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Diversity patterns of vascular and non-vascular epiphytes along tropical dry forest

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ABSTRACT

Introduction: Epiphytes (vascular and non-vascular) are one of the most diverse groups in the Neotropics, but despite their importance in the functioning of many ecosystems, much of their taxonomy and ecology is still unknown in the dry forest of Colombia.

Objective: To compare the diversity patterns and species composition of vascular and non-vascular epiphytes along tropical dry forest remnants of Cauca Valley, Colombia.

Methods: Ten permanent plots (50 x 20 m^2) were established in tropical dry forest remnants. The epiphytes were sampled in 40-50 trees per plot. Alpha and gamma diversity were calculated using the richness (q0) and Shannon index (q1) (alpha was estimated as the average for phorophytes). Beta diversity was measured using the Whitaker index. To evaluate the relationship between diversities and environmental variables, GLM analysis was used.

Results: We found 50 morphospecies of vascular epiphytes, 77 of bryophytes and 290 of lichens. The α and γ diversity of bryophytes from each remnant was significantly explained by temperature. The abundance of lichens per tree was significantly related with the DBH and tree height of each remnant. The α diversity of vascular epiphytes shown can be explained by temperature and precipitation. The γ diversity was strongly influenced by the beta diversity in bryophytes and lichens. This pattern is because the sites with high disturbance present a lower diversity, as a consequence of a homogenizing effect, that is, a low turnover of species between sampling units.

Conclusions: Precipitation and temperature affected the diversity of bryophytes and vascular epiphytes, while it did not show a relationship with the lichen's diversity, for which there is not a high congruence between the diversity and composition of these epiphytes.

Key words: lichens, corticolous, ecology, mosses, liverworts, TDF.

RESUMEN

Patrones de diversidad de epífitas vasculares y no vasculares a lo largo del bosque seco tropical

Introducción: Los epífitos (vasculares y no vasculares) son uno de los más diversos grupos de plantas en el Neotrópico, pero a pesar de su importancia para el funcionamiento de varios ecosistemas, existen grandes vacíos en su conocimiento taxonómico y ecológico en el bosque seco de Colombia.

Objetivo: Comparar los patrones de diversidad y composición de especies de epífitas vasculares y no vasculares a lo largo de remanentes de bosque seco tropical del Valle del Cauca, Colombia.

Métodos: Se establecieron diez parcelas permanentes (50 x 20 m^2) en remanentes de bosque seco tropical. Las epífitas se muestrearon en 40-50 árboles por parcela. La diversidad alfa y gamma se calculó utilizando la riqueza (q0) y el índice de Shannon (q1) (alfa se estimó como el promedio para los forófitos). La diversidad beta se midió utilizando el índice de Whitaker. Para evaluar la relación entre diversidades y variables ambientales se utilizó el análisis GLM.

Resultados: Se encontraron 50 morfoespecies de epífitas vasculares, 77 de briófitas y 290 de líquenes. La diversidad de α y γ de briófitas de cada remanente fue explicada significativamente por la temperatura. La abundancia de líquenes por árbol se relacionó significativamente con el DAP y la altura del árbol de cada remanente. La diversidad α de epífitas vasculares que se muestra puede explicarse por la temperatura y la precipitación. La diversidad γ estuvo fuertemente influenciada por la diversidad beta en briófitas y líquenes. Este patrón se debe a que los sitios con alta perturbación presentan una menor diversidad, como consecuencia de un efecto homogeneizador, es decir, un bajo recambio de especies entre unidades de muestreo.

Conclusiones: La precipitación y la temperatura afectaron la diversidad de briófitas y epífitas vasculares, mientras que no mostró relación con la diversidad de líquenes, por lo que no existe una alta congruencia entre la diversidad y composición de estas epífitas.

Palabras clave: líquenes, cortícolas, ecología, musgos, hepáticas, BST.

INTRODUCTION

Dry forests are ecosystems with a marked seasonality, with dry periods interrupted by rainy months. Formally, a tropical dry forest (TDF) is defined as one with a closed canopy, where the average annual precipitation is less than 1 800 mm, with periods of three to six months with precipitation of less than 100 mm per month, during which the vegetation is deciduous (Gentry, 1995; Murphy & Lugo, 1986; Sánchez-Azofeifa et al., 2005). The topical dry forest also encompasses taxonomic, compositional, and structural variations that depend on climate, topography, and hydrogeography (Ramos & Silverstone, 2018). As these ecosystems normally occur in agriculturally fertile areas, often large human populations have settled there, exacerbating the pressures on these forests, and drastically reducing their extension to only 10 % of the original. In Colombia, dry forest is the most threatened ecosystem, with only 5 % of their original extension left (Ramos & Silverstone, 2018).

The Colombian dry forest is restricted to the inter-Andean valleys, the Caribbean region, part of the plains and rivers. The floristic composition and physiognomy of TDF in Colombia differs markedly between regions, with several endemic species (Ramos & Silverstone, 2018). However, dry forests in Colombia are being destroyed at accelerated rates due to intensive agriculture such as the cultivation of sugarcane, rice and soybeans and transformation into pastures for cattle (Ramos & Silverstone, 2018). This destruction is very noticeable in the region of the geographic valley of the Cauca River, where the sugarcane cultivation and cattle ranching reduced the dry forest to small patches, with an estimated total extension of less than 500 ha. These remnants are largely isolated due to the persistence of the agricultural lands (Ramos & Silverstone, 2018).

One of the most threatened floristic components in the tropics are the epiphytes, plants that use other plants as substrate without parasitizing the host and can be classified into vascular and non-vascular epiphytes (algae, bacteria, bryophytes, and lichens) (Mendieta-Leiva, Porada et al., 2020). Despite the taxonomic heterogeneity of the group, epiphytes show ecological and functional similarities. Epiphytes have important functions in ecosystems ranging from the cycling of nutrients and water to serving as food source for other organisms (Benzing, 1992). The greatest diversity of these plants occurs in the neotropics, with cloud forests being one of the most diverse habitats (Gentry, 1995; Soto et al., 2019). These organisms depend on tree structure, climatic factors, and other epiphytes for their establishment (e.g., non-vascular epiphytes form litter that allows vascular establishment) (Gentry, 1995). Epiphytes also interact with each other (vascular and non-vascular), with variations according to the type of ecosystem, as in cloud forests, where vascular and bryophytes are dominant compared to lichens (Soto et al., 2019; Wolf, 1993). However, there is no consensus regarding the relationship between the diversity of vascular and non-vascular epiphytes, showing patterns of positive, negative, or absent relationship (Affeld et al., 2008; Bacaro et al., 2019). Currently, progress has been made in the study of epiphytes, which has allowed a better understanding of their ecology, conservation, distribution, and large-scale patterns, as well as standardizing sampling protocols (Wolf, 1993; Wolf et al., 2009). However, due to both taxonomic and sampling complexity of these groups, there are few studies that include vascular and non-vascular epiphytes (Affeld et al., 2008; Bacaro et al., 2019, Ramos & Silverstone, 2018; Soto et al., 2015). Therefore, there are still several gaps of knowledge about the interaction and ecological dynamics of the relationship between vascular and non-vascular epiphytes (e.g., relationship between the diversity of vascular vs. non-vascular epiphytes and their responses to environmental gradients).

Currently, vascular epiphytes in the Neotropics are of high interest due to their high diversity, but not well known in ecology, biogeography and macroecology (Mendieta-Leiva, Porada et al., 2020). However, it is known that epiphytes are less diverse in dry ecosystems, but little is known about their ecology (Gentry, 1995; Mendieta-Leiva, Ramos et al., 2020; Werner & Gradstein, 2009). On the other hand, non-vascular epiphytes show growing interest, but are perhaps less well known in the neotropics both taxonomically and ecologically (Benitez et al., 2019; Cornelissen & Steege, 1989). There are also very few ecological studies that integrate vascular and non-vascular epiphytes, despite their obvious interaction (Ramos & Silverstone, 2018; Soto et al., 2015). Interest in the conservation of these plants has increased, with greater representation in management plans and conservation priorities. Because of this, it is necessary to contribute to the knowledge of these groups of organisms, especially in poorly studied ecosystems, such as the dry forest.

Bryophytes and lichens are organisms that are an important part of the primary ecological succession, as well as of the water cycle through horizontal rainfall (Blum, 1973; Kappen, 1973; Proctor, 1982). Furthermore, they can be used as bioindicator organisms of pollution and disturbance since they are poikilohydrous, that is, their water content depends on the environment (Conti & Cecchetti, 2001). Non-vascular epiphytes strongly depend on deterministic factors such as microclimate and stochastic factors such as dispersal, already showing changes in their community composition with small environmental changes. Similarly, vascular epiphytes also depend on factors such as climate, plant structure, characteristics of the phorophyte and dispersal capacity. Due to these similarities, vascular epiphytes have been used as surrogates for establishing nature reserves, identifying conservation priorities, and for environmental planning (Ryti, 1992). In the dry forests of Colombia, fauna and flora are mainly used as priorities for conservation and to establish guidelines for management plans, under the principle that these groups are substitutes for other groups of organisms. However, there are studies that show that the relationship between the diversity of vascular and non-vascular epiphytes is not consistent, with positive or negative relationships, for which there is not a high congruence between these taxa (Bacaro et al., 2019). Thus, understanding the relationship between the diversity and composition of vascular epiphytes, bryophytes and lichens would help improve conservation strategies in the Colombian dry forest.

The objective of this study was to compare the diversity patterns and species composition of vascular and non-vascular epiphytes along tropical dry forest remnants. The hypothesis is that vascular and non-vascular epiphytes will show similar patterns of diversity with respect to an environmental and disturbance gradient of dry forest.

MATERIALS AND METHODS

Study zone: Sampling was carried out in the dry forest of Cauca Valley, a department in the Southwestern part of Colombia. This department ranges from the Pacific coast to the central and western mountain ranges, with elevations above 4 000 m. The dry forest of the geographic Cauca valley is found along the Cauca River, which is located between the two aforementioned mountain ranges. Ten dry forest remnants (sites) were chosen as sampling sites, mainly in the North-central part of Cauca Valley: Chimbilaco (Yotoco), PNR El Vínculo (Buga), Gitana (Riofrío), Higueroncito (Roldanillo), PNR Mateguadua (Tuluá), El Medio (Zarzal), Valenzuela (Tuluá), La Venta (Bugalagrande), Verdun (Andalucia) and El Volcán (Yotoco) (Table 1). The ten localities present dry forests in different states of conservation, with an elevation range between 993-1 150 m and precipitation between 1 057 and 1 593 mm.

Sampling: For vegetation sampling (forest structure) plots of 50 x 20 m^2 were established and all the trees with a diameter at breast height (DBH) > 2.5 cm were counted. For each tree DBH, height and number of branches were noted down. Phorophytes with a DBH > 20 cm were selected from the dominant species of each locality. The phorophytes were at a distance > 10 m from the forest edges. The species and number of vascular epiphyte individuals were counted in three vertical strata (stratum 1: from the base up to the first branching; stratum 2: between the first and second branching; stratum 3: after the second branching) (Gradstein et al., 2003). In total, 50 trees were selected for each plot. One specimen of each species was deposited in the TULV Herbarium.

For the sampling of non-vascular epiphytes, three strata were established: base (between 0.5-1 m), trunk (between 1-2 m) and branches (branches were collected from the upper parts) (Gradstein et al., 2003). In each stratum, a 30 x 20 cm^2 quadrant (divided into 1 cm^2 cells) was placed and the coverage of each non-vascular species was estimated (Déleg et al., 2021). One specimen of each species was deposited in the TULV Herbarium. For more information on the species found, consult Soto & Moncaleano (2021). Additionally, Annual Mean Temperature (Bio 1), Annual Precipitation (Bio 12) and Temperature seasonality (Bio 4) were estimated for each forest remnant using the Worldclim databases (Fick & Hijmans, 2017). Layers were used at a resolution of 2.5 minutes and values of the variables were extracted by site (ten forest remnants). Only these variables were used because they were the ones with the highest correlation between them (Pearson R > 0.7) and variation among the remnants (since the study sites are in the same geographical valley).

Statistical analysis: Initially, the abundance of bryophytes and lichens was measured

Table 1

Location and climate data of the remnants of dry forest that were chosen as study sites.

Locality	Elevation (m)	Latitude	Longitude	Temperature (°C)	Temperature Seasonality	Precipitation (mm)
Chimbilaco	1 092	3.935672	-76.356558	22.5	288	1 176
El Vinculo	1 150	3.836200	-76.296503	23.7	290	1 057
Gitana	1 122	4.166017	-76.333967	22.9	275	1 466
Higueroncito	993	4.497430	-76.109160	23.6	348	1 109
Mateguadua	1 150	4.027992	-76.159331	21.6	248	1 584
Medio	1 000	4.335278	-76.081111	23.9	335	1 239
Valenzuela	1 050	4.010607	-76.171244	21.6	287	1 372
La Venta	1 166	4.198944	-76.065611	23.1	280	1 465
Verdun	1 056	4.215492	-75.996389	22.2	314	1 593
Volcán	1 100	4.021400	-76.362817	22.2	263	1 260

as the cover (cm^2) per sampled quadrant, while the abundance of vascular plants was measured as the number of individuals. Alpha diversity of epiphytes was evaluated by the number of species (Hill number q0) and Shannon diversity indices (Hill number q1) per sampling unit (phorophyte) (Chao et al., 2014). Alpha diversity per site was calculated as the average of q0 and q1 of the phorophytes. Gamma diversity was calculated as q0 (richness) and (q1) (index Shannon's diversity) for the entire remnant (McCune & Grace, 2002) and beta diversity as the Whitaker index for each remnant, which considers the average alpha diversity and gamma diversity of each site (Hammer et al., 2001). In this way, an alpha (average between phorophytes), gamma (Hill number) and beta diversity value was obtained for each remnant. These indices were calculated with the PAST 2.0 ® software (Hammer et al., 2001).

General Linear Models (GLM) were performed to evaluate the relationship between abundance, alpha, beta and gamma diversities, and the environmental variables (temperature, precipitation, and Temperature seasonality, abundance, diversity, DBH and tree height). Previously, Spearman's correlation analysis (between the predictor variables) was performed to select variables with high correlation ($R > 0.7$) and avoid collinearity. These analyzes were also made between the alpha, beta, and gamma diversities. The variables followed a normal distribution (Shapiro Wilk: $P > 0.05$). Statistical analyzes were conducted with the software STATISTICA® 7.0 (StatSoft, 2004).

To evaluate the relationship between the remnants based on their epiphyte composition (similarity), a multidimensional non-metric scaling (NMDS) was performed. The Bray-Curtis similarity index was used to make the NMDS (McCune & Grace, 2002). To evaluate the relationship between environmental variables and epiphyte composition, a Spearman correlation was performed between the NMDS axes and environmental variables. These analyses were conducted with the PAST 2.0 ® software (Hammer et al., 2001).

The 10 remnants were also grouped according to whether they had a conservation status assigned (natural reserve or a similar status) or not (Remnants on farms or without protection), to establish differences in alpha, beta, and gamma diversities of the epiphytes. For this purpose, t-tests were used to compare the remnants with a conservation status vs. no conservation in terms of diversity and abundance of epiphytes. Alpha and gamma diversities were compared between remnants using t-tests (Hammer et al., 2001).

RESULTS

There were 50 morphospecies of vascular epiphytes, 77 of bryophytes and 290 of lichens. The most abundant lichen species were *Cryptothecia striata* (15 743 cm^2), *Coenogonium magdalenae* (11 887 cm^2), *Porina imitatrix* (10 229 cm^2) and *Zwackhia viridis* (Ach.) Poetsch & Schied (8 451 cm^2), while *Emmanuellia tenuis, Bacidia* sp.2, *Bulbothrix isidiza, Byssoloma leucoblepharum, Herpothallon confluenticum*, *Hyperphyscia minor*, *Lopezaria* sp., *Physcia* sp., *Porina* sp., Lichen sp. and *Usnea* sp. had 1 cm^2. The most frequent species in the ten remnants were *Coenogonium linkii* (9 remnants), *Herpothallon rubrocinctum, Diorygma australasicum* (Elix) Lücking et al., *Herpothallon roseocinctum, Zwackhia viridis*, *Porina imitatrix, Coenogonium magdalenae* and *Cryptothecia striata* (8 remnants), while 175 species were very rare (singletons: occurred in only 1 remnant).

For bryophytes, *Lejeunea* sp., *Radula pallens*, *Helicodontium capillare*, *Schiffnerolejeunea polycarpa* and *Lejeunea subsessilis* Spruce were most abundant (13 074, 4 755, 3 488, 3 313 and 3 230 cm^2, respectively), whereas *Plagiochila deflexirama, Bryophyte* sp. and *Leskeadelphus angustatus*, were the least abundant (5, 3 and 3 cm^2, respectively). The most frequent species were *Sematophyllum subpinnatum* (Brid.) E.Britton, *Neckeropsis undulata*, *Frullania ericoides* (Mart.) Mont., *Radula tectiloba* and *Frulania* sp.2., occurring between in 5-6 remnants, while 10 were rare (doubletons: occurred in 2 remnants) and 55 species (71 %) were very rare.

The most abundant species among the vascular epiphytes were *Tillandsia recurvata* (2 221 individuals), *Pleopeltis astrolepis* (160), *Tillandsia usneoides* (159) and *Tillandsia juncea* (115). The most frequent species were *Monstera adansoni* (8 remnants), *Tillandsia recurvata* (7 remnants), *Tillandsia juncea* (6 remnants), *Philodendron barrosoanum* and *Tillandsia elongata* (5 remnants), while 34 species were only present in one remnant.

Diversity α, β and γ in dry forest remnants: The remnants with the highest bryophyte gamma diversity (q0) were Mateguadua (24 species) and Verdun (23 species), while El Vínculo was the place with the lowest diversity (six species). In terms of q1, Verdun was the site with the highest diversity, while the Medio had the lowest bryophyte diversity. Alpha diversity was highest in Mateguadua and lowest in Vínculo (Table 2). Verdun was the remnant with the highest beta diversity, while Vínculo had the least beta diversity. The abundance of bryophytes was highest in the Gitana and lowest in the Volcan.

Regarding lichens, it was found that Higueroncito was the place with the greatest diversity γ, while Chimbilaco was the one with

Table 2

Diversity α, β and γ for epiphytes (bryophytes, lichens and vascular) in ten dry forest remnants.

Epiphyte	Locality	β	α			γ		
			Abundance/tree	Richness	q1	Total abundance	Richness	q1
Bryophytes	Chimbilaco	4.47	427.36	2.83	2.34	10 043	10	4.31
	El Vinculo	4	360.51	2.20	2.08	6 309	6	3.82
	Gitana	4.35	**484.00**	2.87	2.41	**11 132**	10	3.22
	Higueroncito	8.93	205.83	2.51	2.20	4 837	15	5.10
	Mateguadua	7.64	397.00	**3.78**	2.69	7 146	**24**	8.08
	Medio	6.15	407.46	2.54	2.18	5 297	11	2.53
	Valenzuela	8.21	395.88	3.06	2.51	6 334	19	7.54
	Venta	5.25	364.36	3.08	2.48	9 109	13	5.10
	Verdun	**9.36**	477.71	3.22	2.46	9 793	23	11.25
	Volcán	5.6	169.91	2.82	2.39	1 869	12	6.82
Lichens	Chimbilaco	6.6	231.12	3.54	2.27	11 831	28	11.59
	El Vinculo	5.91	474.70	4.34	2.48	24 000	31	16.28
	Gitana	8.36	254.98	5.02	2.64	11 474	47	12.55
	Higueroncito	10.39	312.21	6.94	3.29	14 986	**80**	28.50
	Mateguadua	8.33	327.29	**7.07**	3.60	13 746	66	16.95
	Medio	9.48	313.92	4.49	2.03	11 615	47	13.33
	Valenzuela	9.27	571.06	6.43	3.42	**26 840**	66	23.34
	Venta	9.43	349.96	6.52	3.19	17 498	68	21.33
	Verdun	**11.01**	400.63	6.16	2.86	19 631	74	21.33
	Volcán	8.06	**590.74**	6.40	3.22	20 676	58	16.95
Vascular	Chimbilaco	3.75	18.21	2.47	3.13	173	7	2.20
	El Vinculo	1.77	**123.50**	2.08	1.08	741	3	2.01
	Gitana	3.67	3.50	2.42	3.67	21	6	2.27
	Higueroncito	1.76	49.29	2.45	1.43	**764**	4	2.23
	Mateguadua	4.5	14.53	3.00	7.24	109	11	2.56
	Medio	6.12	21.00	2.55	2.56	231	11	2.23
	Valenzuela	**7**	9.60	2.25	4.39	96	11	2.16
	Venta	6.6	31.53	2.58	2.66	599	13	2.25
	Verdun	6.58	24.61	**3.64**	5.16	443	**20**	2.77
	Volcán	2.08	7.60	2.30	2.34	38	4	2.10

the least diversity. Regarding the diversity α, Mateguadua was the remnant that showed the highest values, while the Medio presented the lowest q1 and Chimbilaco the lowest q0. Diversity β was highest in Verdun, while Vínculo showed the lowest values. The abundance of lichens was highest in Valenzuela (total abundance) and El Volcan (average abundance).

Vascular epiphytes presented a higher diversity γ in Verdun, while it was lower in Vínculo. Diversity α was highest in Verdun (average richness) and Mateguadua (average q1), while it was lowest in Vínculo. Regarding β diversity, the Valenzuela remnant was the one that showed the greatest diversity, while the Vinculo had the lowest values (Table 2). The abundance of vascular epiphytes was highest in Higueroncito (total abundance) and El Vínculo (average abundance per tree), in contrast, La Gitana was the site with the lowest total and average abundance.

Diversities α, β, and γ and environmental variables: The gamma diversity of epiphytic bryophytes from each remnant was significantly explained by alpha and beta diversities (Table 3). The diversities α and γ were related with temperature and precipitation, indicating that the sites with the highest precipitation and lowest temperature tended to present the highest diversity of corticolous bryophytes. The average DBH was significant to the α diversity, suggesting that the sites with the largest trees tended to present the highest diversity of bryophytes per tree.

The diversity γ of corticolous lichens was explained by α and β diversities. The abundance of lichens per tree was significantly related with the DBH and tree height of each remnant (Table 4). Alpha diversity was affected by temperature.

The alpha diversity of vascular epiphytes was explained by temperature with precipitation (Table 5). Gamma diversity was related to precipitation. Gamma diversity was explained only by alpha diversity. The total abundance of vascular epiphytes per tree showed a negative relationship with the DBH.

When comparing the diversity among the remnants with some figure of conservation vs. without conservation, it was observed that the richness and diversity of trees was greater for these last (Table 6). Regarding the epiphytes, no significant differences were found for the diversities α, β and γ.

Composition of epiphytes: The NMDS for vascular epiphytes, lichens, and bryophytes,

Table 3

GLM between diversity and environmental variables for epiphytic bryophytes. Significant Chi- Square are in bold.

	Gamma	Temperature	Precipitation	q1 trees	DBH	Height (m)
Abundance/tree		0.21	3.39	0.00	0.38	2.38
Abundance		0.08	**3.19**	**3.27**	1.95	2.39
Gamma		**8.93**	0.19	0.04	1.99	0.00
Alfa	6.14	**12.62**	**10.96**	3.09	1.31	1.01
Beta	**4.59**	1.33	0.34	0.08	0.06	1.18

Table 4

GLM between diversity and environmental variables for epiphytic lichens. Significant Chi- Square are in bold.

	Gamma	Temperature	Precipitation	q1 trees	DBH	Height (m)
Abundance/tree		3.82	1.34	1.68	**20.74**	**4.82**
Abundance		0.60	1.50	4.67	1.15	0.12
Gamma		0.11	0.00	0.06	0.07	0.76
Alfa	**0.026**	**4.21**	0.06	0.00	0.13	0.01
Beta	**0.018**	0.04	3.49	0.03	1.79	0.30

Table 5

GLM between diversity and environmental variables for vascular epiphytes. Significant Chi- Square are in bold.

	Gamma	Temperature	Precipitation	q1 trees	DBH	Height (m)
Abundance/tree		3.82	1.34	1.68	20.74	4.82
Abundance		4.71	0.01	0.02	4.65	2.22
Gamma		1.80	7.74	0.61	1.42	0.30
Alfa	0.14	9.76	10.17	0.20	1.93	2.13
Beta	0.015	1.03	4.36	0.64	3.10	7.59

Table 6

Comparison of diversity α, β and γ between remnants of dry forest with Conservation vs. without Conservation.

		Without Conservation	Conservation	T	gl	p
	Bio4	294.67	290.00	0.22	8.00	0.83
	Temperature	227.50	227.00	0.09	8.00	0.93
	Precipitation	1 344.83	1 313.00	0.24	8.00	0.81
	Richness trees	21.00	34.50	-2.91	8.00	**0.02**
	Abundance trees	324.00	564.75	-0.83	8.00	0.43
	D tres	0.37	0.11	1.77	8.00	0.12
	H trees	1.72	2.74	-2.37	8.00	**0.05**
	DBH	21.39	20.94	0.10	8.00	0.92
	Height	7.91	7.60	0.17	8.00	0.87
Vascular	β	4.07	4.85	-0.55	8.00	0.60
	Abundance/tree	22.46	42.16	-0.85	8.00	0.42
	α **q0**	2.64	2.47	0.58	8.00	0.58
	α **q1**	1.04	1.12	-0.20	8.00	0.85
	Abundance total	339.67	294.25	0.23	8.00	0.82
	γ **q0**	8.83	8.75	0.02	8.00	0.98
	γ **q1**	0.83	0.80	0.48	8.00	0.64
Bryophytes	β	6.33	6.50	-0.13	8.00	0.90
	Abundance/tree	354.86	390.21	-0.50	8.00	0.63
	α **q0**	2.89	2.89	-0.02	8.00	0.98
	α **q1**	0.87	0.85	0.22	8.00	0.83
	Abundance total	7797.17	6271.50	0.81	8.00	0.44
	γ **q0**	13.83	15.00	-0.29	8.00	0.78
	γ **q1**	1.70	1.59	0.36	8.00	0.73
Lichens	β	8.97	8.25	0.69	8.00	0.51
	Abundance/tree	22.46	42.16	-0.85	8.00	0.42
	α **q0**	5.76	5.58	0.22	8.00	0.83
	α **q1**	1.06	1.03	0.22	8.00	0.83
	Abundance total	16 016.00	19 050.25	-0.85	8.00	0.42
	γ **q0**	59.17	52.50	0.56	8.00	0.59
	γ **q1**	2.88	2.84	0.21	8.00	0.84

showed different clustering patterns related to the different environmental variables evaluated (Fig. 1). The bryophytes were grouped according to precipitation and temperature, with a group formed by Chimbilaco, El Medio and El Vínculo, and another by Volcán, Venta, Mateguadua and Valenzuela. Regarding lichens, the grouping patterns were related to the coordinates (latitude and longitude), and the parameters related to the vegetation. The NMDS of

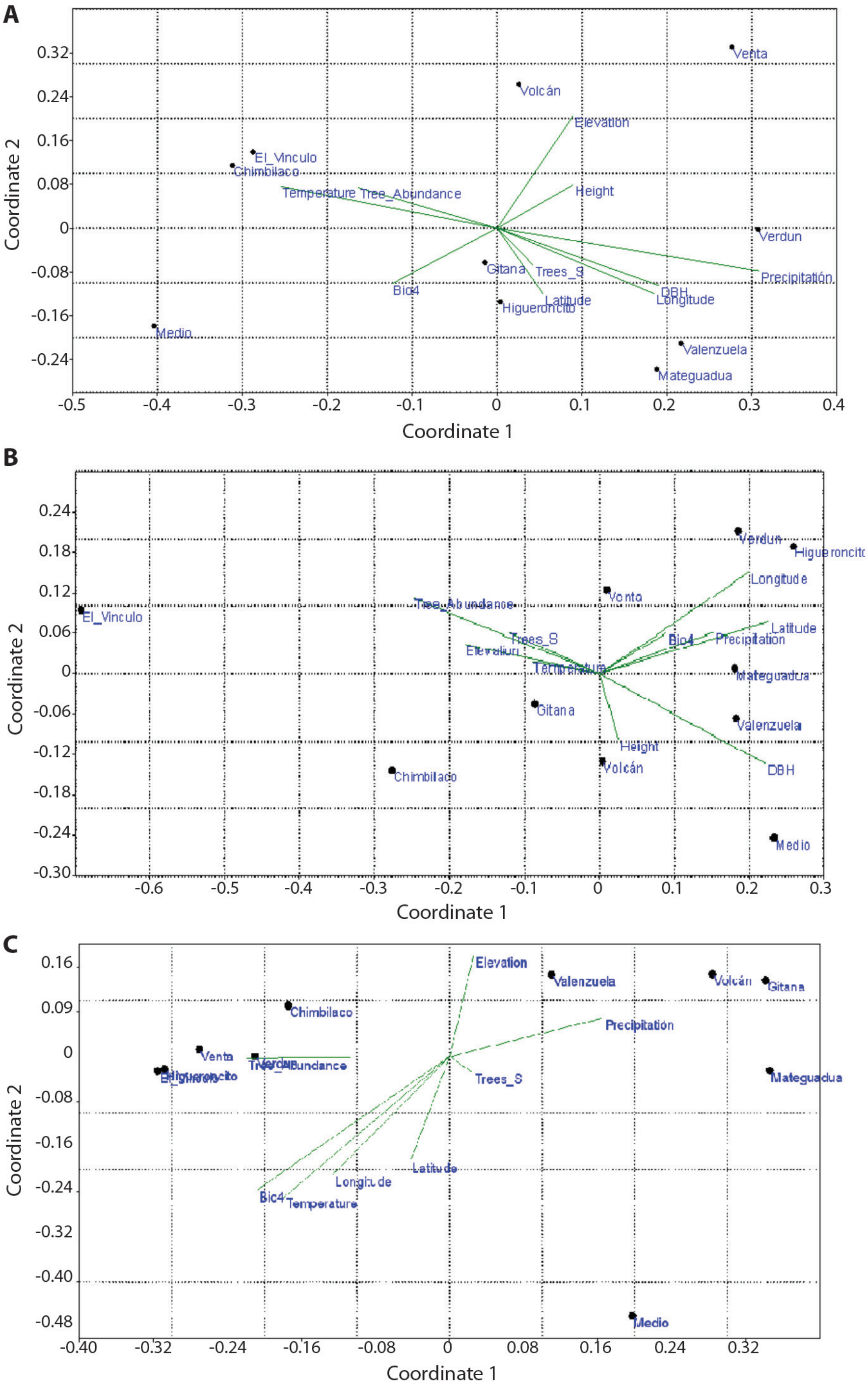

Fig. 1. NMDS epiphytes from TDF Valle del Cauca. **A.** vascular, **B.** bryophytes and **C.** lichens.

vascular epiphytes showed that temperature, temperature seasonality and precipitation were the variables associated with the grouping patterns of the remnants, with Chimbilaco, Venta, Higueroncito, El Vínculo forming a group and Valenzuela, Volcán, Gitana and Mateguadua the other.

DISCUSSION

This study is the first to explore the epiphyte diversity in the dry forest of the geographic valley of the Cauca River. The diversity of vascular epiphytes was low compared to other tropical ecosystems (Mendieta-Leiva, Porada et al., 2020), which may be since the conditions of high temperature and low rainfall negatively impacted the abundance and richness of these organisms (Gentry, 1992). Regarding bryophytes, a low diversity was found compared to the Andean life zones, but like other dry forests in Colombia (García-Martínez & Mercado-Gómez, 2017; Lombo-Sánchez & Suarez-Contento, 2018; Ramírez-Morán et al., 2016). Regarding lichenized fungi, high diversity was observed compared to other dry forests in Colombia (Lücking et al., 2019, Soto et al., 2021). However, this diversity is still low compared to the Andean zone and humid forests at low elevations, which may be because the forests have low precipitation and high temperatures (Sipman, 1996; Soto et al., 2019).

The most frequent and abundant vascular epiphyte species found in this study are common in the dry forest of the geographic valley of the Cauca River, both in artificial and natural ecosystems (Benzing et al., 1992). These species were dominant in remnants with a plant structure with greater dominance than few species, which suggests that these epiphytes are favored by the disturbance.

The most abundant lichen species were *Cryptothecia striata*, *C. magdalenae, Porina imitatrix* and *Zwackhia viridis*. The most frequent species in the ten remnants were *Coenogonium linkii*, *Herpothallon rubrocinctum, Diorygma australasicum*, *H. roseocinctum, Z. viridis*, *Porina imitatrix, Coenogonium magdalenae* y *C. striata*, while 175 species were very rare. Thus, the most important species of lichens belong to the Arthoniaceae, Coenogoniaceae, Porinaceae and Lecanographaceae families, typical families in open and disturbed ecosystems. It should be noted that species of the Graphidaceae, Ramalinaceae and Trypetheliaceae families were not dominant, families that are considered the most diverse in the Neotropics (Menezes et al., 2018). On the other hand, there is a high presence of rare to very rare species, which is a common pattern in communities of lichenized fungi in the Neotropics, since many species of lichens have microclimate and microsite specialists (Cáceres et al., 2007).

The abundance of bryophytes was highest in the Gitana and lowest in the Volcan. The greater abundance of bryophytes in La Gitana may be since this site is a dry forest-premontane transition, for which climatic conditions favor a greater abundance and richness of bryophytes, which are photophobic organisms (Glime, 2007; Proctor, 1999; Proctor & Tuba, 2002). In contrast, Verdun was the site with the highest diversity, although it was not the one with the highest abundance and richness, which indicates that it is the site with the greatest diversity of bryophytes since the Shannon index corrects the effects of abundances. In this way, it is possible that Verdun is a forest with a higher degree of conservation even though it is immersed in a cattle farm, since bryophytes are indicators of habitat quality (Czerepko et al., 2021).

In contrast, it was found that Higueroncito was the place with the greatest diversity γ of corticolous lichens, while Chimbilaco was the one with the least diversity. The β diversity was highest in Verdun, while the Vinculo showed the lowest values. The abundance of lichens was highest in Valenzuela (total abundance) and Volcán (average abundance). These results differ from those of bryophytes because the diversity of lichens is modulated by other factors. Higueroncito was one of the sites with the highest temperature of the ten remnants, in addition to a possible effect of a fog current, which favors a high abundance and diversity of lichens (Stanton, 2015). The sites with the lowest rainfall tended to have the lowest lichen diversity.

Vascular epiphytes presented greater diversity α and γ in Verdun, while it was lower in Vínculo. Regarding β diversity, the Valenzuela remnant was the one that showed the greatest diversity, while the Vinculo had the lowest values. The abundance of vascular epiphytes was higher in Higueroncito (total abundance) and Vínculo (average abundance per tree), in contrast, La Gitana was the site with the lowest total and average abundance. The greater diversity of vascular epiphytes in Verdun may be due to the fact that it is a site with premontane forest characteristics, which are characterized by high epiphytism (Gentry, 1992). On the other hand, the Vínculo was a site with a low diversity and high abundance of epiphytes, which suggests that this site presents a high disturbance.

Regarding the diversity of epiphytic bryophytes, γ diversity of each remnant was significantly related with precipitation and temperature. The diversity α was explained by temperature, indicating that the sites with the highest precipitation and lowest temperature tended to present the highest diversity of corticolous bryophytes. The foregoing is in line with what was previously said that the remnants with higher precipitation and lower temperature tended to present the greatest diversity and abundance of bryophytes (Grass et al., 2015). Bryophytes are poikilohydrous organisms since they do not have mechanisms for regulating their water content. This condition makes them organisms with high water / humidity requirements to maintain adequate hydration and maintain biological processes (Glime, 2007; Proctor, 1999; Proctor & Tuba, 2002). The average DBH was positively related to the diversity α and γ, suggesting that the sites with the largest trees tended to present the greatest diversity of bryophytes. This may indicate that the diversity of bryophytes is higher in potentially more conserved sites (with larger trees), since they are forests with favorable climatic conditions for these organisms (Alvarenga & Pôrto, 2007; Bates et al., 2005; Bisang & Hedenäs, 2005; Czerepko et al., 2021). This response is because bryophytes show particular physiological and ecological aspects related to tolerance to light (photophobic), habitat specialization and reproductive strategies, therefore an alteration of their habitat negatively affects their diversity.

With respect to lichenized fungi, diversity γ was only explained by α and β diversities. The abundance of lichens per tree was positively correlated with the abundance of trees in each remnant. In lichens it has been observed that the total diversity of a place is strongly influenced by the exchange of species among phorophytes (Cáceres et al., 2007; Lücking, 1999). This pattern is since lichens have a strong microclimate and microsite specialization, which is why a high presence of rare and restricted species is observed.

In general terms, in bryophytes and lichens γ diversity was explained by α and β diversities, but in vascular epiphytes it was only alpha diversity. This pattern is because the sites that have a high disturbance, present a lower diversity, is usually due to a homogenizing effect, that is, a low turnover of species between sampling units (Ardila-Ríos et al., 2015). In this way, even though a high diversity α is conserved, the diversity β falls and this is expressed in a low diversity γ; However, in vascular epiphytes, alpha diversity was more important for the total diversity of each site, which can be explained by the fact that microenvironmental factors are less important in modulating the diversity of these epiphytes at a site (Soto-Medina et al., 2015). On the other hand, precipitation and temperature affected the diversity of bryophytes and vascular epiphytes, while it did not show a relationship with the lichen's diversity. In this way, the results show that there are contrasting patterns between the two groups of epiphytes, which is very important when making conservation decisions: e.g., using only vascular epiphytes to take conservation measures could negatively affect epiphytic lichens. In this sense, these results are an important basis for establishing conservation strategies in tropical dry forests.

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