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Changes in functional and taxonomic diversity and composition of corticolous lichens in an altitudinal gradient in Colombia

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Changes in functional and taxonomic diversity and composition of corticolous lichens in an altitudinal gradient in Colombia

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ABSTRACT

The variation of the diversity, composition, functional diversity and species richness of lichen communities along an altitudinal gradient in the Chocó biogeographic region of the department of Valle del Cauca, Colombia, is evaluated basing on 2732 samples belonging to 690 species of corticolous lichens. The dominant families were Graphidaceae, Parmeliaceae, Lobariaceae and Pyrenulaceae. Alpha lichen diversity showed a concave pattern with respect to altitude, and the zones at low and high elevations had greater diversity. Beta diversity and total richness estimated by rarefaction for locality presented a bell-shaped pattern, with a peak at 1600 m. Lichen functional traits strongly changed with the increase of altitude. Functional diversity presented the same pattern of total richness estimated by rarefaction. These results suggest that the lichen communities of the altitudinal extremes are structured by a strong environmental filter effect, while in the intermediate zones there is an overlap of functional traits, which is reflected in both a high functional and taxonomic diversity. The results suggest that the functional traits used are good substitutes for species to study altitudinal patterns. The high number of indicator species for the altitudinal extremes implies that in a context of climate change, these zones will be more susceptible to the loss of species.

KEY WORDS

Chocó,
Rao,
functional diversity,
rarefaction,
traits,
elevation,
mid-domain effect.

RÉSUMÉ

Changements dans la diversité fonctionnelle et taxonomique et la composition des lichens corticoles le long d'un gradient altitudinal en Colombie.

La variation de la diversité, de la composition, de la diversité fonctionnelle et de la richesse en espèces des communautés de lichens le long d'un gradient altitudinal dans la région biogéographique du Chocó du département de Valle del Cauca, en Colombie, est évaluée sur la base de 2732 échantillons appartenant à 690 espèces de lichens corticoles. Les familles dominantes étaient les Graphidaceae, les Parmeliaceae, les Lobariaceae et les Pyrenulaceae. La diversité des lichens alpha a montré un motif concave en ce qui concerne l'altitude, et les zones à basse et haute altitude présentaient une plus grande diversité. La diversité bêta et la richesse totale estimées par raréfaction pour la localité présentaient un motif en forme de cloche, avec un pic à 1600 m. Les traits fonctionnels des lichens ont fortement changé avec l'augmentation de l'altitude. La diversité fonctionnelle présentait le même schéma de richesse totale estimée par raréfaction. Ces résultats suggèrent que les communautés de lichens des extrêmes altitudinaux sont structurées par un fort effet de filtre environnemental, alors que dans les zones intermédiaires il y a un chevauchement des traits fonctionnels, ce qui se traduit par une grande diversité fonctionnelle et taxonomique. Les résultats suggèrent que les traits fonctionnels utilisés sont de bons substituts aux espèces pour étudier les patrons altitudinaux. Le nombre élevé d'espèces indicatrices pour les extrêmes altitudinaux implique que, dans un contexte de changement climatique, ces zones seront plus exposées à la perte d'espèces.

MOTS CLÉS

Chocó,
Rao,
diversité fonctionnelle,
raréfaction,
traits,
altitude,
effet de mi-domaine.

INTRODUCTION

Since the times of Darwin, Wallace, and von Humboldt, it has been known that the natural world changes with elevation (Lomolino 2001). They noted that species richness and habitat type change predictably with altitude and latitude. Since then, the study of these biotic patterns has attracted the attention of many researchers around the world, and several hypotheses have been proposed to try to explain it (Hawkins *et al.* 2003; Storch & Gaston 2004). These hypotheses consider both abiotic and biotic factors that vary with the altitudinal gradient. The most obvious abiotic factor is climatic (i.e. precipitation, solar radiation and temperature), as the gradual change of precipitation and temperature with elevation is well known. The elevation is one of the most important factors explaining richness patterns, because it determines the distribution ranges of species (McCain & Grytnes 2010). Other factors, such as soil, cloud cover and biotic interactions, have been proposed to explain the altitudinal gradients of species richness (McCain & Grytnes 2010). However, the current development of statistics and computational tools has created more uncertainty about the mechanisms that explain these patterns.

The biogeographic Choco region is one of the most diverse regions of the planet and is a hot spot of endemism, with about 1600 species of endemic plants and 68 species of birds (the highest in the world) (Gentry 1986; Forero & Gentry 1989; Faber-Langendoen & Gentry 1991). At present, this region suffers high rates of deforestation due to problems of drug trafficking, indiscriminate cutting of trees, shrimp activities that destroy mangroves and other associated forests, conversion into agricultural fields, domestic pollution by dumping sewage into rivers, and illegal mining (Rangel & Lowy 1993). In addition, the biodiversity of this area is little known and research is scarce, both in terms of inventories and ecological

aspects (Rangel & Lowy 1993; Cárdenas 2003). It is necessary to stimulate research that seeks to document the diversity present in this ecoregion and to understand ecological patterns, at both small and large scale, in order to establish better conservation strategies.

Lichenized fungi or lichens constitute a symbiotic association between an Ascomycota or Basidiomycota fungus, yeast (Basidiomycota) (Spribille *et al.* 2016) and one or more photoautotrophic organisms, which may be cyanobacteria, green algae (Chlorophyta), and even Phaeophyta (Nash 2008). About 14 000 lichen species are estimated for the tropics and 28 000 for the entire world (Lücking *et al.* 2009a). However, the inventories that have been made on these organisms in the tropical zone are insufficient, and there is a great lack of the knowledge of the taxonomy and, even more, of the ecology of these groups for these zones (Lücking *et al.* 2009a). The corticolous lichens are the most diverse group of lichenized fungi in the Neotropics (estimated 4900 species) and taxonomic and ecological knowledge about them is limited (Lücking *et al.* 2009a).

Several studies have been carried out to establish the effect of altitudinal gradients on lichen species richness (Wolf 1993; Pirintsos *et al.* 1995; Bruun *et al.* 2006; Baniya *et al.* 2009; Vittoz *et al.* 2010; Man-Rong & Wei 2012). There are records of lichens observed from 0 to 7400 m (Baniya *et al.* 2009; Man-Rong & Wei 2012). This amplitude of altitudinal distribution is not the same for different morphological groups of lichens (Wolf 1993; Pirintsos *et al.* 1995, Bruun *et al.* 2006, Grytnes *et al.* 2006; Vittoz *et al.* 2010; Man-Rong & Wei 2012). In the studies carried out to date, it has been shown that the different morphological groups of lichens usually are distributed unimodally in an altitudinal gradient (Wolf 1993; Vittoz *et al.* 2010; Man-Rong & Wei 2012). Such distribution may vary between groups (Bruun *et al.* 2006; Baniya *et al.* 2009).

In epiphytic lichens (on bark and leaves), altitudinal distribution is usually unimodal (Wolf 1993; Pirintsos *et al.* 1995), but in terrestrial lichens it can be multimodal (Baniya *et al.* 2009; Man-Rong & Wei 2012). This pattern is caused by different levels of tolerance to light (Wolf 1993; Baniya *et al.* 2009). This affects macroecological patterns and niches, which depend on elevation, climate, communities, isolation, and tolerance patterns (Lomolino 2001; Bruun *et al.* 2006; Rubio-Salcedo *et al.* 2017).

In the biogeographic Chocó region, ecological studies have not been carried out with lichenized fungi, and there are only records of species made by Harrie Sipman and Jaime Aguirre in Chocó and Nariño (Rangel 2004) and by Mateus *et al.* (2012) in Chocó and Valle del Cauca in premontane forests (El Queremal, Dagua) (Soto-Medina & Lüicking in prep.); Soto-Medina *et al.* (2012) reported many new records for Colombia. Based on this, and considering the high rates of deforestation in this area, it is necessary to study the diversity and ecology of vegetation and its associated organisms in this region of high diversity, in order to establish the effect of deforestation on lichen diversity. In addition, these organisms are excellent bioindicators of pollution and ecological continuity, so information on the ecology and taxonomy of these organisms would allow the evaluation of the impact of human intervention on the different ecosystems of this region (Hawksworth & Rose 1976; Hawksworth & Seaward 1990; Rivas-Plata *et al.* 2008).

All of the above shows the lack of knowledge on lichen diversity and ecology in the biogeographic region of Chocó, Valle del Cauca, Colombia. This is a major problem for the establishment of viable conservation strategies, since it is now necessary to know ecological patterns both on a small scale (i.e. local) and on a large scale (i.e. regional, continental) to give an overview of the primary factors affecting diversity. For this, both ecological studies (e.g., traditional ecology) and the strengthening of inventories in the areas of interest are required, which can be used to study the factors that, at the scale of the landscape, are modulating species richness or presence. In addition, lichenized fungi and green plants have been reported as being affected by global warming, which makes them biomonitors of climate change (Aptroot & van Herk 2007; Rubio-Salcedo *et al.* 2017). Thus, the study of altitudinal variation through the establishment of sampling stations would allow monitoring the effects of climate change on plant and lichen communities. The objective of this work was to evaluate the variation of species diversity and composition, besides functional diversity and functional traits composition of lichen communities along an altitudinal gradient in the Choco biogeographic region of the department of Valle del Cauca, Colombia.

MATERIAL AND METHODS

STUDY AREA

The biogeographic region of Chocó ranges from the Darién (Panamá) to Manabí province (Ecuador), reaching

175 000 km². It comprehends 2% of the land surface, but it is home to about 10% of the biodiversity of the planet (Fig. 1). Longitudinally, it extends from the Pacific coast to the watershed of the western cordillera, forming a strip of approximately 865 km long and from 60 to 250 km wide, between latitudes 0°48' and 8°41'N and longitudes 75°51' and 79°02'W. This area rises from sea level to approximately 3700 meters, harboring diverse ecosystems such as paramos, cloud forests, tropical rainforests, and mangroves, among others (Kelleher *et al.* 1995). It is characterized by an average annual rainfall of 9000 mm and average annual temperature of 27°C. The biogeographic Chocó region of Colombia – the Pacific region and the Urabá area – occupies an area of about 113 000 km², representing almost 70% of the entire ecoregion and 10% of Colombian territory (Kelleher *et al.* 1995).

In the department of Valle del Cauca, the Chocó biogeographic region extends between the municipalities of Buenaventura, El Cairo, La Cumbre, Cali and Dagua. This region includes part of protected areas such as the National Natural Park Farallones de Cali, Natural National Park Urabá-Bahía Málaga, and the Serranía de los Paraguas Natural Reserve in the municipality of El Cairo. In this study, samples were collected in five localities of Valle del Cauca at different altitudes (Fig. 1, Table 1), comprising tropical humid forest, premontane, montane and high Andean forest ecosystems. The localities were chosen within the system of natural national parks or regional reserves, to guarantee the good state of conservation of the forests and thus avoid possible biases in the patterns of lichen communities, since these are very sensitive to anthropogenic disturbance (Rivas Plata *et al.* 2007). The sites sampled have never been intervened in the past, many of these had not been sampled previously, which can study the altitudinal patterns without any bias (McCain & Grytnes 2010).

VEGETATION SAMPLING

Ten Gentry transects (linear transects of 50 × 2 m) were established in each locality (following Torres *et al.* 2012). This method allows good estimates of plant diversity and vegetation structure of a site (Gentry 1982; 1993). Basic data, such as breast height diameters (BHD), total height and density, were taken from each individual recorded on each plot (Gentry 1982; 1993). For the taxonomic identification of the arboreal and shrub species, herbarium samples were taken, which were processed and deposited in the CUVC herbarium of the Universidad del Valle. The samples were identified to the highest taxonomic level possible with the help of published taxonomic keys and the CUVC herbarium collection. The diversity of species in each locality, alpha diversity (Shannon Wiener index and species richness per plot) and structural parameters such as basal area, relative frequency and relative density were estimated.

LICHEN SAMPLING

Opportunistic sampling was carried out, which consisted of five 50 m transects at forest edges or along main roads in each

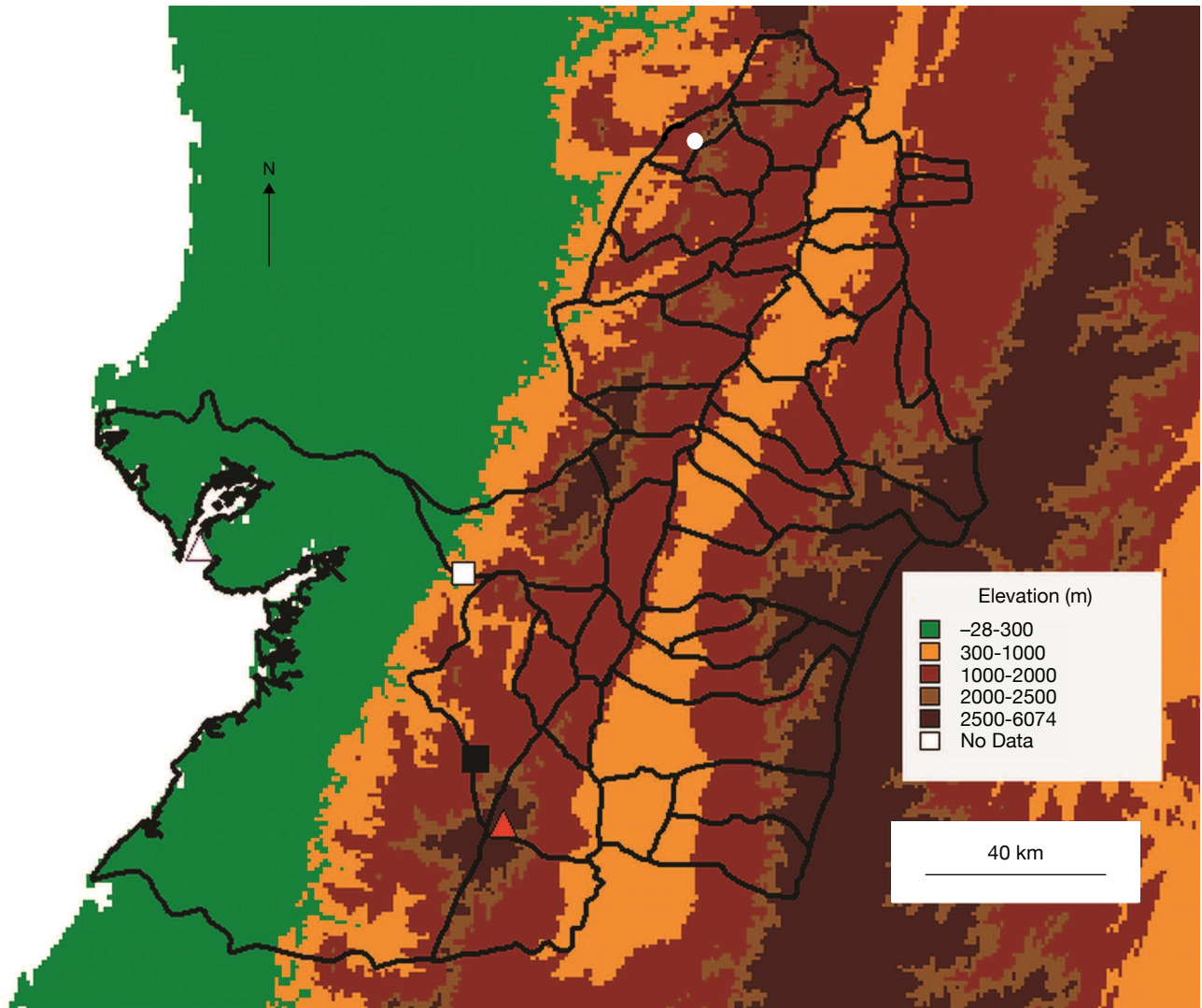


Fig. 1. — Map of the department of Valle del Cauca, Colombia, showing the sampling points: Δ , Chucheros; \square , Pericos; \blacksquare , El Queremal; \circ , Cerro El Inglés; \blacktriangle , Pico Pance.
1— please check location for Cerro El Inglés: brown 1000-2000 (on the map) vs 2250-2350 (in the table);
2— Confirm that the legend added on the map "Elevation " is OK

locality, where all corticolous lichens present in each tree up to 2 m high were collected. This method was also used in each of the Gentry transects used for vegetation. The abundance of each lichen species was estimated by the number of specimens collected (Sipman 1996; Cáceres *et al.* 2007).

To improve the estimation of the species richness of each locality (gamma diversity), climbing equipment was used to sample three vertical strata on five trees (i.e. high, medium, and low) (Komposch & Hafellner 2000; Boonpragob & Polyiam 2007). In each stratum, a strip of trunk 1 m high was sampled and the abundance of each species was estimated.

CLIMATIC PARAMETERS

Interpolated bioclimatic parameters for different areas based on records since 1950 were taken into account. These parameters correspond to mean annual precipitation, variability of

TABLE 1. — Sampling locations in the Chocó region of Valle del Cauca, Colombia.

Locality	Elevation (m)	Ecosystem	Natural reserve
Chucheros	35	Tropical rainforest	Uramba-Bahía Málaga
Pericos	655	Tropical rainforest	Pericos Reserve
El Queremal	1600	Premontane humid forest	Farallones de Cali
Cerro El Inglés	2250-2350	Montane forest	Serranía de los Paraguas Natural Reserve
Alto Pance	3650	subpáramo	Farallones de Cali

precipitation, mean annual temperature, and temperature variability. These data were taken from the WorldClim (Global Climate Data) databases (Hijmans *et al.* 2005). We also use cloud cover data such as Cloud Forest Prediction (CFP), Cloud

Cover Mean Annual (CCMA), Interannual Variability (IAV) and Spatial Variability (SV) (Wilson & Jetz 2016).

LICHEN FUNCTIONAL TRAITS

In this case, the characteristics of thallus (i.e. crustose, foliose, fruticose), photobiont (e.g., green algae, cyanobacteria), presence of rhizines, ascoma (i.e. apothecia, lirelae, perithecia), ascoma color, ascospore size (i.e. small <30 µm, large > 30 µm), ascospore septa (i.e. single, septate, muriform), ascospore color (hyaline, dark), ascospore wall thickness (i.e. thin, thick), isidia and soredia were recovered. These traits were determined based on literature or on the field samples. Based on these traits, we performed a detrended correspondence analysis (DCA) to establish the patterns of these traits together along the altitudinal gradient.

DATA ANALYSIS

Based on the information collected, alpha diversity (species richness by transect), beta diversity (Sørensen index) and gamma diversity (for locality) (McCune & Grace 2002) were estimated. Structural parameters (DBH, basal area, density and height) and richness of plant species were also estimated for each locality. Based on the data of the lichen and vegetation communities, and the climatic parameters, correlations (Spearman's correlation) were made to establish the factors determining the altitudinal patterns of species diversity (McCune & Grace 2002). For each locality, correlations were also made between vegetation parameters by transect, besides richness and abundance of lichens.

The sampling units (transects) were grouped *a priori* in open habitats (forest edge) or closed sites (forest interior). Thus, this variable was taken as a factor in the analysis of variance.

Given that there are strong differences in lichen abundance between localities, we decided to make a rarefaction to effectively compare the lichen richness between localities. Rarefaction has been shown as a good tool to compare the richness of species independently of abundance and thus better understand the patterns of species richness without effect of the number of individuals. The rarefaction was made with respect to the locality with the least number of samples (El Queremal) (Gotelli & Colwell 2001). To evaluate the sampling efficiency, the Jackknife estimator was used. These analyzes were carried out in the PAST® 4.0 software (Hammer *et al.* 2001).

We also assessed to what extent the Mid domain effect (MDE) could contribute to the observed richness patterns across the forest types using RANGEMODEL v.5 (Colwell 2005). We calculated empirical richness as interpolated richness, based on the assumption that each specie inhabited all sampling sites between its lowest and highest recorded occurrences regardless of whether or not it was recorded at all intermediate sites. Expected richness under the influence of MDE was generated by randomizing the placement of the complete set of empirical ranges along a continuous gradient, as suggested by McCain & Grytnes (2010) and Colwell & Lees (2000). We did Spearman's correlation

between the species richness observed, the empirical and the expected by MDE.

Non-metric multidimensional scaling (NMS) was used with the Sørensen index, since it takes into account the abundances of each lichen species (McCune & Grace 2002). This was done to establish changes in lichen composition along the altitudinal gradient. These analyzes were carried out in the PAST® 4.0 software (Hammer *et al.* 2001). An analysis of indicator species was also carried out to find the species with preference for an elevation zone (McCune & Grace 2002). The latter was made in PC-ORD® 5.0 (McCune & Mefford 2006).

The incidence of functional traits per sampling unit (community weight mean trait) in each locality also was estimated (Lavorel *et al.* 2008). These calculations were made with the F Diversity program (Casanoves *et al.* 2010). A correlation analysis was also carried out between the CWM of each trait, functional diversity and climatic and vegetation parameters. Additionally, detrended correspondence analysis was performed based on the incidence of traits per sampling unit. The DCA was performed to see the patterns of clustering of the elevations based on the features of the species. These analyzes were carried out in the Past software (Hammer *et al.* 2001).

Functional diversity was estimated using the relative Rao index (rRao) and Simpson functional dominance (D) taking into account all traits. The similarity measure used was Jaccard (Casanoves *et al.* 2010). These calculations were made with the FDiversity program (Casanoves *et al.* 2010). All parameters were compared using two-way ANOVA (Locality and Microhabitats). In each case, the sampling units within forest were considered as closed microhabitats, while those of forest edge as open habitats.

RESULTS

LICHEN DIVERSITY ALONG THE ALTITUDINAL GRADIENT

We found 2732 samples belonging to 690 species of corticolous lichens in all localities. The dominant families were Graphidaceae, Parmeliaceae, Lobariaceae and Pyrenulaceae. Graphidaceae showed the greatest richness in lower altitude zones; species richness in this family decreased with increasing altitude. On the other hand, the Parmeliaceae presented an opposite pattern, with a peak in Alto Pance (71 species) and without records in the lower zone. Lobariaceae showed greater diversity at 2300 m (Fig. 2). The greatest number of families was recorded in the middle of the altitude gradient, and decreased towards the extremes.

ALPHA, BETA AND GAMMA LICHEN DIVERSITY AND SPECIES RICHNESS ALONG THE GRADIENT

The sampling efficiency in each locality was high, between 79 and 84% (Table 2), thus giving good support to the ecological analyzes. Alpha lichen diversity showed a concave pattern with respect to altitude, and the zones at low and high elevations had greater diversity per unit of sampling (Fig. 3A). The localities of Pericos, El Queremal, and Cerro

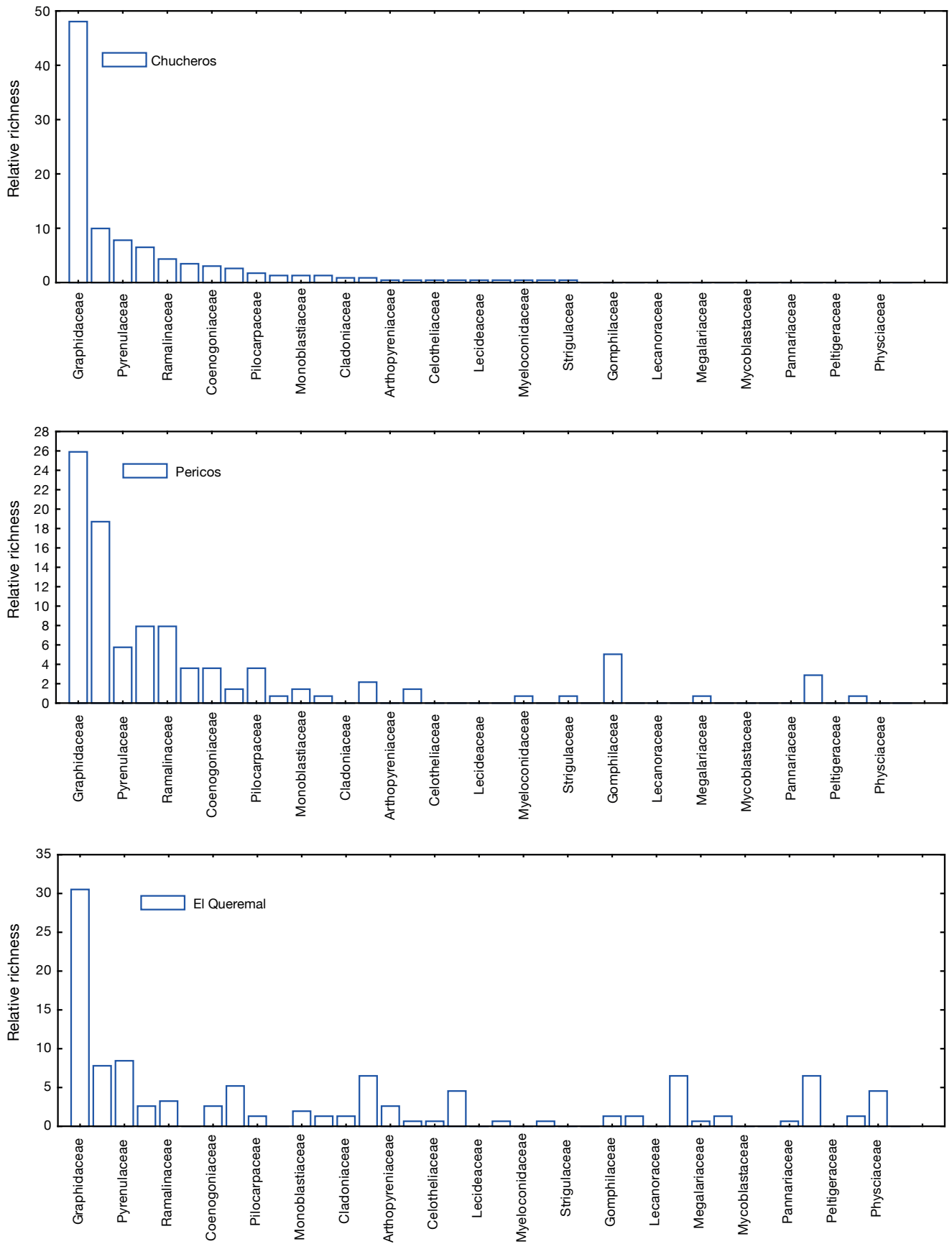


Fig. 2. — Number of species of the lichen families with higher diversity at each locality in the Chocó region of Valle del Cauca, Colombia.

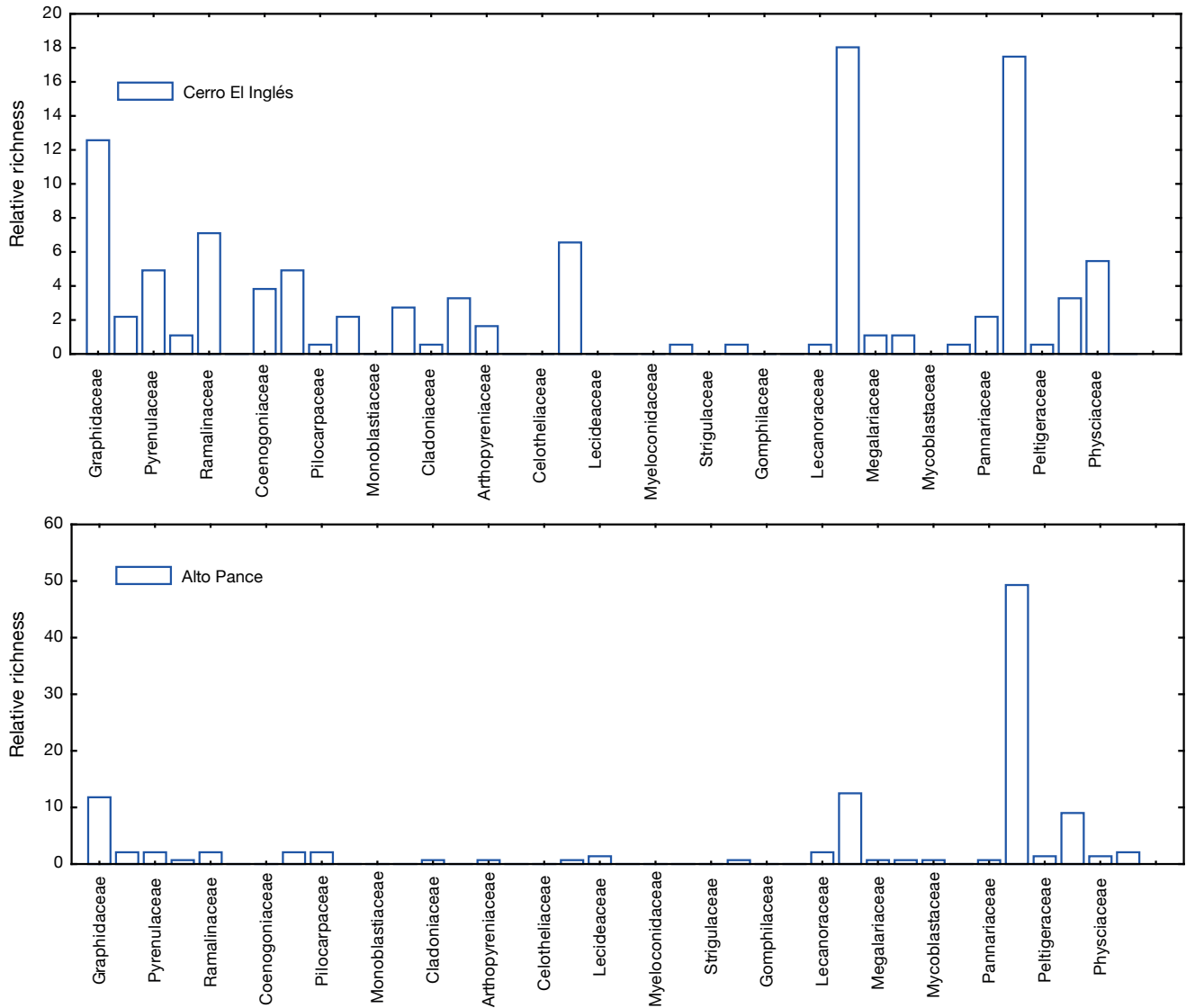


FIG. 2. — Continuation.

El Inglés did not show significant differences in alpha diversity, although Pericos presented the lowest value. It was also observed that microhabitat diversity (Forest edge vs. Forest interior) tended to be more different in intermediate altitude zones, whereas in the high and low elevation zones it tended to be similar (Fig. 3B).

In contrast, for beta lichen diversity the opposite pattern was found, with the highest values in El Queremal (1500 m) and lowest in low and high altitudes; the latter had the least beta diversity (Fig. 3C). When analyzing the beta diversity between altitudes, the pattern was of greater similarity between closer altitudes, and a decrease of similarity as the distance increased.

Gamma lichen diversity was highest at Chucheros (231 species), followed by Cerro El Inglés (183 species), and El Queremal (154 species). The observed richness (OR) showed a tendency to a decreasing pattern with altitude initially, although then, from 650 altitude, showed a bell-shaped pattern (Fig. 3D).

On the other hand, the result of rarefaction showed a non-symmetric bell-shaped species richness pattern, with a peak of richness near the middle of the domain (1600 m), and sites of lower elevation with greater species richness than those of higher elevation (Fig. 3D). The best model that explains species richness with respect to altitude was the quadratic model. Climatic variables and vegetation structure were correlated with lichen species richness. Thus, the diversity of lichens showed a pattern that fits the mid-domain effect model, contrary to what is shown by the species richness of trees (Moreno *et al.* 2018). Observed species richness (OR) by locality was not correlated with that estimated by the MDE model.

VEGETATION STRUCTURE AND DIVERSITY

The Chucheros locality had the greatest plant species richness and abundance with 472 individuals of 201 species, belonging to 34 families; 49 individuals from 37 different morphospecies could not be identified at the family level (Table 2). On

TABLE 2. — Environmental variables and lichen species richness by locality in the Chocó region of Valle del Cauca, Colombia.

Parameters	Chucheros	Pericos	El Queremal	Cerro El Inglés	Alto Pance
Elevation (m)	36.8	650	1573	2300	3650
Average annual temperature (°C)	25.9	24.6	20.2	17.8	12.3
Standard Temperature Deviation	307	281	313	235	175
Average annual precipitation (mm)	7.41	3423	1621	2479	2214
Standard deviation of average annual precipitation	33	28	33	27	36
Cloud forest Pred (CFP)	0.01	0.03	1.22	1.99	1.24
Mean Annual cloud (MACC)	77.2	91.7	96.5	95	89.7
IAV	8	6	3	4	7
Spatial variation cloud (SV)	8	8	10	10	11
Plant richness	201	154	98	99	27
Number of trees/0.1ha	472	345	329	371	312
Basal area (m ²)	5.98	5.03	3.70	8.90	0.93
Tree height (m)	9.5	7.6	10.3	11.1	3.1
Standard deviation of tree height	5.5	6.1	6.8	6.6	1
Lichen samples	737	364	345	502	784
Rarefied lichen richness	155	136	177	152	100
Observed lichen richness	231	139	154	183	144
Estimated lichen Richness (Jackknife)	282	174	196	229	171
Sampling efficiency (%)	82	80	79	80	84
Number of families	25	22	31	28	26

the other hand, El Queremal and Cerro El Inglés had similar richness and abundance, with 329 individuals of 98 species and 31 families in El Queremal, and 371 individuals of 99 species and 33 families in Cerro El Inglés.

The majority of the individuals were trees or shrubs; only ten lianas were recorded in Chucheros (2.1%), eight in El Queremal (2.4%), and four in Cerro El Inglés (1%). Cerro El Inglés had the highest value of basal area with 8.90 m², followed by Playa Chucheros with 5.98 m², Pericos 5.03 m², El Queremal 3.70 m², and Alto Pance 0.929 m².

RELATIONSHIP OF LICHEN DIVERSITY, VEGETATION STRUCTURE, AND CLIMATE

Alpha lichen diversity was higher at the altitudinal extremes, and at these extremes showed a strong correlation with the vegetation structure. In the locality of Chucheros (36 m), the species richness of lichens was negatively correlated with the density of trees (Fig. 4). An opposite pattern was found in Alto Pance, with a positive correlation between lichen species richness and tree density and DBH. This suggests that in areas of low elevation, the increase in tree density decreases the lichen species richness, while the opposite happens in high elevation sites, the increase in tree density and DBH increases lichen species richness. Plant richness was negatively related to altitude and positively related to temperature (Table 3).

Total lichen diversity observed and estimated by locality was positively related to the number of trees/0.1ha (Table 3). Lichen diversity also had a high relation to plant species richness and the average annual precipitation, although the relation was not significant. Lichen species richness corrected through rarefaction was only correlated with the standard deviation of temperature. Species richness estimated by the MDE model was correlated with CCMA and IAV (Table 3).

LICHEN SPECIES COMPOSITION

Species composition was statistically different among the five localities (MRPP, $p < 0.05$), although El Queremal showed slight overlap with Pericos and Cerro El Inglés (Fig. 5A). The clustering at the highest locality was more compact, whereas that of the Cerro El Inglés was looser. There were 148 indicator species, 72 in Alto Pance (50%), 28 in Chucheros (12%), 22 in El Queremal (14%), 17 in Cerro El Inglés (9%), and nine in Pericos (6%). These results suggest a marked change in the composition of lichens along the altitudinal gradient and a higher frequency of indicator species in the highest locality (Table 4).

LICHEN FUNCTIONAL TRAITS AND FUNCTIONAL DIVERSITY ALONG THE ALTITUDINAL GRADIENT

When analyzing the lichen functional traits along the altitudinal gradient, several patterns were observed. In terms of growth forms, it was found that the crustose forms were dominant at low elevations, and their importance decreased with altitude (Fig. 6). On the other hand, foliose and fruticose forms gained dominance as the elevation increased. At the locality at 2300 m, foliose lichens were more abundant.

The incidence of rhizines increased with increasing altitude, and they were more common in open sites; it is important to note that although this trait is associated mainly with foliose lichens, it was not correlated with the incidence of this type of thallus (Fig. 6C, F). The abundance of cyanolychens showed an increase with altitude up to 2300 m, and decreased again to 3600 m. The presence of cyanobacteria did not show significant differences among microhabitats, although in Cerro El Inglés it tended to be greater in closed sites.

Regarding the reproductive traits, the incidence of soredia did not show significant differences between altitudes, although it showed a tendency to increase with increase in altitude. *Isidia* were more frequent at 650 m, coinciding with the

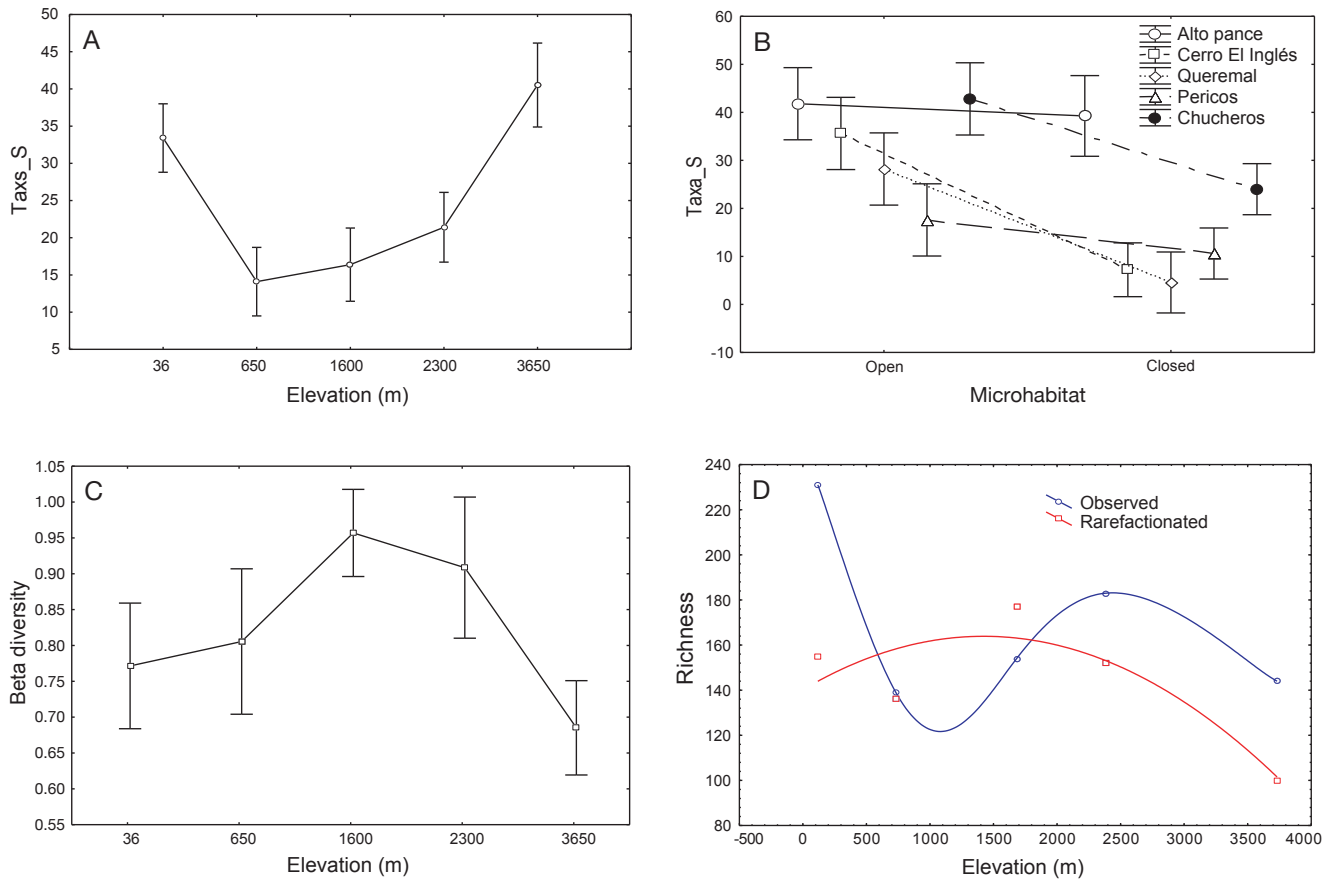


Fig. 3. — Lichen diversity and vegetation richness in the Chocó region of Valle del Cauca, Colombia: **A**, mean and standard error for alpha lichen diversity along the altitudinal gradient; **B**, mean and standard error for alpha lichen diversity by locality and microhabitat; **C**, beta lichen diversity; **D**, total lichen species richness (observed and rarefied) by locality.

strong influence of the family Arthoniaceae and Roccellaceae in this locality (mainly represented by the genus *Herpothallon* and *Dichosporidium*). The incidence of apothecia was higher at 2300 m, and tended to be higher in closed microsites. The CWM of lirelae did not show differences with altitude, although in the locality of Chucheros they were more frequent in open places. The occurrence of perithecia was higher in Chucheros and El Queremal, and was more frequent in closed microsites in the latter. At low-altitude locations (36 and 650 m), the abundance of dark-colored as compared to light-colored ascomas tended to be lower, while in the higher elevation zones, the opposite occurred.

The relative frequency of simple vs. septate or muriform ascospores showed that the latter tend to decrease with increasing elevation, whereas simple ascospores increased with altitude. The size of the ascospores presented a pattern of higher incidence of small spores compared to large ones at low to medium elevations (0-1600 m), while at higher elevations large spores were dominant. On the other hand, the frequency of septate/muriform spores was greater than that of simple spores at almost all elevations, but the pattern was reversed in the highest locality. The incidence of thick ascospore walls was greater than that of thin walls at lower and higher elevations.

The incidence of traits was correlated with the climatic parameters. The CWM of crustose was strongly correlated with average annual temperature (+), average annual precipitation (+), cloud forest predicted (-) and spatial variation (-) (Table 5), pattern opposite to that shown by fruticose lichens. Gelatinous, rhizines, light ascomata, dark ascomata, hyaline ascospores dark ascospores, thin ascospores wall, thick ascospores wall, muriform ascospores and septate ascospores showed correlations with the climatic variables (Table 5).

The DCA result (Fig. 5B) showed that the sampling units at each altitude are grouped per trait composition, with overlap between the two lowest elevation locations and between the two locations at 1600 and 2300 m. The locality at the highest altitude was separated from the other localities. In this way, the functional traits were markedly different for Alto Pance, while in the other localities there was a slight overlap, although a clear gradient was observed from low to high elevations, showing a high degree of replacement in the traits used.

The functional diversity presented higher values at 1500 m, and decreased towards the extremes (Fig. 7A). This pattern coincides with that shown by the richness corrected for rarefaction and with beta diversity (Fig. 3). In contrast, the functional dominance was greater in altitudinal extremes (Fig. 7B), indicating that in these areas there is less functional diversity

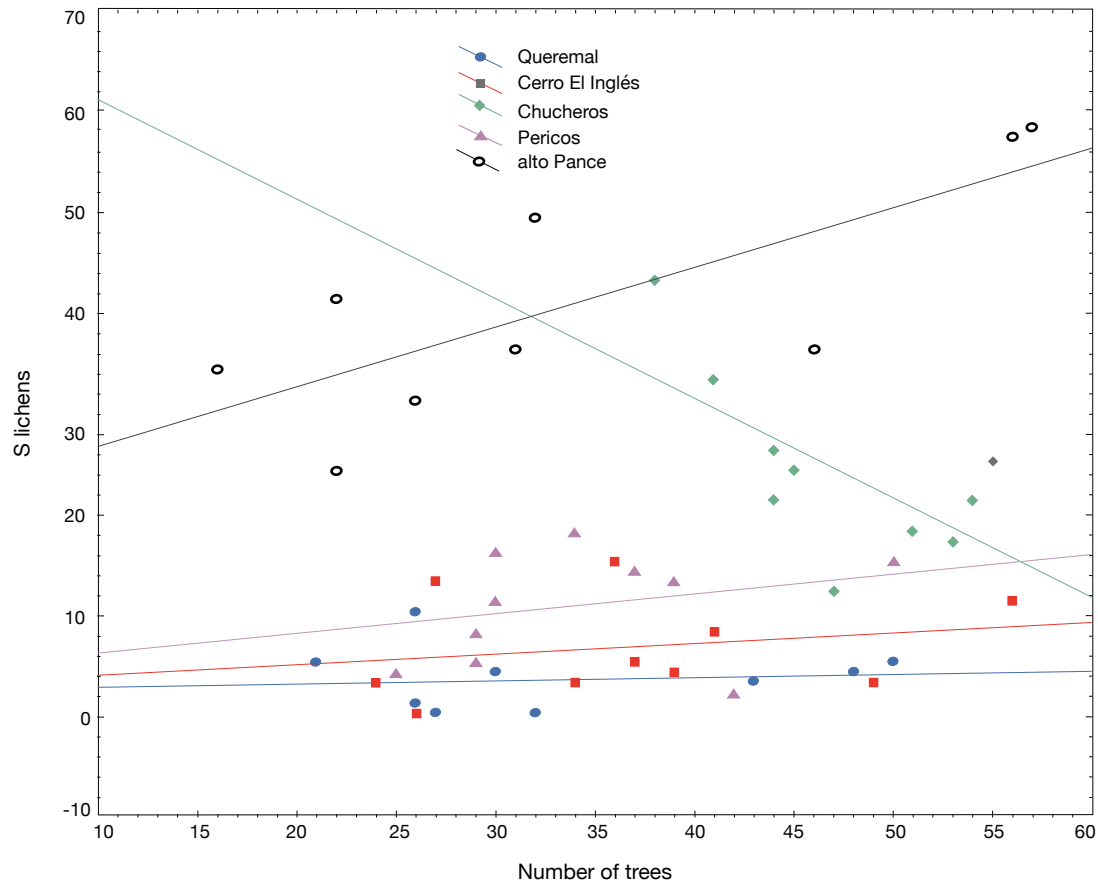


Fig. 4. — Scatter plot for the alpha lichen diversity and tree density ratio in each study site in the Chocó region of Valle del Cauca, Colombia.

and high redundancy of traits. The Rao index was correlated with the estimated richness due to rarefaction.

DISCUSSION

LICHEN DIVERSITY ALONG THE ALTITUDINAL GRADIENT

In total, 689 species of lichens were found throughout the altitudinal gradient, with greatest richness at Chucheros (250 species, 36 m altitude) and lowest value at Pericos (139 species, 650 m altitude). Compared to other tropical regions, the Chocó biogeographic region of the department of Valle del Cauca has a very high diversity of lichens, with Chucheros being one of the most widely reported sites (Wolf 1993; Komposch & Hafellner 2000; Holz 2003; Nöske 2004; Cáceres *et al.* 2007). In the most recent list of lichens for Colombia, about 1350 species are recorded (Bernal *et al.* 2015), which shows the great diversity of lichens found in this study.

The dominant families in this study (Graphidaceae, Parmeliaceae, Arthoniaceae, Lobariaceae, and Trypetheliaceae) are the families with the greatest species richness in the world (Lücking *et al.* 2009b; Lücking *et al.* 2016). Other studies have found that the families Graphidaceae, Arthoniaceae, Pyrenulaceae, and Trypetheliaceae are the dominant elements in low elevation forests with dry and very humid tropical forests, whereas the families Parmeliaceae, Lobariaceae, Ramalinaceae,

Hygrophoraceae, Arthoniaceae, and Pyrenulaceae, are more frequent in montane forests at higher elevations (Hekking & Sipman 1988). This can be explained because at low elevations there is higher solar radiation and high humidity, which does not favor the presence of foliose or fruticose lichens, whose thallus will be supersaturated with water, inhibiting photosynthesis. On the other hand, crustose lichens exhibit strategies to avoid supersaturation and can survive in these high humidity environments (Lakatos *et al.* 2006).

Alpha lichen diversity showed the highest values at the altitudinal extremes, while beta diversity was highest in the premontane and montane areas. Thus, at the low and high elevations, gamma lichen diversity was more influenced by alpha diversity, while in the intermediate zones, gamma diversity was more influenced by beta diversity. This is because at the altitudinal extremes there is high irradiance, which favors a high abundance of lichen thalli (these sites had highest abundance) in both open and closed sites. This increases the probability of species overlap. On the other hand, in montane sites there is high cloudiness, which allows a high coverage of bryophytes. This limits the abundance of lichens, which increases the exchange of species between borders and forest interior (Wilson & Jetz 2016). However, in montane sites, lichen richness in open sites is high and together with the high turnover of species causes high gamma diversity.

TABLE 3. — Spearman correlations among environmental variables, lichen species richness and functional diversity in the Chocó region of Valle del Cauca, Colombia. Significant correlations are marked with *.

	Observed lichen richness	Rarefied	Rao	Empirical richness of lichens	Expected richness MDE	Plant richness	Tree height	Tree number/0.1ha	Basal area
Cloud forest Pred	-0.1	-0.3	0.1	-0.1	0.36	-0.7	0.3	-0.4	0
Mean Annual cloud IAV	-0.2	0.4	0.7	-0.2	0.97*	-0.4	0.6	-0.3	0
Spatial variation	0.2	-0.4	-0.7	0.2	-0.97*	0.4	-0.6	0.3	0
Elevation	-0.16	-0.32	-0.11	-0.16	0.08	-0.95*	-0.11	-0.74	-0.53
Observed lichen richness	-0.3	-0.5	-0.2	-0.3	0.1	-0.90*	-0.1	-0.7	-0.4
Rarefied lichen species richness		0.6	0.5	1.00*	-0.05	0.4	0.6	0.7	0.6
Rao	0.23		0.9*	0.6	0.56	0.3	0.7	0.4	0.3
Empirical richness of lichens	0.45	0.02		0.5	0.82	0.1	0.90*	0.3	0.4
Expected richness MDE	0.02	0.23	0.45		-0.05	0.4	0.6	0.7	0.6
Temperature media anual	-0.1	0.46	-0.21	-0.5		-0.21	0.72	-0.1	0.15
Temperature SD	0.3	0.5	0.2	0.3	-0.1	0.90*	0.1	0.7	0.4
Temperature media anual	0.3	0.9*	0.7	0.3	0.46	0.4	0.4	0.3	0.1
Precipitacion SD	0.4	0.3	0.1	0.4	-0.21	1.00*	0.2	0.90*	0.7
Plant richness	-0.1	-0.15	-0.41	-0.1	-0.5	-0.46	-0.67	-0.56	-0.82
Tree height	-0.1	0.46	-0.21	-0.5	0.73		0.2	0.90*	0.7
Tree number/0.1ha	0.23	0.23	0.02	0.23	0.17	0.68		0.5	0.7
Basal area	0.23	0.45	0.52	0.23	0.90*	0.02	0.45		0.90*
	0.23	0.52	0.45	0.23	0.83	0.23	0.23	0.02	

VEGETATION STRUCTURE AND DIVERSITY

In previous works with birds (Kattan & Franco 2004) and plants (Gentry 1982; Givnish 1999), a decreasing pattern of richness with altitude in the Chocó biogeographic region was found. To explain this pattern, several hypotheses have been proposed, such as the mass effect (Shmida & Wilson 1985) or dynamic sink source (Pulliam 1988), the species-area relationship (Rosenzweig 1995), gradual climate change (Sanders 1968; Palmer 1994), and primary productivity at low to high elevations. In this study, the same pattern was found for arboreal vegetation, and was strongly related to temperature and elevation. In the tropics, a consistent pattern is the decrease of temperature with altitude, but precipitation shows different patterns, depending on the mountain system. In Colombia, precipitation may have a unimodal pattern in the inter-Andean valleys, while, in the regions near the Amazon and Chocó biogeographic regions, it presents a decreasing pattern with altitude. Thus, in these regions a pattern of high precipitation and high temperatures in the lower elevations is expected, which would imply a higher primary productivity in these sites compared to the higher areas of low temperatures and precipitation. Thus, the pattern of tree vegetation richness along the altitudinal gradient could be explained by the hypotheses of gradual climate change and primary productivity, since the species richness is concentrated in more stable and more productive climatic zones. Because this work was carried out through standardized sampling, the area has no effect on the richness pattern (Gotelli & Colwell 2001; Grytnes & Vetaas 2002; McCain & Grytnes 2010).

Contrary to what was seen in plants, the observed and estimated total richness of corticolous lichens by locality presented a peak at the lowest elevation, but then behaved in quadratic form with a richness peak at 2300 m of altitude. The richness of lichens showed a high correlation with

the number of trees per locality and was highly correlated with the average precipitation and the diversity of trees, but was not significant. This suggests that the total diversity of lichens is influenced by the number of trees, which in turn is influenced by precipitation. However, after rarefaction, lichen species richness showed an asymmetric unimodal pattern, and it was related to the mean tree height and the standard deviation of temperature. The rarefaction allows effective comparison the diversity between sites when there is too much discrepancy between abundances (Gotelli & Graves 1996). In this case, some sites duplicate the number of samples from other sites, so the rarefaction would be well justified. Many authors suggest that lichen richness presents a pattern that fits a bell, with a peak at the midpoint of the altitudinal gradient (Wolf 1993; Wolseley & Aguirre-Hudson 1997; Negi 2000; Pinokiyo *et al.* 2008; Baniya 2010; Rai *et al.* 2014). The underlying mechanism that explains this pattern has been the mid-domain effect. This hypothesis states that, in an altitudinal range, there are strong barriers or constrictions at the ends of the range, which causes a peak of richness to occur in the middle of the domain (Colwell & Lees 2000; Zapata *et al.* 2005). However, in this case we did not obtain support for this hypothesis since the MDE Model did not adjust to the observed richness pattern.

RELATIONSHIP OF LICHEN DIVERSITY, VEGETATION STRUCTURE, AND CLIMATE

In this case, the data suggest that temperature, precipitation and cloud cover structure the asymmetric bell-like richness pattern: that is, at low elevations the species richness is higher than in the high ones, given that there is a higher temperature and humidity. On the other hand, towards the middle of the gradient, the highest levels of cloud cover and intermediate values of temperature and precipitation occur, which allows

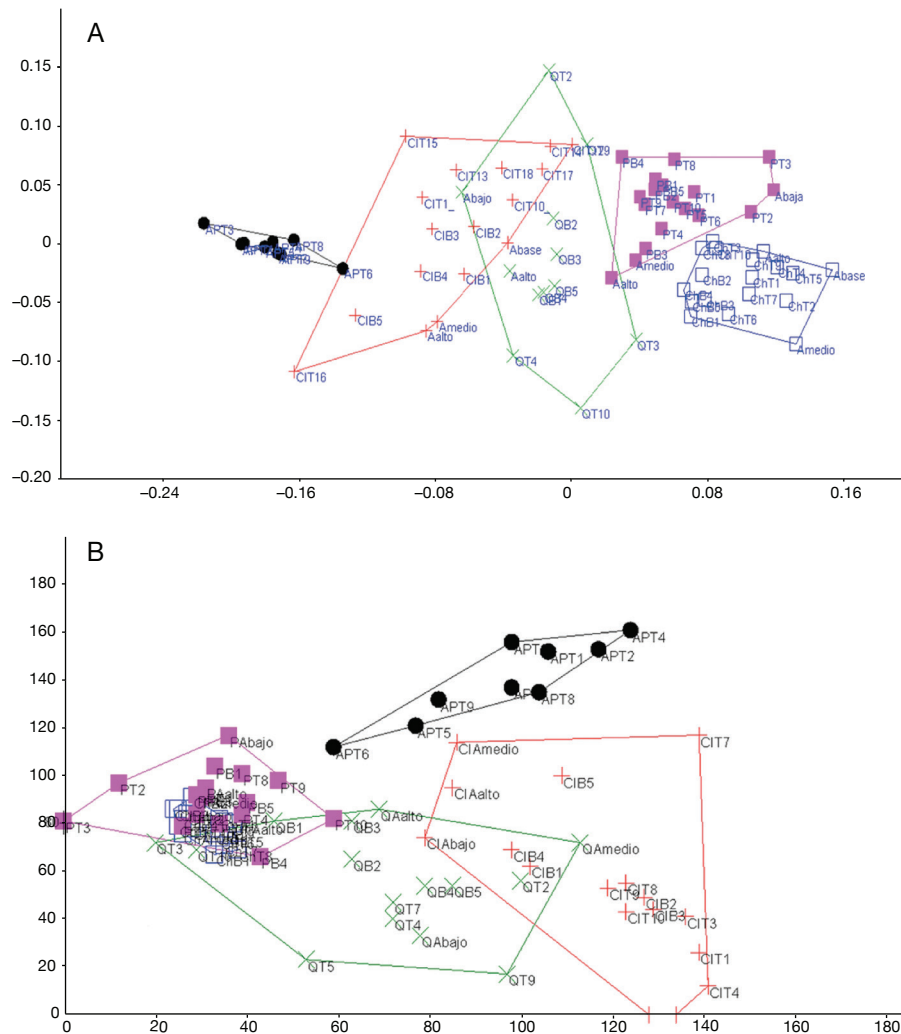


Fig. 5. — **A**, non-metric multidimensional scaling for composition of lichen species along the gradient (Stres=0.21); **B**, detrended correspondence analysis for the lichen functional traits along the gradient. In both graphs there is a clear separation between elevations, showing a gradient of species composition and functional traits along the altitudinal gradient. Locations: ●, Alto Pance; +, Cerro El Inglés; ×, El Queremal; ■, Pericos; □, Chucheros.

a greater number of functional and taxonomic groups to occur, which would explain the greater richness of species at this point of the altitudinal gradient.

LICHEN SPECIES COMPOSITION

With regard to species composition, a marked change of species was observed along the altitudinal gradient. It was also found that the samples of Alto Pance were different from the other of localities. This suggests that the altitudinal gradient and the subsequent environmental gradient have a strong role structuring of lichen communities. This also occurs in other groups of fungi (Geml *et al.* 2017). In lichenized fungi, this effect may be more pronounced due to the microenvironmental preferences of many lichen species (Soto-Medina *et al.* 2012; Benítez *et al.* 2012). The high number of indicator species in the zone of higher elevation indicates that the species of this zone are unique and have particular requirements at this locality. This high number of indicator species in Alto Pance

also implies that these high altitudinal regions will be the most affected by global climate change.

LICHEN FUNCTIONAL TRAITS AND FUNCTIONAL DIVERSITY ALONG THE ALTITUDINAL GRADIENT

Functional lichen traits showed several patterns along the altitudinal gradient. The abundance of crustose thalli decreased with altitude, but the abundance of foliose and fruticose thalli increased. As mentioned previously, crustose lichens have adaptations to the high humidity conditions of low elevations and can photosynthesize using low light intensity that enters the forests (Lakatos *et al.* 2006). On the other hand, foliose lichens begin to dominate with higher altitude, because they no longer have problems of water supersaturation and can outcompete crustose lichens because their thalli are larger (Sipman 1996; Lakatos *et al.* 2006). In addition, the increase of mist favors the growth of foliose lichens because of their three-dimensional morphology (Stanton & Horn 2013; Stanton 2015). Fruticose growth forms, in well-lit higher

TABLE 4. — Indicator lichen species ($p < 0.05$) by locality in the Chocó region of Valle del Cauca, Colombia.

Locality		Indicator Species	
Chucheros (35 m)	Arthoniaceae	<i>Herpothallon roseocinctum</i> , <i>Herpothallon</i> sp. 2	
	Graphidaceae	<i>Ampliotrema palaeoamplius</i> , <i>Chapsa alborosella</i> , <i>Chapsa defectosorediata</i> , <i>Chapsa lassae</i> , <i>Chapsa platycarpella</i> , <i>Fissurina chroodiscoides</i> , <i>Fissurina dumastii</i> , <i>Graphis oxyclada</i> , <i>Graphis sitiana</i> , <i>Gyrotrema álbum</i> , <i>Myriotrema pulverulentum</i> , <i>Ocellularia crocea</i> , <i>Ocellularia mauritiana</i> , <i>Ocellularia perforata</i> , <i>Ocellularia vezdana</i> , <i>Ocellularia volcanisorediata</i> , <i>Stegobolus auberianus</i> , <i>Stegobolus granulatus</i> , <i>Wirthotrema glaucopallens</i> .	
	Myeloconidiaceae	<i>Myeloconis guyanensis</i>	
	Porinaceae	<i>Porina imitatrix</i>	
	Pyrenulaceae	<i>Pyrenula santensis</i> , <i>Pyrenula</i> sp.	
	Ramalinaceae	<i>Eschatogonia prolifera</i>	
	Trypetheliaceae	<i>Trypethelium nitidiusculum</i>	
Pericos (655 m)	Arthoniaceae	<i>Cryptothecia striata</i> , <i>Herpothallon aurantiacoflavum</i> , <i>Herpothallon</i> sp. 13, <i>Herpothallon</i> sp. 14, <i>Herpothallon</i> sp. 5, <i>Neosergipea</i> sp.	
	Coenogoniaceae	<i>Coenogonium linkii</i>	
	Ramalinaceae	<i>Phyllopsora nigrocincta</i>	
	Roccellaceae	<i>Dichosporidium nigrocinctum</i>	
El Queremal (1600 m)	Arthoniaceae	<i>Herpothallon</i> sp. 8	
	Collemataceae	<i>Leptogium azureum</i>	
	Coccocarpiaceae	<i>Coccocarpia domingensis</i> , <i>Coccocarpia erythroxyli</i> , <i>Coccocarpia microphyllina</i>	
	Coenogoniaceae	<i>Coenogonium disjunctum</i>	
	Gomphillaceae	<i>Gomphillus hyalinus</i>	
	Graphidaceae	<i>Clandestinotrema leucomelaenum</i> , <i>Graphis angustata</i> , <i>Graphis flavominiata</i> , <i>Graphis sarawakensis</i> , <i>Graphis</i> sp., <i>Graphis subchrysocharpa</i> , <i>Graphis virescens</i> , <i>Phaeographis brasiliensis</i> , <i>Phaeographis intricans</i>	
	Hygrophoraceae	<i>Cora bovei</i> , <i>Dictyonema</i> sp. 3	
	Lobariaceae	<i>Sticta arbuscula</i> , <i>Sticta luteola</i>	
	Physciaceae	<i>Heterodermia reagents</i>	
	Ramalinaceae	<i>Eugeniella ortizii</i>	
Cerro El Inglés (2300 m)	Arthoniaceae	<i>Crocodia aurata</i>	
	Collemataceae	<i>Leptogium</i> sp. 2, <i>Leptogium</i> sp. 3, <i>Leptogium</i> sp. 9	
	Graphidaceae	<i>Graphis argentata</i> , <i>Phaeographis</i> sp.	
	Megalosporaceae	<i>Megalospora tuberculosa</i>	
	Lobariaceae	<i>Sticta</i> aff. <i>venosa</i> , <i>Sticta cometia</i> , <i>Sticta granatensis</i> , <i>Sticta lumschiana</i> , <i>Sticta subfilicinella</i> , <i>Sticta venosa</i>	
	Parmeliaceae	<i>Hypotrachyna flavovirens</i>	
	Pannariaceae	<i>Pannaria andina</i>	
	Physciaceae	<i>Heterodermia</i> sp. 2, <i>Heterodermia</i> sp. 3	
Alto Pance (3650 m)	Arthoniaceae	<i>Arthonia</i> sp. 2	
	Corticaceae	<i>Acantholichen variabilis</i>	
	Graphidaceae	<i>Clandestinotrema clandestinum</i> , <i>Graphidaceae</i> sp., <i>Graphis dupaxana</i> , <i>Graphis snudaeformis</i> , <i>Graphis</i> sp. 4, <i>Graphis</i> sp. 2, <i>Ocellularia</i> sp., <i>Reimnitzia</i> sp., <i>Thelotrema diplotrema</i>	
	Hygrophoraceae	<i>Cora</i> sp. 2, <i>Corella</i> sp.	
	Lecanoraceae	<i>Lecanora</i> sp. 1, <i>Lecanora</i> sp. 2	
	Lecideaceae	<i>Lecidea lactea</i> , <i>Lecidea</i> sp.	
	Lobariaceae	<i>Sticta</i> sp.	
	Megalariaceae	<i>Megalaria</i> sp. 1	
	Parmeliaceae	<i>Anzia leucobates</i> , <i>Everniastrum catawbiense</i> , <i>Everniastrum columbiense</i> , <i>Everniastrum fragile</i> , <i>Everniastrum lipidiferum</i> , <i>Everniastrum sorocheilum</i> , <i>Hypotrachyna andensis</i> , <i>H. costaricensis</i> , <i>H. degelii</i> , <i>H. densirhizinata</i> , <i>H. gondylophora</i> , <i>H. lopezii</i> , <i>H. paramense</i> , <i>H. prolongata</i> , <i>H. reducens</i> , <i>H. sinuosa</i> , <i>Oropogon bicolor</i> , <i>Oropogon herzogii</i> , <i>Oropogon lopezii</i> , <i>Oropogon loxensis</i> , <i>Rimelia</i> sp., <i>Usnea ceratina</i> , <i>U. chaetophora</i> , <i>U. cornuta</i> , <i>U. cornuta</i> 2, <i>U. cornuta</i> 3, <i>U. diplotypus</i> , <i>U. esperantiana</i> , <i>U. fragileszens</i> , <i>U. rubicunda</i> , <i>U. scabrata</i> , <i>U. sp.</i> , <i>U. subfloridana</i> , <i>U. wasmuthii</i>	
		Pertusariaceae	<i>Pertusaria</i> sp. 16, <i>Pertusaria</i> sp. 10, <i>Pertusaria</i> sp. 11, <i>Pertusaria</i> sp. 12, <i>Pertusaria</i> sp. 14, <i>Pertusaria</i> sp. 15, <i>Pertusaria</i> sp. 7, <i>Pertusaria</i> sp. 8, <i>Pertusaria</i> sp. 9
		Physciaceae	<i>Heterodermia podocarpa</i>
		Pyrenulaceae	<i>Pyrenula dermatodes</i> , <i>Pyrenula</i> sp. 5
		Ramalinaceae	<i>Phyllopsora</i> sp. 3, <i>Ramalina usnea</i>
		Sphaerophoraceae	<i>Bunodophoron melanocarpum</i> , <i>Bunodophoron</i> sp.
		Trypetheliaceae	<i>Pseudopyrenula media</i>
	Verrucariaceae	<i>Normandina pulchella</i>	

elevations, have the advantage of being able to use light from all directions better than foliose lichens, which can maximize

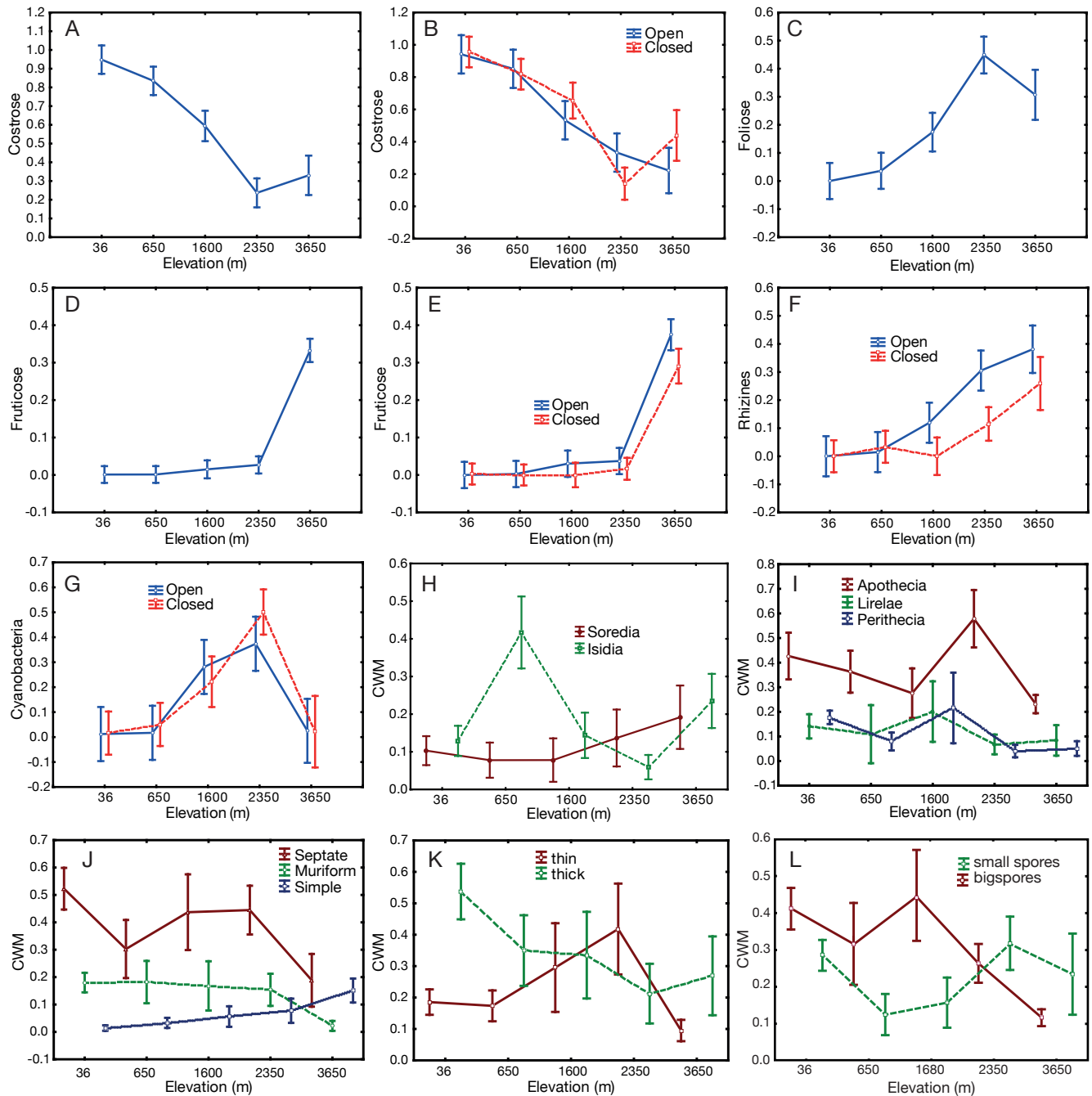


Fig. 6. — Community Weighted Means (CWMs) of functional lichen traits along the altitudinal gradient in the Chocó region of Valle del Cauca, Colombia: A, crustose thallus; B, crustose thallus by microhabitat; C, foliose thallus; D, fruticose thallus; E, fruticose thallus by microhabitat; F, rhizines by microhabitat; G, cyanobacterial photobiont; H, vegetative propagules; I, ascoma; J, ascospore septation (septate, muriform and simple); K, thickness of the ascospore wall; L, size of the ascospores.

the harvest of more or less unidirectional light (Gauslaa *et al.* 2009). Moreover, the dissected fruticose lichens have a high surface area: volume ratio, making them more closely coupled to ambient atmosphere than flat foliose lichens, and they absorb moisture more readily from air (Baniya 2010). This argument also explains the greater frequency of fruticose thalli in open sites.

Rhizines were more abundant at high elevations. This can be due to the fact that these structures allow the capture of

atmospheric water, and as altitude increases, precipitation decreases, so the presence of rhizines would favor obtaining the scarce water that lichens need for photosynthesis (Stanton & Horn 2013). The occurrence of rhizines was much higher in open sites, where there is a higher intensity of light and low humidity, so rhizines could allow lichens to survive in these microhabitats. The frequency of cyanolichens was higher at 2300 m and was lower in low and high elevation areas. This can be related to the fact that these lichens require high

TABLE 5. — Spearman correlations for lichen traits, diversity (functional and taxonomic) and climatic parameters in the Chocó region of Valle del Cauca, Colombia. Significant correlations and highly significant correlations are marked respectively * and **.

	Average annual temper- ature	Temper- ature Season- ality	Average annual precip- itation	Standard deviation of precip- itation	Plant richness	Rao	Cloud forest Pred	Mean Annual cloud	IAV	Spatial variation	Altitud
Plant	0.90*	0.40	1.00*	-0.46	0.00	0.78**	-0.70	-0.40	0.40	-0.95	-0.90
Richness											
Rao	0.20	0.70	0.10	-0.41	0.10	0.00	0.10	0.70	-0.70	-0.11	-0.20
Crustose	1.00*	0.70	0.90*	-0.21	0.90*	0.20	-0.90	-0.30	0.30	-0.95	-1.00
Dimorphic	-0.35	0.00	-0.35	0.36	-0.35	0.35	0.35	0.00	0.00	0.56	0.35
Squamulose	0.00	0.53	-0.16	-0.46	-0.16	0.74**	0.21	0.95	-0.95	-0.03	0.00
Filamentose	0.46	0.82*	0.21	-0.34	0.21	0.67	-0.31	0.67	-0.67	-0.43	-0.46
Foliose	-0.60	-0.10	-0.50	-0.21	-0.50	0.60	0.80	0.60	-0.60	0.63	0.60
Fruticose	-0.80*	-0.30	-0.90*	0.62	-0.90*	0.00	0.60	0.20	-0.20	0.95	0.80
Gelatinous	-0.22	0.45	-0.34	-0.29	-0.34	0.89*	0.45	0.89	-0.89	0.29	0.22
Rhizines	-1.00*	-0.70**	-0.90*	0.21	-0.90*	-0.20	0.90	0.30	-0.30	0.95	1.00
Soredia	-0.67	-0.15	-0.56	-0.29	-0.56	0.56	0.87	0.72	-0.72	0.65	0.67
Isidia	0.05	0.21	-0.21	0.08	-0.21	-0.15	-0.21	0.36	-0.36	-0.11	-0.05
Apothecia	0.10	0.40	0.20	-0.67	0.20	0.90*	0.30	0.60	-0.60	-0.11	-0.10
Lirelae	0.21	0.74**	0.05	-0.14	0.05	0.95*	0.00	0.53	-0.53	-0.03	-0.21
Perithecia	0.70**	1.00*	0.40	-0.05	0.40	0.70**	-0.60	0.30	-0.30	-0.53	-0.70
Light ascomata	1.00*	0.70**	0.90*	-0.21	0.90*	0.20	-0.90	-0.30	0.30	-0.95	-1.00
Dark ascomata	-0.20	0.20	-0.10	-0.36	-0.10	0.80	0.50	0.50	-0.50	0.26	0.20
Hyaline ascospores	0.60	0.50	0.70**	-0.41	0.70**	0.60	-0.30	-0.10	0.10	-0.53	-0.60
Dark ascospores	-0.10	0.50	-0.20	-0.10	-0.20	0.90*	0.30	0.60	-0.60	0.26	0.10
Thin ascospores wall	0.10	0.40	0.20	-0.67	0.20	0.90	0.30	0.60	-0.60	-0.11	-0.10
Thick ascospores wall	0.90*	0.90*	0.70**	-0.05	0.70**	0.50	-0.80	-0.10	0.10	-0.74	-0.90
Muriform ascospores	0.10	0.60	0.00	-0.56	0.00	0.90	0.20	0.90	-0.90	-0.11	-0.10
Septate ascospores	0.67	0.67	0.67	-0.29	0.67	0.67	-0.41	-0.05	0.05	-0.54	-0.67
Simple ascospores	0.00	0.10	0.20	-0.36	0.20	0.60	0.30	0.10	-0.10	0.05	0.00
Small ascospores	0.70**	1.00*	0.40	-0.05	0.40	0.70*	-0.60	0.30	-0.30	-0.53	-0.70
Longer ascospores	-0.10	0.50	-0.20	-0.10	-0.20	0.90*	0.30	0.60	-0.60	0.26	0.10
Cyanobacteria	-0.67	-0.15	-0.56	-0.29	-0.56	0.56	0.87	0.72	-0.72	0.65	0.67
Chlophyta	0.70*	0.20	0.60	0.36	0.60	-0.50	-0.90	-0.80	0.80	-0.63	-0.70
Rarefied lichen richness	0.50	0.90*	0.30	-0.15	0.30	0.90*	-0.30	0.40	-0.40	-0.32	-0.50

humidity and low luminosity conditions in montane forests, especially in the forest interior (Lakatos *et al.* 2006; Rai *et al.* 2014, Soto-Medina *et al.* 2015). On the other hand, at low elevations, higher temperatures reduce the presence of cyanolichens, whereas at high elevations there is a high intensity of light because of low forest cover, which is a limiting factor for this type of lichens.

Regarding the characteristics of the ascospores, it was found that, at low elevations, septate ascospores are more common, whereas, at high elevations, simple ascospores are more common. The size of the ascospore also showed a contrasting pattern, with a higher abundance of small spores at low elevations. This can be explained by considering that larger ascospores have less

dispersal capacity (Gregory 1961); thus at high elevation sites with lower forests and a more open canopy, large ascospores are more abundant. In addition, a large ascospore has a low volume: area ratio, which minimizes the damage produced by prolonged desiccation (Pentecost 1981). Another adaptation of the large ascospores is that they contain more nutritional reserves, which allow them to survive longer than smaller spores. In contrast, in low-elevation forests, the canopy is more closed and there is a greater number of individuals and tree species, which causes greater competition. In this habitat, the strategy is to produce a greater number of propagules by means of septate or muriform spores, of medium to small size (Pentecost 1981). Additionally, ascospores can also decrease

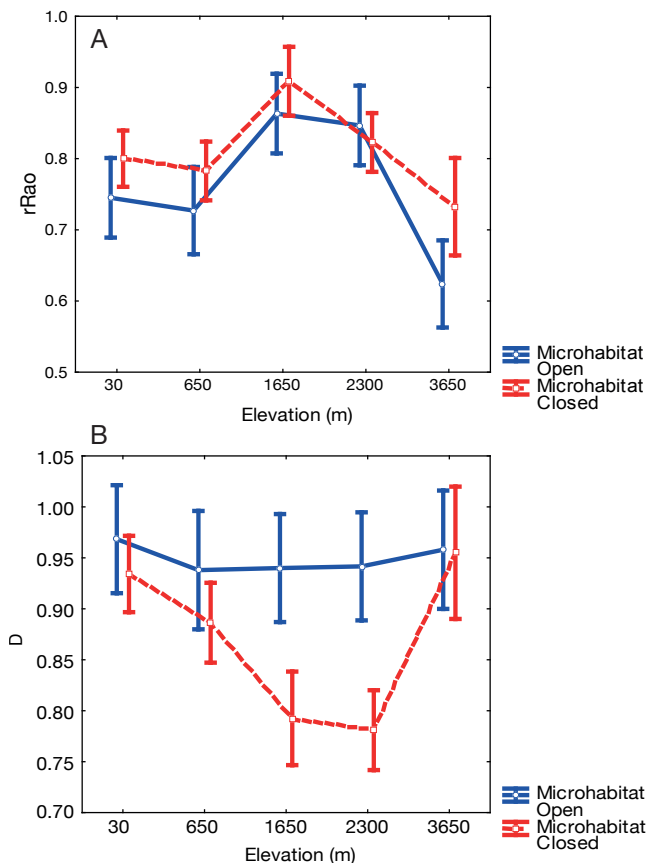


Fig. 7. — Functional diversity along the altitudinal gradient: **A**, relative Rao Index; **B**, functional Dominance.

desiccation damage by reducing the volume: area ratio through aggregation, as in muriform spores. An additional adaptation to extreme conditions of low and high altitudes may be the presence of a thick wall.

Functional diversity showed a greater value at the midpoint of the altitudinal gradient (El Queremal, 1600 m), while at the altitudinal extremes (Alto Pance and Chucheros) there was greater dominance and functional redundancy (“functionally clustered”) (Weiher & Keddy 1999; Kraft *et al.* 2007; Prieto *et al.* 2017). This suggests that environmental filtering processes are occurring at low and high elevations, which can be explained by the extreme climatic conditions of these sites: Alto Pance has low temperatures, a strong temperature variation (high temperatures during the day and low temperatures at night) and low average precipitation, which favors the presence of macrolichens species (mainly fruticose) with few common features; on the other hand, Chucheros presents high temperatures and precipitation, which is a favorable environment only for crustose or filamentous lichens and some microfoliose and squamulose that can survive in high humidity conditions. In this way, altitudinal extremes seem to be strong barriers for functional diversification of lichens. On the other hand, in the middle of the gradient several functional features may coincide, which explains the greater functional diversity of this site (functional overdispersion)

(Kraft *et al.* 2007; Mayfield & Levine 2010). Thus, in the middle of the gradient, occur mainly competition effects and biotic interactions.

The DCA for the functional traits showed a clear separation between altitudes. This pattern was similar to that found in the NMS based on species composition. Thus, the functional traits used in this study respond similarly to the taxonomic diversity. Recently, it has been found that morphological features can be used as taxonomic substitutes in lichens to evaluate the effect of environmental changes or anthropic disturbance (Ramírez-Morán *et al.* 2016; Arango *et al.* in press).

Finally, it was found that the alpha diversity showed a concave pattern with the altitude, whereas the beta diversity had a convex pattern, with a peak in the middle part of the gradient. This implies in a greater contribution of beta diversity to gamma diversity in the middle of the gradient, while at the altitudinal extremes alpha diversity dominates. On the other hand, the total diversity estimated by rarefaction showed a unimodal pattern, with a higher value at 1600 m (El Queremal). This pattern is not explained by MDE, but by the interaction of climatic variables. With respect to the functional traits, a strong change of the characteristics of the lichens with the increase of the altitude was observed. Crustose lichens were more frequent at low elevations, while foliose and fruticose were gaining dominance with altitude. A higher incidence of cyanolichens was also found in the middle part of the altitudinal gradient, regions of high cloudiness and shadow, while these types of lichens were less dominant in the low and high elevations, since they are zones with greater sun exposure. The presence of rhizines showed a higher incidence in the higher altitude localities, because these structures allow the capture of water from the fog, which is one of the main sources of water in high elevations where the precipitation is lower than in low altitude localities. Functional diversity showed a similar pattern to that found with species richness corrected by rarefaction, which implies that the number of specimens collected or the abundance obscures the real richness patterns along the altitudinal gradient. In this way, it is recommended to consider rarefaction in studies in which lichen abundance can be notoriously different between ecosystems or sites to be compared.

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