of the refuges during the dry climatic periods associated with glacial episodes, the populations of Araceae that occupied these refuges differentiated (allopatric speciation). Grayum (1996) mentions that there is morphological evidence of this in *Philodendron* subgenus *Pteromischum*, which may suggest the existence of intergradation due to isolation, given past historical events associated with glaciation episodes. The endemism patterns can also be related to specific ecological features such as dispersal. Croat (1986a) mentions that for the Panamanian *Anthurium*, the high rate of endemism may be related to seed dispersal processes. The same author mentions that many of the *Anthurium* species grow in areas of dense understorey, where it is more probable that their fruits are consumed by birds from forest areas, instead of migratory birds or those that live and forage in more open areas (at the edge of the forest). It is important to note that many of the bird species present in Cerro Pirre are also endemic (Robbins et al. 1985; Angehr et al. 2004; Hruska et al. 2017; Renjifo et al. 2017), some of which could be involved in specific dispersal patterns.

From the conservation point of view, the information presented in this study is highly relevant. Currently, the areas surrounding the sites under study are under increased anthropogenic pressure from various indigenous communities that gradually expand their communities, build new villages and transform the land into terrains suitable for farming or livestock. The areas of endemism (MR) and high diversity (MS) identified in this study should be a priority in the conservation programmes of the Darién National Park.

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