Lichen community assemblages and functional traits as indicators of vegetation types in central Mexico, based on herbarium specimens

Diego SIMIJACA
Centro de Ciencias Básicas, Universidad Autónoma de Aguascalientes,
Avenida Universidad 940, Ciudad Universitaria, C.P. 20100, Aguascalientes,
Aguascalientes (Mexico)

Gilberto OCAMPO
Jaime ESCOTO-MORENO
Departamento de Biología, Centro de Ciencias Básicas, Universidad Autónoma de Aguascalientes,
Avenida Universidad 940, Ciudad Universitaria, C.P. 20100, Aguascalientes,
Aguascalientes (Mexico)

Rosa Emilia PÉREZ-PÉREZ
Facultad de Ciencias Biológicas, Benemérita Universidad Autónoma de Puebla,
Ciudad Universitaria, Building 1 BIO 1 C.P. 72570, Puebla (Mexico)
emilia.perez@correo.buap.mx (corresponding author)

Submitted on 9 February 2023 | Accepted on 16 May 2023 | Published on 26 July 2023

Simijaca D., Ocampo G., Escoto-Moreno J. & Pérez-Pérez R. E. 2023. — Lichen community assemblages and functional traits as indicators of vegetation types in central Mexico, based on herbarium specimens. *Cryptogamie, Mycologie* 44 (6): 83-102. https://doi.org/10.5252/cryptogamie-mycologie2023v44a6. http://cryptogamie.com/mycologie/44/6

ABSTRACT

Despite the growing interest in the lichen communities of Mexico, little is known about the assemblages from the central part of the country. For that reason, we defined the following research objectives: 1) to compare species richness, composition, and dissimilarity of lichen communities among three vegetation types; 2) to explore the incidence of environmental variables on lichen community species composition; and 3) to identify species and functional traits indicative of each vegetation type. Based on lichens' collection of Aguascalientes (HUAA herbarium), the relationships between species, traits, and environmental variables were represented through beta diversity components, non-metric multidimensional scales, Indicator Species Analysis, and Fourth Corner Analysis. In total, 218 lichen species were found, 132 in *Quercus* L. forests, 90 in subtropical shrubland, and 85 in xerophytic shrubland. Vegetation types had beta diversity total values higher than 0.8, although paired comparisons revealed variations in species replacement and richness. The indicator species identified for *Quercus* forests were *Parmotrema acutatum* Kurok., while for subtropical shrubland *Phaeophyscia nashii* Essl. and *Physcia biziana* (A.Massal.) Zahlbr. No indicator species were identified for xerophytic shrubland. Functional traits indicative of xerophytic shrubland were crustose lichens and the saxicolous substrate. Subtropical shrubland indicators comprised soredia and foliose narrow lobes, whereas indicators of *Quercus* forest consisted of foliose wide lobes and the epiphyte substrate. The functional trait approach used in the study of Mexican lichen communities is highly recommended given the observed similarities between taxonomical and functional community assemblages and the ease with which the functional traits approach links species composition to environmental variables.

KEY WORDS
Bioindicators,
community assemblages,
diversity,
response traits,
shrublands.

Downloaded From: https://complete.bioone.org/journals/Cryptogamie,-Mycologie on 02 Aug 2023
Terms of Use: https://complete.bioone.org/terms-of-use Access provided by Institute of Botany of the Czech Academy of Sciences

RÉSUMÉ

Assemblages et traits fonctionnels des communautés de lichens comme indicateurs des types de végétation du centre du Mexique, basés sur des spécimens d'herbier.

Malgré l'intérêt croissant pour les communautés lichéniques du Mexique, on connaît peu de choses sur les assemblages de la partie centrale du pays. Pour cette raison, nous avons défini les objectifs de recherche suivants : 1) comparer la diversité des espèces, la composition et la dissimilarité des communautés de lichens parmi trois types de végétation ; 2) explorer l'incidence des variables environnementales sur la composition des espèces des communautés de lichens ; et 3) identifier les espèces et les traits fonctionnels indicatifs de chaque type de végétation. Sur la base de la collection de lichens de la ville d'Aguascalientes (herbier HUAA), les relations entre les espèces, les traits et les variables environnementales ont été représentées par des composantes de diversité bêta, des analyses multidimensionnelles non paramétriques, une analyse des espèces indicatrices et une analyse des quatre coins. Au total, 218 espèces de lichens ont été trouvées, 132 dans les forêts de *Quercus* L., 90 dans les zones arbustives subtropicales et 85 dans les zones arbustives xérophiles. Les types de végétation présentaient des valeurs totales de diversité bêta supérieures à 0,8, bien que les comparaisons par paires aient révélé des variations dans le remplacement et la richesse des espèces. Les espèces indicatrices identifiées pour les forêts de *Quercus* sont *Parmotrema acutatum* Kurok., tandis que pour les zones arbustives subtropicales, *Phaeophyscia nashii* Essl. et *Physcia biziana* (A.Massal.) Zahlbr. Aucune espèce indicatrice n'a été identifiée pour la zone arbustive xérophile. Les traits fonctionnels indicatifs de la zone arbustive xérophile sont les lichens crustacés et le substrat saxicole. Les indicateurs de la zone arbustive subtropicale comprennent les sorédies, et les lobes foliacés et étroits, tandis que les indicateurs de la forêt de *Quercus* comprennent les lobes foliacés larges, et le substrat épiphyte. L'approche des traits fonctionnels utilisée dans l'étude des communautés de lichens mexicains est fortement recommandée étant donné les similitudes observées entre les assemblages de communautés taxonomiques et fonctionnelles et la facilité avec laquelle l'approche des traits fonctionnels relie la composition des espèces aux variables environnementales.

MOTS CLÉS
Bioindicateurs,
assemblages
de communautés,
diversité,
traits de réponse,
zones arbustives.

INTRODUCTION

Lichenized fungi, or "lichens" as symbioses are considered evolutionarily ubiquitous and play fundamental roles in structuring ecosystems (Nelsen *et al.* 2020). They constitute a complex, but self-supporting association, that results from interactions among fungi (the primary mycobiont) and a unicellular to filamentous algae and/or a cyanobacterium (the primary and/or secondary photobiont), along with other obligately associated elements of the fungal and bacterial microbiome contained on the thallus (Hawksworth & Grube 2020; Lücking *et al.* 2021). Currently, over 20 000 species of lichenized fungi have been described in the world (Lücking *et al.* 2016b).

Lichens have several roles in the ecosystem dynamics. A good example is found in the *Quercus* L. forest (Oak forest) in tropical regions of South America, where lichens reach 40% to 60% of the total epiphyte species richness per plot, and accumulate among 16 to 24 g/dm^2 of biomass (Wolf 1993). In Mexican tropical dry forests, crustose lichens amass at least 0.18 g/dm^2, accounting for 61% of the foliar biomass in that vegetation type (Miranda-González & McCune 2020). Furthermore, lichens are involved in nitrogen-fixing processes (Belnap 2002; Gutiérrez-Larruga *et al.* 2020), mineral degradation (Belnap & Lange 2001), and water and energy fluxes (Palmqvist & Sundberg 2000; Lakatos *et al.* 2006; Gauslaa 2014; Matos *et al.* 2019). Even vascular plants (Ellis 2012), arthropods, and vertebrates, interact with lichenized fungi (Brodo *et al.* 2001; Lalley *et al.* 2006).

Researchers have shown interest in the sensitivity of lichens in response to environmental disturbances (Hawksworth *et al.* 2005) in addition to their role in ecosystem dynamics (Nimis *et al.* 2002; Branquinho *et al.* 2015). Several studies have revealed strong relationships among substrate features and species richness or lichen community composition, which are influenced by climatic and substrate features (Cáceres *et al.* 2007; Rosabal *et al.* 2013), which have effects on lichen community diversity (Wolf 1994; Boonpragob & Polyiam 2007; Zárate-Arias *et al.* 2019). This sensitivity has allowed the use of lichens as indicators of forest continuity (McCune 2000; Rivas-Plata *et al.* 2008; Benítez *et al.* 2015), successional stages (Hedenås & Ericson 2000; Nordén *et al.* 2012), and the effect of alien tree species on the richness and composition of lichens (Käffer *et al.* 2009, 2010, 2011; Calviño-Cancela *et al.* 2013; Ardila *et al.* 2014; Simijaca *et al.* 2018).

In the same sense, beta diversity is an essential component of community ecology, because it allows to understand species assemblages in terms of differences and similarities, both in space and time (Anderson *et al.* 2011). One of the prevalent approaches to measure beta diversity is to split beta components into replacement and richness differences (Calderón-Patrón *et al.* 2013; Heino *et al.* 2019). Replacement (β_{-3}) refers to changes in species identities (turnover), and richness differences (βrich) to the loss-gain in species richness between two sites (Carvalho *et al.* 2012).

In addition to species diversity, functional traits can be used to improve our understanding of lichen community assemblage mechanisms and how they respond to different gradients of environmental change (Díaz & Cabido 2001; Lavorel & Garnier 2002). In fact, functional traits are defined as any morphological, physiological or phenological feature that varies in response to changes in environmental conditions (Violle *et al.* 2007). Regarding lichens, the use of soft functional traits such as growth forms, photobiont types, and reproductive strategies is a common and reliable practice to highlight responses of communities to environmental gradients or substratum (Cornelissen *et al.* 2007; Concostrina-Zubiri *et al.* 2014a; Tripp *et al.* 2016; Asplund & Wardle 2017; Soto-Medina *et al.* 2019; Hurtado *et al.* 2020). Therefore, lichens have been used as air quality indicators (Pinho *et al.* 2011; Llop *et al.* 2017) and a particular set of soft traits such as foliose narrow lobes, asexual reproduction (soredia), and pruinose lichens has been a common feature of urban and polluted sites (Koch *et al.* 2019; Lucheta *et al.* 2019). Additionally, photobiont types responded to water availability (Gauslaa 2014; Matos *et al.* 2015) and has been sensitive to global warming (Aptroot & Van Herk 2007; Marini *et al.* 2011). Consequently, field and herbarium samples are suitable to obtaining information on functional traits, which can be classified as hard or soft traits, depending on the nature of the data (continuous or categorical, respectively) (Ellis 2012).

Lichen soft functional traits and phylogenetic structure of lichen communities show similar patterns, allowing to evaluate ecological interactions and the evolutionary meaning of those assemblages (Prieto *et al.* 2017; Hurtado *et al.* 2019). That congruence highlights the importance of local and regional inventories in making ecosystem conservation decisions (Nascimento *et al.* 2021), as well as the implications of functional diversity parameters and phylogenetic dispersion on the vulnerability of ecosystem services (Koch *et al.* 2013; Soto-Medina *et al.* 2019). The interpretation of lichen ecological phenomena using a functional trait approach, provides advantages to the non-specialists in lichen taxonomy and offers the appropriate tools to comprehend how traits have an important role on lichen community structure and dynamics (Benítez *et al.* 2018; Ellis *et al.* 2021).

Lichen epiphyte communities in Mexico have been evaluated using several approaches and the lichen biota of *Alnus acuminata* Kunth (Betulaceae), *Juniperus flaccida* Schltdl. (Cupressaceae), and *Quercus laurina* Humb. & Bompl. (Fagaceae), among other phorophytes has been documented (Pérez-Pérez *et al.* 2008, 2015; Córdova-Chávez *et al.* 2016; Ramirez-Péña 2019; Castillo-Campos *et al.* 2019; León-González & Pérez-Pérez 2020). Lichen diversity has also been used to assess air quality and the impact of urbanization on the composition and abundance of lichen communities (Zambrano *et al.* 2000; Pérez-Pérez & Guzmán 2015), to evaluate the effect of forest management on lichen richness and composition (Pérez-Pérez 2005; Pérez-Pérez *et al.* 2011), and to recognize distributional patterns and phylogenetical structure of Parmeliaceae (Lücking *et al.* 2016a). Crustose lichen biomass has been linked to carbon economy, trophic chains, and nutrient fluxes (Miranda-González & McCune 2020). However, functional trait-based methodologies have yet to be employed.

Notably, some parts of the central region of the country have remained understudied despite increasing research on lichen ecology of Mexican ecosystems. For instance, in the Mexican state of Aguascalientes lichen diversity has only been studied through floristic approaches (Álvarez & Guzmán-Dávalos 2009; Miguel-Vázquez *et al.* 2021). This may obscure its real and current status and prevents the use of lichens as evidence for the decision-making processes impacting ecosystems conservation. For this reason, the objectives of the present study were: 1) to compare species richness, composition, and dissimilarity of lichen communities among three common vegetation types of the central part of Mexico; 2) to explore the effect of environmental variables on lichen community species composition; and 3) to identify species and functional traits indicative of each vegetation type. Changes in precipitation and elevation were hypothesized to impact lichen community species richness and composition, thus allowing to distinguish between xerophytic shrublands, subtropical shrublands, and *Quercus* forests. Furthermore, traits and species with crustose or narrow lobe growth forms and sexual reproduction were expected to relate to low elevation and low precipitation, whereas broad size lichens and asexual reproduction were related to changes in vegetation type, elevation, and precipitation.

MATERIAL AND METHODS

DATA COLLECTION AND STUDY AREA

Data collection was based on the revision of 849 samples deposited at herbarium HUAA (Universidad Autónoma de Aguascalientes, Mexico). Those herbarium specimens were result of non-quantitative opportunistic samplings (Sipman 1996) applied in the state of Aguascalientes from 2018 to 2022. Field information was taken from the herbarium specimen label and the name of the collecting localities was classified considering the vegetation types (INEGI 2017).

The state of Aguascalientes, located in the central portion of the country, upon the Mexican Plateau and borders the states of Jalisco and Zacatecas. The state has a land area of 5680.33 km^2 and is located between meridians 101°53’ and 102°52’W, and parallels 22°27’ and 21°28’N (Ávila-Villegas *et al.* 2008). The physiography of the state is the result of the convergence of three biogeographic regions (Toledo & Ordoñez 2009). It encompasses plains and low hills covered by shrubs, as well as mountainous landscapes dominated by *Quercus* and coniferous forests (Martínez-Calderón *et al.* 2017; Siqueiros-Delgado *et al.* 2017).

TAXONOMIC WORK

We used specialized taxonomic literature to identify the specimens (Nash III *et al.* 2002, 2004, 2007; Otálora *et al.* 2014; Mongkolsuk *et al.* 2015; Brodo *et al.* 2016; Kitaura *et al.* 2019). Lichen morphological structures were recognized by means of light microscopy (Leica EZ400, Leica DM 100) and lichen substances were detected using spot tests and UV light exposition (Brodo *et al.* 2001). Lichen nomenclature follows the Consortium of North American Lichen Herbaria (CNALH 2022) and the identifications correspond to the list presented in Simijaca *et al.* (2023) (Appendix 1).

DIVERSITY INDEXES

The number of species per site was used to calculate alpha diversity and a Mann-Whitney test was used to discover significant differences in average alpha diversity among vegetation types. Richness values completeness for each vegetation type and among vegetation types were tested using Chao 2 and first-order Jackknife estimators (Jackknife 1). Gamma diversity was estimated as the total richness per vegetation type. Because the number of sites per vegetation type was unequal, gamma diversity was logarithmically transformed as follows: $\gamma' = \gamma/100 \times \log(N)$ (where γ' is transformed gamma diversity, γ is original gamma diversity and N corresponds to the number of sites per vegetation type) (Cáceres *et al.* 2008). Beta diversity was estimated as Beta total (β_{cc}), including beta replacement (β_{-3}) and beta richness differences (β_{rich}) (Carvalho *et al.* 2012). In addition, exclusive and shared species among vegetation types were counted and depicted in a Venn diagram, using the ggVennDiagram function of the ggplot R package (Wickham 2011).

ENVIRONMENTAL DATA

Vegetation types were selected based on soil uses and plant communities classification (INEGI 2017), where *Quercus* forest, subtropical shrubland, and xerophytic shrubland were the most represented plant communities across Aguascalientes (Siqueiros-Delgado *et al.* 2016). Annual mean temperature and annual mean precipitation data for the study sites were obtained for years 1980 to 2009 (Cuervo-Robayo *et al.* 2020), available in raster format at CONABIO Geoportal (CONABIO 2021). Elevation data was extracted from Guevara & Arroyo-Cruz (2016). The information was compiled and visualized using QGIS 3.4 (QGIS Development Team 2016). After confirming through PCA loading scores that temperature and elevation were linearly correlated, the annual mean precipitation and elevation were selected as explanatory variables.

LICHEN COMMUNITIES

Lichen species composition heterogeneity among and within vegetation types was evaluated using a Multi-Response Permutation Procedure (MRPP) and the Sørensen distance (Koch *et al.* 2019). The spatial relationship of sampling sites (lichen communities) and the incidence of environmental variables was visualized using non-metric multidimensional scaling (NMDS), and a randomized test with 500 runs was implemented to determine stress and dimensionality (Ardila *et al.* 2014; Ramírez-Morán *et al.* 2016). Additionally, a cluster analysis using the Sørensen distance was performed with a flexible beta = –0.25. Species affinity to specific vegetation types was evaluated by means of an Indicator Species Analysis (ISA) using a Monte Carlo test with 1000 runs (Cáceres *et al.* 2008). The analyses were performed with PCORD version 7.08 (McCune & Mefford 2018).

FUNCTIONAL TRAITS

Substrate type data (rock, soil, wood, multiple) data per species were compiled in a presence/absence matrix. Growth forms (crustose, dimorphic, foliose broad lobed, foliose narrow lobed, fruticose, squamulose, and jelly lichens), photobiont type (Cyanophyta, Chlorophyta), and reproductive structure (absent, apothecia, isidia, lobules, perithecia, soredia, mixed types) were considered as functional traits (Chuquimarca *et al.* 2019). This information (Appendix 1), along with the species relative abundance, was used to calculate the Community Weighted Mean (CWM) to reflect the functional composition of each vegetation type (Lucheta *et al.* 2019).

The affinity of functional traits to each vegetation type was tested using the Indicator Species Analysis (ISA) with 1000 runs (Lucheta *et al.* 2019). An NMDS was performed to search for lichen composition patterns, functional features, and environmental factors; however, only significant values were considered and displayed in the final schematic result (Matos *et al.* 2015). Finally, to test the strength of the relationships among environmental and traits data in the matrix, a Fourth Corner Analysis (FCA) was performed using a combined randomization model with 1000 runs (Legendre *et al.* 1997; McCune 2015). The analyses were performed in PCORD version 7.08 (McCune & Mefford 2018) and represented using the ggcorrplot function of the ggplot R package (Wickham 2011).

RESULTS

Twenty-five sites were identified during herbarium specimen study, including 11 in xerophytic shrubland, eight in subtropical shrubland, and six in *Quercus* forest (Table 1). Species richness values were between seven and 50 species per site, with the *Quercus* forest having the highest average value for alpha diversity (mean = 33.3); sampling site EBAZ (*Quercus* forest) was the richest throughout the study. Subtropical shrubland (mean = 20.3) and xerophytic shrubland (mean = 13.8), had lower richness values, where the 75th percentile did not exceed 29 species (Fig. 1). In addition, the subtropical shrubland (Terrero de la Labor) had the lowest value of species richness, grouping seven species. Furthermore, a site with subtropical forest with 40 species, was registered as an outlier (Los Adobes).

Sample completeness in the xerophytic shrubland surpassed 95% (Chao 2 = 97.70%, Jackknife 1 = 96.59%), while the subtropical shrubland reached 92% (Chao 2 = 92.78%, Jackknife 1 = 97.83%). The *Quercus* forest had the lowest value for the in Chao 2 Estimator (Chao 2 = 88.59%, Jackknife 1 = 99.25%). The sample completeness estimation for all the 25 sites resulted in more than 96% (Table 2).

The xerophytic shrubland-*Quercus* forest pairwise comparison showed a significant difference in richness averages (U = 2, $p = 0.002$). In contrast, the comparisons *Quercus* forest-subtropical shrubland (U = 9) and subtropical-xerophytic shrublands (U = 24) did not have significant differences in average richness values ($p > 0.05$). On the other hand, gamma diversity values were the highest for the *Quercus* forest with 132 species ($\gamma' = 2.8$), followed by the subtropical shrubland with 90 species ($\gamma' = 1.76$), and the xerophytic shrubland with 85 species ($\gamma' = 1.64$) summing up a total of 218 species (see Appendix 1 for species names).

Beta diversity

The pairwise comparisons showed high dissimilarities between the *Quercus* forest and the xerophytic shrubland with $\beta cc = 0.86$ and the subtropical shrubland with $\beta cc = 0.84$. The lowest value ($\beta cc = 0.8$) resulted from the comparison between xerophytic and subtropical shrublands (Fig. 2A). The highest replacement (turnover) value derived from the pairwise comparison between the *Quercus* forest and the subtropical shrubland ($\beta_{-3} = 0.74$), which contrasts with the comparison of the *Quercus* forest and the xerophytic shrubland, where the turnover value reaches $\beta_{-3} = 0.57$. The pairwise comparison between the xerophytic and the subtropical shrublands showed equal values for replacement and richness differences (0.4).

The three vegetation types shared less than 20% of the species (25 taxa; Fig. 2A, B), including *Caloplaca microphyllina* (Tuck.) Hasse, *Flavopunctelia soredica* (Nyl.) Hale, and *Leptogium joergensenii* Marcelli & Kitaura. Notably, the *Quercus* forest had the highest value of unique species (85) and the subtropical shrubland had the lowest (33).

Communities

The heterogeneity among and within vegetation types was evaluated through a MRPP pairwise comparison, which showed statistical index (A) values < 0.5 and were significant ($p < 0.05$). This indicated that the lichen species composition per sampling site and each vegetation type (as a grouping variable) differed significantly (Fig. 3A).

Spatial ordination of communities based on the NMDS analysis (stress = 0.139) resulted in a compositional gradient guided by changes in elevation (R^2 with axis 1 = 0.55) and annual mean precipitation (R^2 with axis 1 = 0.56). From the highest number of unique species contained within the *Quercus* forest communities, few isolated elements were promoted by high elevations and mean precipitation (vectors with the same direction). However, one sampling site of the xerophytic shrubland (Cerro Juan El Grande) showed similar lichen composition and climatic conditions to the *Quercus* forest. In the opposite direction, some communities of the xerophytic shrubland were grouped by lower elevations and annual mean precipitation (Fig. 3A). An intermediate position was observed for the subtropical shrubland communities. However, some sites were closer to the xerophytic shrubland due to similar climatic conditions (Table 1) and to the *Quercus* forest due to similarities in species composition. The NMDS and the cluster analyses showed shared elements among lichen communities of the three vegetation types and an isolated set of sites depicting each vegetation type. After setting a 20% cutoff in the cluster dendrogram, four groups were displayed, one per vegetation type. An additional group corresponds to two xerophytic shrubland sites (Cerro Juan el Grande and Cerro el Capulín), which are more similar to the *Quercus* forest community (Fig. 3B).

The ISA analysis detected 14 species as indicators of the vegetation types (Table 3). Twelve of those species were associated to the *Quercus* forest with importance values (IV) ranging between 33.3 and 66.7 ($p < 0.05$). The species with the highest IV (66.7) were *Leptogium pseudofurfuraceum* P.M.Jørg., *Ochrolechia mexicana* Vainio, and *Parmotrema acutatum* Kurok. The remaining two indicator species were *Phaeophyscia nashii* Essl. and *Physcia biziana* (A.Massal.) Zahlbr. which were related to the subtropical shrubland. Those species belong to the family Physciaceae and exhibit the same growth form (foliose with narrow lobes), although *Physcia biziana* showed the highest importance value among the overall studied species (70.4). The ISA analysis did not detect any species with a significant association to the xerophytic shrubland.

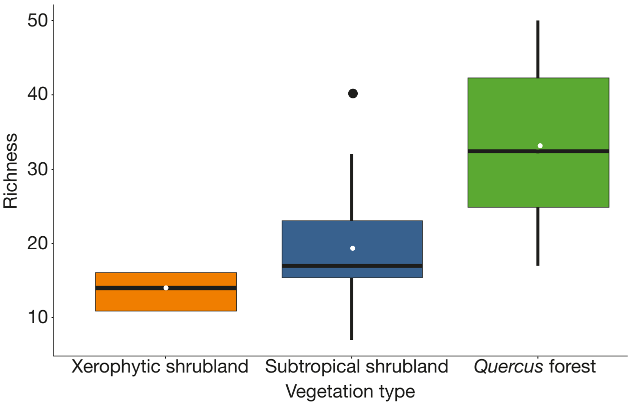

FIG. 1. — Amplitude and mean values of alpha diversity (species richness) per vegetation type. Symbols: **black dot**, outlier; **white dots**, mean values.

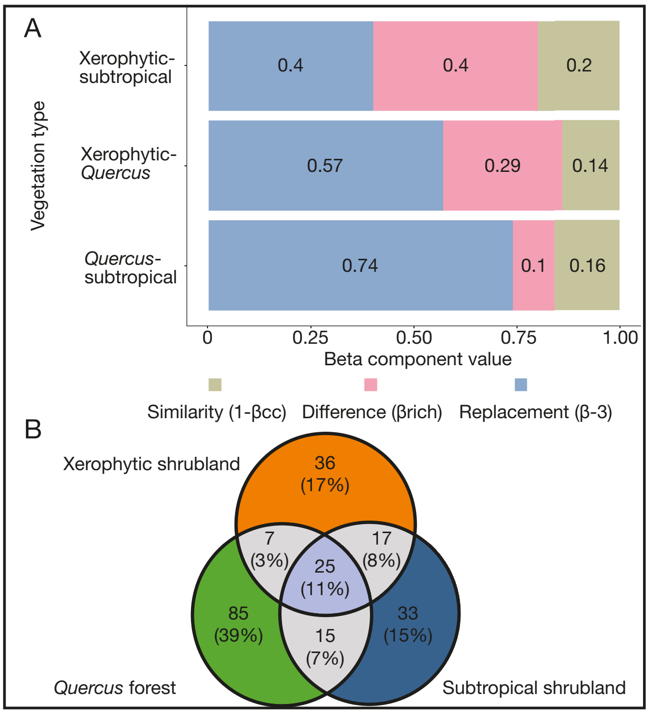

FIG. 2. — Beta diversity and shared species per vegetation type: **A**, pairwise comparisons of the different elements of beta diversity (**Xerophytic**, xerophytic shrubland; ***Quercus***, *Quercus* forest; **Subtropical**, subtropical shrubland); **B**, Venn diagram showing exclusive and shared species among the vegetation types included in this study.

TABLE 1. — Environmental variables and species richness values of the study sites.

Vegetation	Site	Latitude	Longitude	Elevation	Temperature (°C)	Precipitation (mm/y)	Richness
Xerophytic shrubland	Boca de Túnel	22.2344	–102.4368	2113	16.4	517.5	14
	Buenos Aires	21.9225	–102.5795	2272	16.2	635.6	13
	Campus sur UAA	21.7794	–102.2942	1900	17.4	522.3	17
	Cerro El Capulín	22.2445	–102.1532	2172	16.2	476.1	12
	El Tule	22.0738	–102.0771	2001	16.8	458.2	14
	Gracias a Dios	21.9312	–102.4837	2028	17.1	568.3	9
	Jocoqui	22.1466	–102.3662	2032	16.9	493.7	10
	Juan el Grande	21.9350	–101.9264	2238	16.2	495.4	15
	Mirasoles	22.3068	–102.4313	2291	15.8	543.1	21
	Pabellón Hidalgo	22.1856	–102.3409	2051	16.9	474.3	10
	Presa de Natillas	22.3486	–102.3298	2220	16.3	476.3	17
Quercus forest	Barranca del Toro	22.2585	–102.6348	2880	13.5	661.1	17
	Cerro Picacho	21.8779	–102.4229	2272	15.8	624.4	24
	EBAZ	22.0937	–102.5615	2280	16.1	597.9	50
	Los Alamitos	21.7345	–102.7135	2357	15.2	717.7	37
	Montegrande	22.2836	–102.6031	2872	12.7	654.9	44
	Sierra Fría	22.0618	–102.7409	2758	14.7	695.9	28
Subtropical shrubland	Adobes	21.8022	–102.6877	1936	17.4	643.7	40
	Arquitos	21.9204	–102.4019	2005	17.3	532	18
	Codorniz alto	22.0130	–102.6677	1830	17.4	596.2	16
	Codorniz bajo	22.0101	–102.6732	1821	17.4	596.2	32
	Jaltiche de Abajo	21.7773	–102.8167	1553	19.0	595.7	20
	Palo Alto	22.0564	–102.6688	2027	16.7	602.4	16
	Posta UAA	21.9827	–102.3757	1946	17.0	533.3	14
	Terrero de la Labor	22.0743	–102.6872	2480	15.6	648.2	7

TABLE 2. — Completeness of opportunistic sampling in all sites and vegetation types.

Index	All sites	Xerophytic shrubland	Subtropical shrubland	*Quercus* L. forest
Observed species	218	85	90	132
Chao 2	224	87	97	149
Chao 2 completeness (%)	97.32	97.70	92.78	88.59
Jacknife 1	226	88	92	133
Jacknife 1 completeness (%)	96.46	96.59	97.83	99.25

TABLE 3. — Lichen indicator species analysis for the three vegetation types. No indicator species was retrieved for the xerophytic shrubland.

Species	Group	Importance value	Mean	SD	*p*
Physcia biziana (A.Massal.) Zahlbr.	Subtropical shrubland	70.4	26.1	8.3	0.002
Leptogium pseudofurfuraceum P.M.Jørg. & Wallace	*Quercus* forest	66.7	18.1	9.21	0.004
Ochrolechia mexicana Vain.	*Quercus* forest	66.7	17.3	8.52	0.001
Parmotrema acutatum Kurok.	*Quercus* forest	66.7	17.9	9.36	0.003
Parmotrema reticulatum (Taylor) M.Choisy	*Quercus* forest	51.1	22.6	9.43	0.015
Flavopunctelia praesignis (Nyl.) Hale	*Quercus* forest	50	15.9	8.85	0.011
Haematomma flexuosum Hillm.	*Quercus* forest	50	15.2	8.34	0.007
Lecanora caesiorubella Ach.	*Quercus* forest	50	16.1	8.57	0.009
Polyblastidium hypoleucum (Ach.) Kalb	*Quercus* forest	50	15.1	8.22	0.008
Usnea florida (L.) Weber ex F.H.Wigg.	*Quercus* forest	50	16.2	9.13	0.018
Phaeophyscia nashii Essl.	Subtropical shrubland	46.2	19.1	9.25	0.019
Punctelia caseana Lendemer & Hodk.	*Quercus* forest	39.8	16.9	8.7	0.035
Parmotrema subtinctorium (Zahlbr.) Hale	*Quercus* forest	33.3	13.1	7.05	0.046
Usnea subfusca Stirton	*Quercus* forest	33.3	13	7.19	0.046

Functional traits and relation to environmental variables

The *Quercus* forest grouped all growth forms considered in this study and the foliose broad lobed lichens were the growth form with the highest CWM proportion. The crustose and squamulose lichens showed dominant proportions in xerophytic shrubland but lower proportions in the *Quercus* forest; otherwise, the foliose narrow lobed lichens showed the highest proportion in the subtropical shrubland. The fruticose lichens were only found in the *Quercus* forest, reaching 6% of the CWM (Fig. 4A).

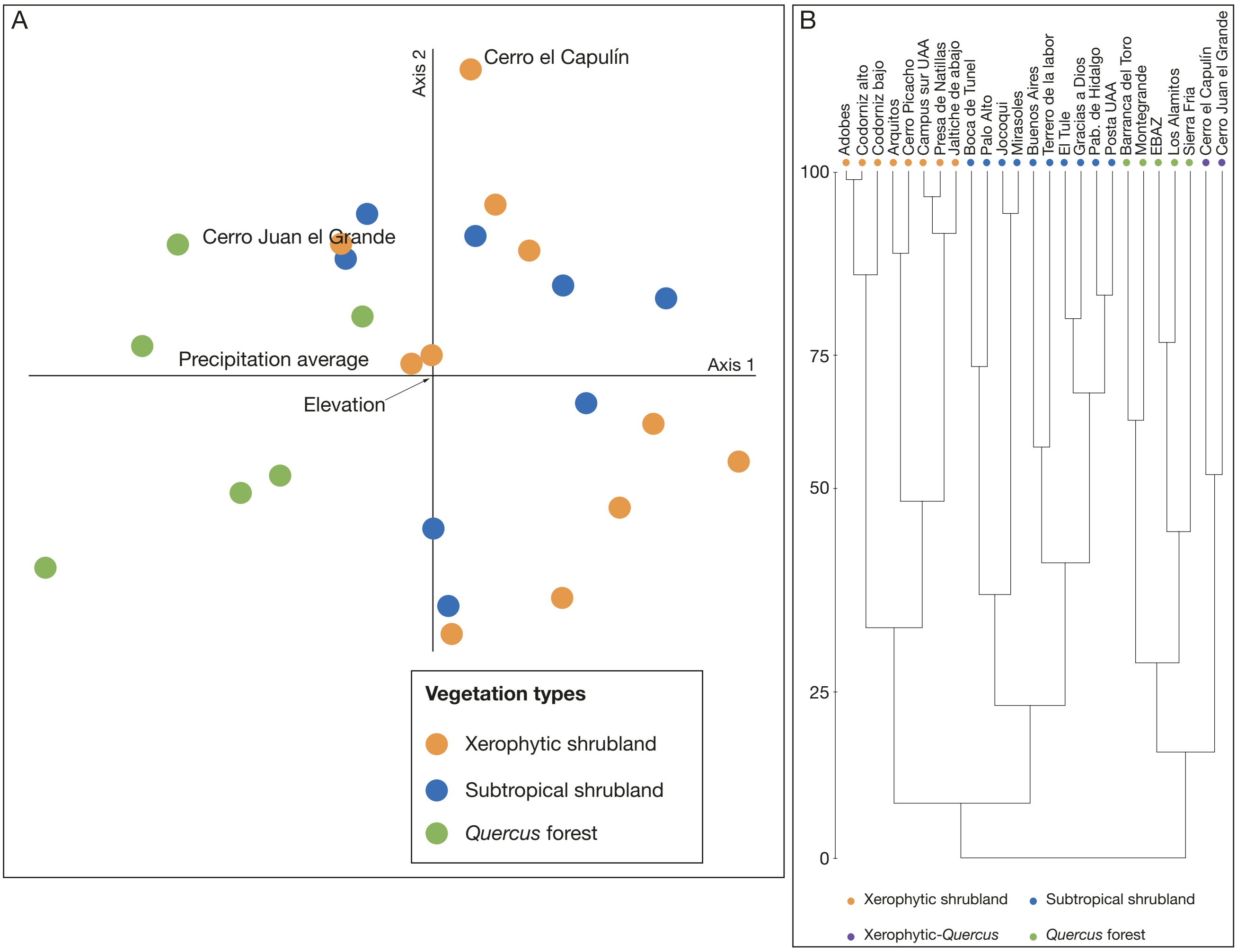

Fig. 3. — Ordination and clustering of lichen communities from the different vegetation types: **A**, non-parametric multidimensional scaling (NDMS); **B**, cluster analysis dendrogram. The sites Cerro el Capulín and Cerro Juan el Grande show different affinities in both analyses (part of the xerophytic shrubland in the NDMS, but more similar to the *Quercus* L. forest in the dendrogram, labeled as the Xerophytic-*Quercus* group in the latter).

For substrate CWM, the saxicolous lichens were predominant in the xerophytic shrubland, the epiphytic lichens had the highest proportion in *Quercus* forest, while the edaphic lichens had the lowest in the subtropical shrubland. Lichens colonizing more than one substrate (multiple) ranged between 14 and 20% in the different vegetation types (Fig. 4B).

The apothecia were the reproductive structure predominating in the three vegetation types. However, the soredia exhibited a high value in the subtropical shrublands (Fig. 4C). The lobules were the reproductive structure with the lowest values in the vegetation types. The isidia had its highest value in the *Quercus* forest, whereas the perithecia did the same in the xerophytic shrubland.

Chlorophyta photobionts predominated with more than 80% of the CWM in every vegetation type. There was an increased proportion of Cyanophyta photobionts from xerophytic shrubland (lowest CWM values) to *Quercus* forest (highest CWM values) (Fig. 4D).

The spatial ordination of functional traits, lichen communities, and environmental variables supported the patterns and gradients observed in the CWM analyses. The NMDS and ISA results applied to functional traits were combined to represent those traits that may be used as indicators of each type of vegetation (Fig. 5). The assemblage of crustose and squamulose growth forms with perithecia (reproduction) and saxicolous substrate (rock) was associated to xerophytic shrubland communities and responded to low precipitation and elevation. Foliose narrow lobed lichens and sorediated lichens indicated subtropical shrubland. Finally, the *Quercus* forest showed the highest number of significant traits, such as the dimorphic, fruticose, and foliose broad lobed lichens, isidia, and epiphytic substrate.

The NMDS, ISA, and FCA analyses showed similarities regarding the statistical significance of the gradient and relationships among functional traits and environmental variables. However, those results differed on the strength of the association of several traits. The FCA analysis showed that traits related to substrate were strong indicators, while others represented weak association.

According to the FCA, epiphytic lichens were positively influenced by precipitation (R = 0.3) and favored by the micro-

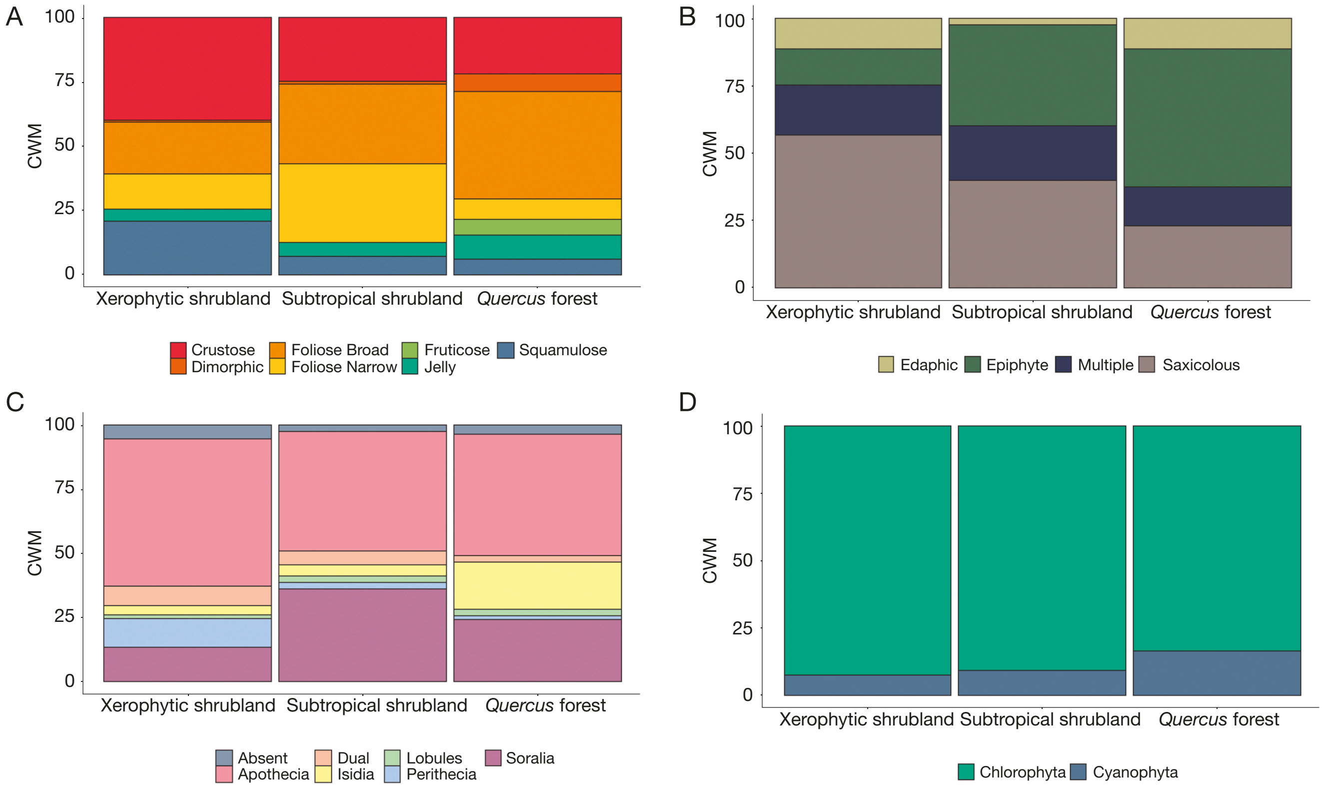

FIG. 4. — Community weighted mean proportions of functional traits for each vegetation type: **A**, growth forms; **B**, substrate; **C**, reproductive structure types; **D**, photobionts.

environmental conditions in the *Quercus* forest (R = 0.26), and negatively associated with the xerophytic shrubland (R = –0.33). On the other hand, saxicolous lichens decreased with increasing precipitation (R = –0.22). A weak but positive relationship (R = 0.17), was detected between elevation and edaphic lichens (Fig. 6).

Similar trends were detected when squamulose and foliose wide lobed lichens were compared (Fig. 6). The former decreased with higher precipitation regimes (R = –0.22) and was positively associated to xerophytic shrublands (R = 0.2). The foliose wide lobed lichens showed the inverse tendency. Like in the NMDS analysis, foliose narrow lobed lichens were indicators of the subtropical shrubland (R = 0.22).

Finally, the analysis of the reproductive strategies showed that isidia were positively associated with elevation and precipitation and, therefore, to the *Quercus* forest. Soredia were positively related to the subtropical shrubland and negatively associated with the xerophytic shrubland. Perithecia were negatively associated with precipitation and positively with the xerophytic shrubland.

DISCUSSION

DIVERSITY PATTERNS

Plant and fungal collections deposited in herbaria are a permanent and often a well-documented source to not only evaluate species taxonomy and distribution but to recognize and track global changes based on verifiable, repeatable, sustainable, and persistent information (Nualart *et al.* 2017; James *et al.* 2018), allowing the online mobilization of vast amounts of specimen data, combined to the use novel tools and extensive interdisciplinary collaborations (Davis 2023). For instance, herbarium specimens have been used to trace the composition and diversity of thelotremoid Graphidaceae as an indicator or signal of forest integrity (Rivas-Plata *et al.* 2008) and to evaluate the distribution and phylogenetic structure of lichen taxa in different vegetation types (Nascimento *et al.* 2021), where the existence of phylogenetic clustering in Parmeliaceae was revealed as a response to water stress in Mexican ecosystems (Lücking *et al.* 2016a). In addition, herbarium specimens' data in combination with published papers on lichen growth forms have been used to predict epiphytic lichen abundance in a wide variety of forest types (Aragón *et al.* 2019).

Herbarium collections have been used to recognize regional richness patterns of lichenized and no lichenized fungi of Colombia (Corrales *et al.* 2022; Moncada *et al.* 2022), which has helped not only to detect the richest ecosystems, but also the less explored areas. In this sense, our study shows suitable completeness in the exploration of vegetation types, even if the exploration was based on herbarium specimens. However, it is recognized that the observed richness depends on the sampling effort and almost unavoidably underestimates the value of total richness in a given community (Coddington *et al.* 2009). On the other hand, it has been discussed that highly geographically heterogeneous sampling efforts can result in

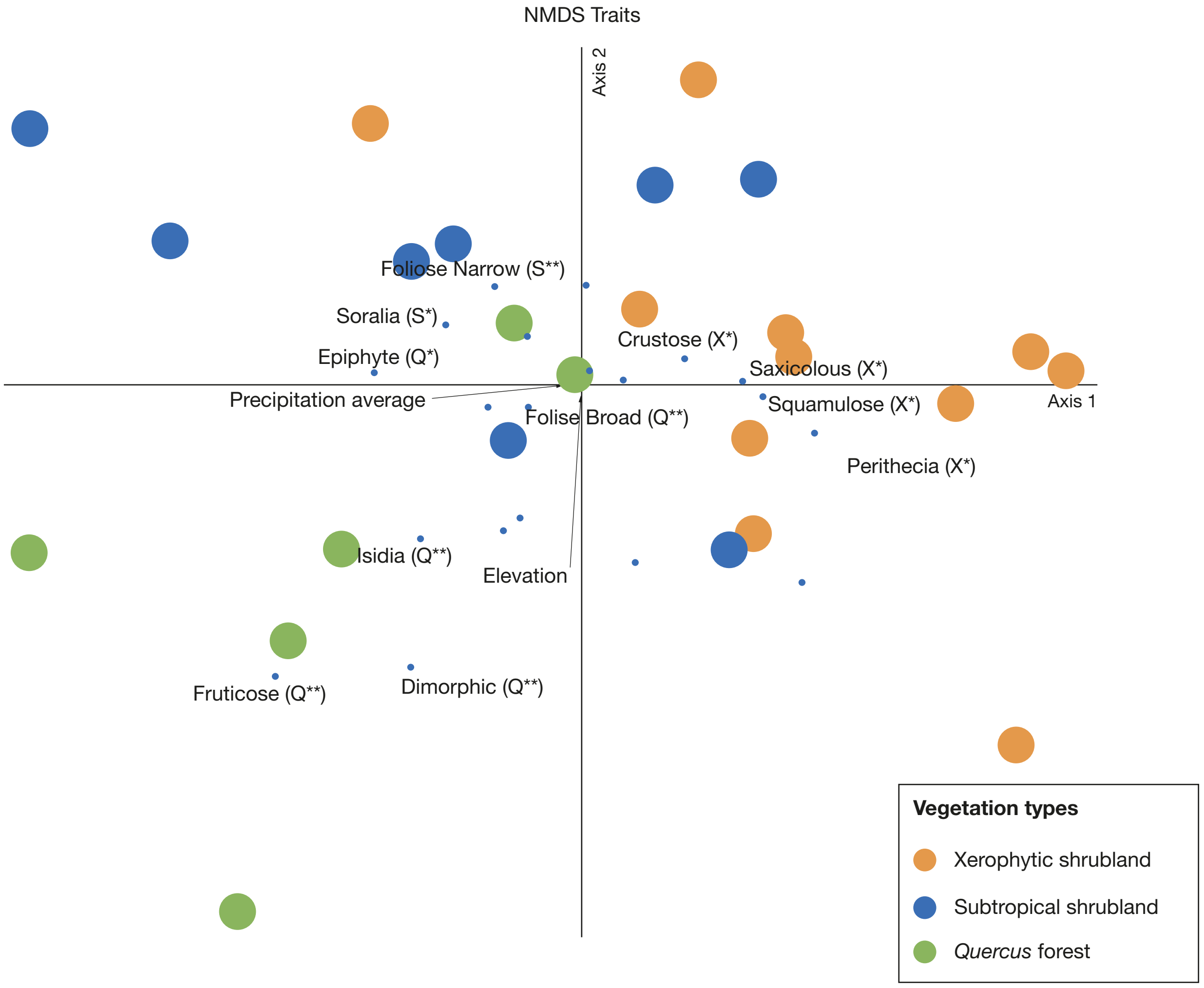

Fig. 5. — Non-metric Multidimensional Scaling analysis of lichen community functional traits and environmental variables in three vegetation types. * ($p < 0.05$) and ** ($p < 0.005$) represent the significance of functional traits related to the Xerophytic shrubland (**X**), Subtropical shrubland (**S**), and *Quercus* L. forest (**Q**).

a biased description of diversity gradients (Petřík *et al.* 2010; Droissart *et al.* 2012). Despite the sampling heterogeneity of individual localities in Aguascalientes for including non-opportunistic sampling, and differences in the number of sampling sites for each vegetation type, we used two approaches to make richness values comparable. First, we did not directly compare the values of richness among individual sites but explored the mean richness value among vegetation types. Second, we used the logarithmic transformation suggested by Cáceres *et al.* (2008) to compare the gamma diversity of vegetation types, and we included a trait-based approach to overcome the scale-dependency issue (Benítez *et al.* 2018; Zhou *et al.* 2018; Ellis *et al.* 2021).

Regarding inventories of specific vegetation types, one of the most impressive inventories of lichen richness in dry ecosystems of North America is the Lichen Flora of the Greater Sonoran Desert (Nash III *et al.* 2002, 2004, 2007), with more than 1900 species, some of which are distributed in Mexico. Another example for dry lands is the list of the Great Basin Desert, where 195 species are recorded (Hollinger & Noell 2020), and the richness of the Colorado Plateau, with 244 species (Leavitt *et al.* 2021). Compared with the Aguascalientes xerophytic shrubland, the 85 species recorded in this study would demonstrate low diversity, taking into account that previous studies considered the same substrate types as our research. This study is the second effort that records the arid land diversity of lichens in Aguascalientes (Miguel-Vázquez *et al.* 2021). Here, 15% of known lichen diversity in Mexican xerophytic ecosystems, according to Herrera-Campos *et al.* (2014) were registered.

Lichens are a fairly ubiquitous group in subtropical forests and constitute an important but scarcely studied component of this ecosystem (Marmor *et al.* 2011). The 90 species recorded for the subtropical shrubland of Aguascalientes (central Mexico) would seem few when compared with the 255 species of the subtropical forest of the northeastern region of Rio Grande do Sul, southern Brazil (Koch *et al.* 2016) or moderately diverse when compared with the 217 epiphytic species of the Xujiaba region of China, with an alpha range of 43 to 175 (Li *et al.* 2013). However, a similar diversity pattern is obtained after including the subtropical forest of Florida, with 101 species and an alpha diversity ranging between 12 and 51 species

(DeBolt *et al.* 2007), which also has more geographic and climatic similarities with the central part of Mexico.

Temperate forests, some of which are dominated by *Quercus* species, are considered the most studied ecosystems regarding lichen richness (over 947 species; Herrera-Campos *et al.* 2014) and lichen community ecology in Mexico (Herrera-Campos & Lücking 2003; Pérez-Pérez *et al.* 2008; Gregorio-Cipriano *et al.* 2016; León-González & Pérez-Pérez 2020). The records obtained in this study moderately represent the lichen richness in the *Quercus* forest, with *c.* 14% of the species known for this vegetation type.

Beta diversity was used here to support the framework of lichen community comparisons across Mexican ecosystems, as it has been successfully applied to lichens in the discernment of the causes of beta diversity patterns (Nascimbene & Spitale 2017) along latitudinal, biogeographic, or ecological gradients (Ramírez-Peña 2019; Castillo-Campos *et al.* 2019). Beta diversity pairwise comparisons among vegetation types resulted in high beta diversity values (≥ 0.8), coinciding with other studies that showed that different vegetation types sustain different lichen communities (Wolf 1993; Cáceres *et al.* 2008; Nascimbene *et al.* 2013). The differences referred to elevation, precipitation, and temperature, which influence the vascular composition of vegetation types and lichen composition in different communities (Cáceres *et al.* 2007; Benítez *et al.* 2015). Thus, the compositional pattern and high values of beta diversity among vegetation types observed in Aguascalientes support the hypothesis that environmental changes impact the richness and composition of lichen communities.

The species replacement was the main component of beta (Fig. 2A), indicating a change in taxonomic entities among vegetation types and a positive relationship between elevation, increasing richness, and species pool (Nascimbene & Marini 2015). The highest turnover was observed between the subtropical shrubland and the *Quercus* forest, which is related to temperature and elevation gradients. On the other hand, a decrease in precipitation may be related to species loss (richness differences), as evidenced after comparing the xerophytic shrubland with the *Quercus* forest, highlighting in turn the sensitivity of lichens to desiccation (Concostrina-Zubiri *et al.* 2014b). Therefore, a homogeneous habitat with low precipitation may thus promote competition among the species pool of the two types of shrublands, in addition to the colonization of the best-adapted species (Kraft *et al.* 2015), as reported for lichen communities in Eucalyptus stands (Calviño-Cancela *et al.* 2013; Ardila *et al.* 2014). Moreover, the high richness differences may be related to additional environmental factors such as vegetation density (Pérez-Pérez *et al.* 2011; Benítez *et al.* 2012, 2015) or canopy cover (Cáceres *et al.* 2007; Koch *et al.* 2013), although such variables were not considered in this study.

LICHEN COMMUNITIES

Cerro El Capulin (elevation = 2172; annual mean precipitation = 476.1 mm) and Cerro Juan El Grande (elevation = 2104.6 m; annual mean precipitation = 502.5 mm) are climatically similar to the xerophytic shrubland (mean elevation = 2119.8 m; annual mean precipitation = 514.6 mm). Moreover, the lichen species composition in these sites was similar to that of the *Quercus* forest. Four underlying factors may explain those similarities: 1) the lack of epiphytic substrate in those areas promotes the colonization of edaphic and saxicolous substrates, resulting in a distinctive set of species (Giordani *et al.* 2012; Jüriado *et al.* 2016); 2) the compositional affinities would be due to the abundance and frequency of *Quercus* species in Aguascalientes, which are even found in xerophytic shrublands (Martínez-Calderón *et al.* 2017); 3) the incorrect classification of the vegetation types due to the use of coarse-grain cartographical classification (INEGI 2017); and 4) the proportion of generalist species (11.4%) with a higher tolerance to local environmental factor variations, as often seen in the xerophytic shrubland and grassland ecosystems (Concostrina-Zubiri *et al.* 2014b).

Sites like Cerro Picacho, Presa de Natillas, and Campus Sur, were at first classified as xerophytic shrubland communities (Table 1), but their lichen composition resulted closer to the subtropical shrubland. This may be explained by the fact that, on average lower elevations of the subtropical shrubland and the higher precipitation regimes allow the colonization of several shared species including *Circinaria contorta* (Hoffm.) A.Nordin, Savić & Tibell, *Flavopunctelia soredica*, and *Phaeophyscia hirsuta* (Mereschk.) Essl. The differences among those vegetation types may be better understood through the relation of functional traits to reproduction strategies and growth forms, which in turn depend on water and shade availability (Lakatos *et al.* 2006; Ellis & Coppins 2007; Gauslaa 2014), factors that favor exclusive species to the subtropical shrubland.

FUNCTIONAL TRAITS AND INDICATOR SPECIES

The influence of elevation and precipitation gradients on functional traits and indicator species is shown by the prevalence of foliose wide lobe lichens (*Flavopunctelia praesignis* (Nyl.) Hale, *Parmotrema acutatum*) in the *Quercus* forest, the shift to narrow lobed lichens (*Physcia biziana*, *Phaeophyscia nashii*) in the subtropical shrubland, and the predominance of crustose (*Circinaria contorta*) or squamulose lichens (*Peltula hassei* (Zahlbr.) Büdel, *Protoparmeliopsis muralis* (Schreb.) M.Choisy) in the xerophytic shrubland. Those results suggest that the volume of lichen thallus decreases in response to water availability, compromising the photosynthetic area and keeping a wide exposure surface (Giordani *et al.* 2012, 2014; Nelson *et al.* 2015a; Lucheta *et al.* 2019).

The response to high precipitation of crustose and foliose wide lobed lichens in Mediterranean ecosystems (Matos *et al.* 2015) and tropical rainforests (Koch *et al.* 2022), has been reported to differ by a particular combination of traits. Those enhance the performance of crustose lichens, coupled with diverse reproductive strategies and hydrophobic surfaces (Lakatos *et al.* 2006), or may be due to the influence of geographical differences not only on environmental variables, but on the phylogenetic diversity (Cáceres *et al.* 2008; Rivas-Plata *et al.* 2008; Nascimento *et al.* 2021; Koch *et al.* 2022). An additional indicative trait is the fruticose growth form, which is positively related to precipitation and constitutes an exclusive attribute of the *Quercus* forest (Figs 4A; 5). This agrees with the positive relation to water availability found in Mediterranean ecosystems (Giordani *et al.* 2014; Matos *et al.* 2015) and Alaskan shrublands (Nelson *et al.* 2015b), whereas in the tropical rainforest (Koch *et al.* 2013, 2022; Benítez *et al.* 2018; Soto-Medina *et al.* 2019) the trait is associated with open sites.

In this study, the CWM proportion of Cyanophyta photobionts had a positive relation to precipitation and elevation, with a change among the vegetation types. However, the photobiont type as a trait appears to not be significantly associated with any vegetation type or environmental variable. Despite this, it has been used as an indicator of late successional states, which relates cyanolichens (lichens with Cyanophyta photobionts) to ancient forests or less fragmented habitats (Koch *et al.* 2013; Benítez *et al.* 2018; Chuquimarca *et al.* 2019), because of its dependence on liquid water to perform photosynthesis (Lakatos *et al.* 2006; Gauslaa 2014). Conversely, other studies have reported an increase in Cyanophyta photobionts in the early stages of perturbed (burned) forests or sites where water is scarce (Giordani *et al.* 2014, 2016; Matos *et al.* 2015; Nelson *et al.* 2015a). In such places, cyanolichens are found in sites with stagnant water, like rocks or shaded soil, where liquid water supply is enough to reactivate photosynthesis (Hauck *et al.* 2007).

On the other hand, the Chlorophyta photobionts were predominant in all vegetation types included in this study, a situation negatively related to elevation and the *Quercus* forest (see FCA). It has been documented that Chlorophyta photobionts have a better performance under low water supply conditions by using of dew and environmental humidity (Lakatos *et al.* 2006; Gauslaa 2014). This, in addition to the ISA results, supports the notion that Chlorophyta photobionts are generalists because they are not particularly associated with any vegetation type. However, derived from the association of lichens with Chlorophyta photobionts to high elevations (Rapai *et al.* 2012), the altitudinal gradients could be used as framework in the evaluation of the predictive power of photobionts as functional traits and the differentiation of Chlorophyte photobionts in Trebuxioid and Trentepohlioid groups to test climate change (Aptroot & Van Herk 2007; Marini *et al.* 2011; Koch *et al.* 2022).

The precipitation gradient observed in this study may be negatively related to the CWM of sexual structures. Perithecia was an indicator trait of the xerophytic shrubland, which decreased in other vegetation types. This pattern contrasts with the dominance of perithecia in late-successional stages of tropical forests (Koch *et al.* 2013; Benítez *et al.* 2018), where this structure indicates a healthy forest (Rivas-Plata *et al.* 2008). However, sexual structures have also been linked to harsh climatic conditions, where the perennial nature of lichen fruiting bodies constitute an advantage, providing a continual source of spores but with less metabolic investment per propagule when compared to asexual structures (Seymour *et al.* 2005). Furthermore, sexual reproduction generates novel genetic diversity within populations, facilitating the response to environmental change by genotype selection (Murtagh *et al.* 2000).

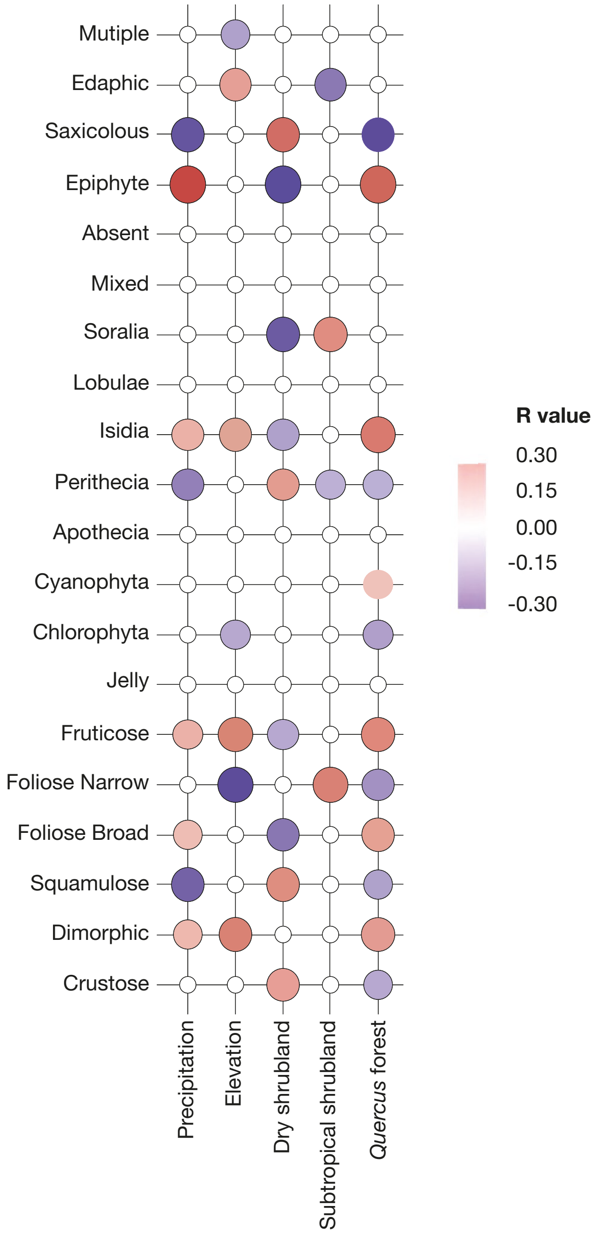

Fig. 6. — Correlation of lichen community functional traits and environmental variables in three vegetation types.

On the other hand, isidia have been associated with less harsh conditions (Ramírez-Morán *et al.* 2016; Chuquimarca *et al.* 2019), because the larger size of propagules implies a higher investment in the production of lichen substances and a shorter dispersion, fostering their competitive ability in stable and preserved habitats (Ellis & Coppins 2007). The isidia structure enhances dispersion capabilities by means of fragmentation and increases the exposition of thallus surface in low light conditions, thus enhancing its photosynthetic rate (Koch *et al.* 2013). The isidia is also an efective reproductive structure in both low wind flow and high rain flow conditions (Giordani *et al.* 2014). In this study, isidia constituted an indicative trait of *Quercus* forest, reaching high proportions of CWM and being positively related to precipitation and elevation, but negatively to xerophytic shrubland, in agreement with the previous studies.

It has been demonstrated that soralia represent a successful long-distance dispersion strategy (Nelson *et al.* 2015a), an efficient colonizer on smooth surfaces (Giordani *et al.* 2014), and a resistant diaspore that can colonize high pH substrates (Giordani *et al.* 2012), because its small size carries both partners of the lichen symbiosis. Those features provide resistance to substrates like *Bursera fagaroides* (Kunth) Engl., *Ipomoea murucoides* Roem. & Schult. and *Manihot caudata* Greenm., where soralia has been frequently recorded and which are representative of subtropical shrublands (Siqueiros-Delgado *et al.* 2017).

Finally, this is the first study that examines lichen communities in different vegetation types in central Mexico and the first in Mexico to evaluate lichen community assemblages and the composition of functional traits. It is essential to highlight that there is a correspondence between indicator species and functional traits, which is also related to diversity patterns studied in many ecosystems (e.g. Hurtado *et al.* 2019; Soto-Medina *et al.* 2019; Koch *et al.* 2022). The above reinforces the proposal of using lichens as bioindicators and functional traits as innovative but easy tool to study community assemblages and lichen responses to environmental gradients (Ellis *et al.* 2021).

CONCLUSION

Beta diversity and functional composition analyses were able to differentiate among lichen communities in vegetation types of central Mexico, showing that several lichen species could be used as targets in conservation programs. Elevation and precipitation were important features of each vegetation type, influencing lichen community composition (inherently including a set of indicator species and functional traits). In addition, lichen growth forms, substrates, and reproductive structures were indicative traits of the different vegetation types, rather than photobionts.

Acknowledgements

To the Consejo Nacional de Ciencia y Tecnología (Mexico) for the scholarship number 762521 provided to the first author and for giving financial support to the second author through grant 321671. To the Centro de Ciencias Básicas and the Biological Sciences Doctoral Program of the Universidad Autónoma de Aguascalientes (Mexico) for the academic and logistical support. To the anonymous referees for the suggestions that allowed to improve the manuscript.

REFERENCES

Álvarez I. & Guzmán-Dávalos L. 2009. — Flavopunctelia y Punctelia (Ascomycetes liquenizados) de Nueva Galicia, México. *Revista Mexicana de Micología* 29: 15-29. https://www.scielo.org.mx/pdf/rmm/v29/v29a4.pdf

Anderson M. J., Crist T. O., Chase J. M., Vellend M., Inouye B. D., Freestone A. L., Sanders N. J., Cornell H. V., Comita L. S., Davies K. F., Harrison S. P., Kraft N. J .B., Stegen J. C. & Swenson N. G. 2011. — Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters* 14 (1): 19-28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Aptroot A. & Van Herk C. M. 2007. — Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. *Environmental Pollution* 146 (2): 293-298. https://doi.org/https://doi.org/10.1016/j.envpol.2006.03.018

Aragón G., Martínez I., Hurtado P., Benítez Á., Rodríguez C. & Prieto M. 2019. — Using growth forms to predict epiphytic lichen abundance in a wide variety of forest types. *Diversity* 11 (4): 1-14. https://doi.org/10.3390/d11040051

Ardila A. I., Moncada B. & Lücking R. 2014. — Epiphyte homogenization and de-diversification on alien *Eucalyptus* versus native *Quercus* forest in the Colombian Andes: a case study using lirellate Graphidaceae lichens. *Biodiversity and Conservation* 24 (5): 1239-1252. https://doi.org/10.1007/s10531-014-0855-7

Asplund J. & Wardle D. A. 2017. — How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews* 92 (3): 1720-1738. https://doi.org/10.1111/brv.12305

Ávila-Villegas H., Melgarejo E. D. & Cruz-Angón A. 2008. — *La Biodiversidad en Aguascalientes: Estudio de Estado*. CONABIO [Comisión Nacional para el Conocimiento y Uso de la Biodiversidad], IMAE [Instituto del Medio Ambiente del Estado de Aguascalientes], UAA [Universidad Autónoma de Aguascalientes], Mexico, 384 p.

Belnap J. 2002. — Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils* 35 (2): 128-135. https://doi.org/10.1007/s00374-002-0452-x

Belnap J. & Lange O. L. 2001. — *Biological soil crusts: Structure, Function and Management*. Springer, Würzburg, 496 p.

Benítez A., Prieto M., González Y. & Aragón G. 2012. — Effects of tropical montane forest disturbance on epiphytic macrolichens. *Science of the Total Environment* 441: 169-175. https://doi.org/10.1016/j.scitotenv.2012.09.072

Benítez A., Prieto M. & Aragón G. 2015. — Large trees and dense canopies: key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. Forestry: *An International Journal of Forest Research* 88 (5): 521-527. https://doi.org/10.1093/forestry/cpv022

Benítez A., Aragón G., González Y. & Prieto M. 2018. — Functional traits of epiphytic lichens in response to forest disturbance and as predictors of total richness and diversity. *Ecological Indicators* 86: 18-26. https://doi.org/https://doi.org/10.1016/j.ecolind.2017.12.021

Boonpragob K. & Polyiam W. 2007. — Ecological groups of lichens along environmental gradients on two different host tree species in the tropical rain forest at Khao Yai National Park, Thailand. *Bibliotheca Lichenologica* 96: 25-48.

Branquinho C., Matos P. & Pinho P. 2015. — Lichens as ecological indicators to track atmospheric changes: future challenges, *in* Lindenmayer D., Barton P. & Pierson J. (eds), *Indicators and Surrogates of Biodiversity and Environmental Change*. CSIRO Publishing, Melbourne, Clayton South: 77-90.

Brodo I. M., Sharnoff S. D. & Sharnoff S. 2001. — *Lichens of North America*. Yale University Press, New Haven, 794 p.

Brodo I., Sharnoff S. D. & Sharnoff S. 2016. — *Keys to lichens of North America: revised and expanded*. Yale University Press, New Haven, 427 p.

Cáceres M., Lücking R. & Rambold G. 2007. — Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. *Mycological Progress* 6 (3): 117-136. https://doi.org/10.1007/s11557-007-0532-2

Cáceres M., Lücking R. & Rambold G. 2008. — Corticolous microlichens in northeastern Brazil: habitat differentiation between coastal Mata Atlântica, Caatinga and Brejos de Altitude. *The Bryologist* 111 (1): 98-117. https://doi.org/10.1639/0007-2745(2008)111[98:CMINBH]2.0.CO;2

Calderón-Patrón J. M., Moreno C. E., Pineda-López R., Sánchez-Rojas G. & Zuria I. 2013. — Vertebrate dissimilarity due to turnover and richness differences in a highly beta-diverse region: The role of spatial grain size, dispersal ability and distance. *PLoS ONE* 8 (12): 1-10. https://doi.org/10.1371/journal.pone.0082905

Calviño-Cancela M., De Silanes M. E. L., Rubido-Bará M. & Uribarri J. 2013. — The potential role of tree plantations in providing habitat for lichen epiphytes. *Forest Ecology and Management* 291: 386-395. https://doi.org/10.1016/j.foreco.2012.11.023

Carvalho J. C., Cardoso P. & Gomes P. 2012. — Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography* 21 (7): 760-771. https://doi.org/10.1111/j.1466-8238.2011.00694.x

Castillo-Campos G., Pérez-Pérez R. E., Córdova-Chávez O., García-Franco J. G. & Cáceres M. 2019. — Vertical distribution of epiphytic lichens on *Quercus laurina* Humb. & Bonpl. in a remnant of cloud forest in the state of Veracruz, México. *Nordic Journal of Botany* 37 (12): 1-11. https://doi.org/10.1111/njb.02459

Chuquimarca L., Gaona F. P., Iñiguez-Armijos C. & Benítez Á. 2019. — Lichen Responses to Disturbance: Clues for Biomonitoring Land-use Effects on Riparian Andean Ecosystems. *Diversity* 11 (5): 73-98. https://doi.org/10.3390/d11050073

CNALH 2022. — Consortium of North American Lichen Herbaria. Available from https://lichenportal.org/cnalh/index.php (accessed on 22 February 2022).

Coddington J. A., Agnarsson I., Miller J. A., Kuntner M. & Hormiga G. 2009. —Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology* 78: 573-584.

CONABIO 2021. — Portal de geoinformación 2021. Available from http://www.conabio.gob.mx/informacion/gis/ (accessed on 19 September 2021).

Concostrina-Zubiri L., Martínez I., Rabasa S. & Escudero A. 2014a. — The influence of environmental factors on biological soil crust: from a community perspective to a species level approach. *Journal of Vegetation Science* 25 (2): 503-513. https://doi.org/10.1111/jvs.12084

Concostrina-Zubiri L., Pescador D. S., Martínez I. & Escudero A. 2014b. — Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands. *Biodiversity and Conservation* 23 (7): 1757-1770. https://doi.org/10.1007/s10531-014-0683-9

Córdova-Chávez O., Castillo-Campos G., Pérez-Pérez R., García-Franco J. & Cáceres M. 2016. — Alpha diversity of lichens associated with *Quercus laurina* in a Mountain Cloud Forest at Cofre de Perote eastern slope (La Cortadura), Veracruz, Mexico. *Cryptogamie, Mycologie* 37 (2): 193-204. https://doi.org/10.7872/crym/v37.iss2.2016.193

Cornelissen J., Lang S. I., Soudzilovskaia N. A. & During H. J. 2007. — Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany* 99 (5): 987-1001. https://doi.org/10.1093/aob/mcm030

Corrales A., Benjumea C. & Gomez-Montoya N. 2022. — Diversity, Functional Groups, and Community Structure of Fungi of Colombia, *in* de Almeida R. F., Lücking R., Vasco-Palacios A., Gaya E. & Diazgranados M. (eds), *Catalogue of Fungi of Colombia*. Kew Publishing, Royal Botanic Gardens, Kew, London: 139-150.

Cuervo-Robayo A. P., Ureta C., Gómez-Albores M. A., Meneses-Mosquera A. K., Téllez-Valdés O. & Martínez-Meyer E. 2020. — One hundred years of climate change in Mexico. *PLoS ONE* 15 (7): e0209808. https://doi.org/10.1371/journal.pone.0209808

DeBolt A. M., Rosentreter R. & Martin E. P. 2007. — Macrolichen diversity in subtropical forests of north-central Florida. *Bryologist* 110 (2): 254-265. https://doi.org/10.1639/0007-2745(2007)110[254:MDISFO]2.0.CO;2

Davis C. C. 2023. — The herbarium of the future. *Trends in Ecology & Evolution* 38 (5): 412-423. https://doi.org/10.1016/j.tree.2022.11.015

Díaz S. & Cabido M. 2001. — Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16 (11): 646-655. https://doi.org/https://doi.org/10.1016/S0169-5347(01)02283-2

Droissart V., Hardy O. J., Sonké B., Dahdouh-Guebas F. & Stévart T. 2012. — Subsampling herbarium collections to assess geographic diversity gradients: a case study with endemic Orchidaceae and Rubiaceae in Cameroon. *Biotropica* 44 (1): 44-52. https://doi.org/10.1111/j.1744-7429.2011.00777.x

Ellis C. 2012. — Lichen epiphyte diversity: A species, community and trait-based review. *Perspectives in Plant Ecology, Evolution and Systematics* 14 (2): 131-152. https://doi.org/10.1016/j.ppees.2011.10.001

Ellis C. & Coppins B. 2007. — Reproductive strategy and the compositional dynamics of crustose lichen communities on aspen (*Populus tremula* L.) in Scotland. *The Lichenologist* 39 (4): 377-391. https://doi.org/10.1017/S0024282907006937

Ellis C. J., Asplund J., Benesperi R., Branquinho C., Nuzzo L. Di, Hurtado P., Mart I., Matos P., Nascimbene J., Pinho P., Rocha B., Rodr C., Thüs H. & Giordani P. 2021. — Functional Traits in Lichen Ecology: A Review of Challenge and Opportunity. *Microorganisms* 9 (4): 776. https://doi.org/10.3390/microorganisms9040766

Gauslaa Y. 2014. — Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *The Lichenologist* 46 (1): 1-16. https://doi.org/10.1017/S0024282913000753

Giordani P., Brunialti G., Bacaro G. & Nascimbene J. 2012. — Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecological Indicators* 18: 413-420. https://doi.org/10.1016/j.ecolind.2011.12.006

Giordani P., Incerti G., Rizzi G., Rellini I., Nimis P. L. & Modenesi P. 2014. — Functional traits of cryptogams in Mediterranean ecosystems are driven by water, light and substrate interactions. *Journal of Vegetation Science* 25 (3): 778-792. https://doi.org/10.1111/jvs.12119

Giordani P., Rizzi G., Caselli A., Modenesi P., Malaspina P. & Mariotti M. G. 2016. — Fire affects the functional diversity of epilithic lichen communities. *Fungal Ecology* 20: 49-55. https://doi.org/https://doi.org/10.1016/j.funeco.2015.11.003

Gregorio-Cipriano M., Gómez-Peralta M. & Álvarez I. 2016. — Líquenes cortícolas de las áreas urbanas y suburbanas de Morelia, Michoacán, México. *Botanica Complutensis* 40: 9-21 https://doi.org/10.5209/BOCM.53195

Guevara M. & Arroyo-Cruz C. E. 2016. — Modelo digital de elevaciones sin oquedades resolución 1 km. Available from http://www.conabio.gob.mx/informacion/metadata/gis/filled_demgw.xml?_httpcache=yes&_xsl=/db/metadata/xsl/fgdc_html.xsl&_indent=no%0ADescripción (accessed on 12 February 2022).

Gutiérrez-Larruga B., Estébanez-Pérez B. & Ochoa-Hueso R. 2020. — Effects of Nitrogen Deposition on the Abundance and Metabolism of Lichens: A Meta-analysis. *Ecosystems* 23 (4): 783-797. https://doi.org/10.1007/s10021-019-00431-4

Hauck M., Dulamsuren C. & Mühlenberg M. 2007. — Lichen diversity on steppe slopes in the northern Mongolian mountain taiga and its dependence on microclimate. *Flora – Morphology, Distribution, Functional Ecology of Plants* 202 (7): 530-546. https://doi.org/https://doi.org/10.1016/j.flora.2006.11.003

Hawksworth D. L. & Grube M. 2020. — Lichens redefined as complex ecosystems. *New Phytologist* 227 (5): 1281-1283. https://doi.org/10.1111/nph.16630

Hawksworth D. L., Iturriaga T. & Crespo A. 2005. — Líquenes como bioindicadores inmediatos de contaminación y cambios medioambientales en los trópicos. *Revista Iberoamericana de Micología* 22 (2): 71-82. https://doi.org/10.1016/S1130-1406(05)70013-9

Hedenås H. & Ericson L. 2000. — Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biological Conservation* 93 (1): 43-53. https://doi.org/https://doi.org/10.1016/S0006-3207(99)00113-5

Heino J., Alahuhta J., Fattorini S. & Schmera D. 2019. — Predicting beta diversity of terrestrial and aquatic beetles using ecogeographical variables: insights from the replacement and richness difference components. *Journal of Biogeography* 46 (2): 304-315. https://doi.org/10.1111/jbi.13485

Herrera-Campos M. A. & Lücking R. 2003. — The foliicolous lichen flora of Mexico II. New species from the montane forest in Oaxaca and Puebla. *The Bryologist* 106 (1): 1-8. https://doi.org/10.1639/0007-2745(2003)106[0001:TFLFOM]2.0.CO;2

Herrera-Campos M. A., Lücking R., Pérez-Pérez R. E., Miranda-González R., Sánchez N., Barcenas-Peña A., Carrizosa A., Zambrano A., Ryan B. & Nash T. 2014. — Biodiversidad de líquenes en México. Revista Mexicana de Biodiversidad 85: 82-99. https://doi.org/10.7550/rmb.37003

Hollinger J. & Noell N. 2020. — New Reports of Great Basin Desert Lichens in California. *Bulletin of the California Lichen Society* 27 (2): 47-55

Hurtado P., Prieto M., Aragón G., Escudero A. & Martínez I. 2019. — Critical predictors of functional, phylogenetic and taxonomic diversity are geographically structured in lichen epiphytic communities. *Journal of Ecology* 107 (5): 2303-2316. https://doi.org/10.1111/1365-2745.13189

Hurtado P., Prieto M., Martínez-Vilalta J., Giordani P., Aragón G., López-Angulo J., Košuthová A., Merinero S., Díaz-Peña E. M., Rosas T., Benesperi R., Bianchi E., Grube M., Mayrhofer H., Nascimbene J., Wedin M., Westberg M. & Martínez I. 2020. — Disentangling functional trait variation and covariation in epiphytic lichens along a continent-wide latitudinal gradient. *Proceedings of the Royal Society B: Biological Sciences* 287: 20192862. https://doi.org/10.1098/rspb.2019.2862

INEGI 2017. — Uso del suelo y vegetación, escala 1:250000, serie VI. Available from http://www.conabio.gob.mx/informacion/gis/ (accessed on 12 February 2022).

James S. A., Soltis P. S., Belbin L., Chapman A. D., Nelson G., Paul D. L. & Collins M. 2018. — Herbarium data: Global biodiversity and societal botanical needs for novel research. *Applications in Plant Sciences* 6 (2): e1024. https://doi.org/10.1002/aps3.1024

Jüriado I., Kämärä M.-L. & Oja E. 2016. — Environmental factors and ground disturbance affecting the composition of species and functional traits of ground layer lichens on grey dunes and dune heaths of Estonia. *Nordic Journal of Botany* 34 (2): 244-255. https://doi.org/10.1111/njb.00936

Käffer M. I., Ganade G. & Marcelli M. P. 2009. — Lichen diversity and composition in Araucaria forests and tree monocultures in southern Brazil. *Biodiversity and Conservation* 18 (13): 3543-3561. https://doi.org/10.1007/s10531-009-9659-6

Käffer M. I., Marcelli M. P. & Ganade G. 2010. — Distribution and composition of the lichenized mycota in a landscape mosaic of southern Brazil. *Acta Botanica Brasilica* 24 (3): 790-802. https://doi.org/10.1590/S0102-33062010000300022

Käffer M. I., Martins S., Alves C., Pereira V. C., Fachel J. & Vargas V. 2011. — Corticolous lichens as environmental indicators in urban areas in southern Brazil. *Ecological Indicators* 11 (5): 1319-1332. https://doi.org/10.1016/j.ecolind.2011.02.006

Kitaura M. J., Koch N., Lucheta F., Käffer M. I., Schmitt J. L., Pedroso J., Martins S., Rodrigues A. S. & Canêz L. S. 2019. — A new species and new records of *Leptogium* (Ach.) Gray (Collemataceae, Peltigerales) from Rio Grande do Sul State with an identification key for the genus. *Anais da Academia Brasileira de Ciencias* 91 (1): e20180313. https://doi.org/10.1590/0001-3765201920180313

Koch N., Martins S., Lucheta F. & Müller S. C. 2013. — Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. *Ecological Indicators* 34: 22-30. https://doi.org/10.1016/j.ecolind.2013.04.012

Koch N., Branquinho C., Matos P., Pinho P., Lucheta F., Martins S. & Vargas V. 2016. — The application of lichens as ecological surrogates of air pollution in the subtropics: a case study in South Brazil. *Environmental Science and Pollution Research* 23 (20): 20819-20834. https://doi.org/10.1007/s11356-016-7256-2

Koch N., Matos P., Branquinho C., Pinho P., Lucheta F., Martins S. & Vargas V. 2019. — Selecting lichen functional traits as ecological indicators of the effects of urban environment. *Science of the Total Environment* 654: 705-713. https://doi.org/10.1016/j.scitotenv.2018.11.107

Koch N., Stanton D., Müller S. C., Duarte L. & Spielmann A. 2022. — Nuanced qualitative trait approaches reveal strong environmental filtering and phylogenetic constraints on lichen communities during tropical forest succession. *Ecosphere* 13 (4): e4042. https://doi.org/10.1002/ecs2.4042

Kraft N. J. B., Adler P. B., Godoy O., James E. C., Fuller S. & Levine J. M. 2015. — Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29 (5): 592-599. https://doi.org/https://doi.org/10.1111/1365-2435.12345

Lakatos M., Rascher U. & Büdel B. 2006. — Functional characteristics of corticolous lichens in the understory of a tropical lowland rain forest. *New Phytologist* 172 (4): 679-695. https://doi.org/10.1111/j.1469-8137.2006.01871.x

Lalley J. S., Viles H. A., Henschel J. R. & Lalley V. 2006. — Lichen-dominated soil crusts as arthropod habitat in warm deserts. *Journal of Arid Environments* 67 (4): 579-593. https://doi.org/10.1016/j.jaridenv.2006.03.017

Lavorel S. & Garnier E. 2002. — Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology* 16 (5): 545-556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Leavitt S. D., Hollinger J., Summerhays S., Munger I., Allen J. & Smith B. 2021. — Alpine lichen diversity in an isolated sky island in the Colorado Plateau, USA – Insight from an integrative biodiversity inventory. *Ecology and Evolution* 11 (16): 11090-11101. https://doi.org/10.1002/ece3.7896

Legendre P., Galzin R. & Harmelin-Vivien M. L. 1997. — Relating behavior to habitat: solutions to thefourth-corner problem. *Ecology* 78 (2): 547-562. https://doi.org/10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2

León-González D. & Pérez-Pérez R. E. 2020. — Líquenes epífitos en *Juniperus flaccida* Schltdl. (Cupressaceae) – Componente importante de los bosques templados de Oaxaca, México. *Acta Biológica Colombiana* 25 (2): 235-245. https://doi.org/10.15446/abc.v25n2.77238

Li S., Liu W. Y. & Li D. W. 2013. — Epiphytic lichens in subtropical forest ecosystems in southwest China: Species diversity and implications for conservation. *Biological Conservation* 159: 88-95. https://doi.org/10.1016/j.biocon.2012.12.027

Llop E., Pinho P., Ribeiro M. C., Pereira M. J. & Branquinho C. 2017. — Traffic represents the main source of pollution in small Mediterranean urban areas as seen by lichen functional groups. *Environmental Science and Pollution Research* 24 (13): 12016-12025. https://doi.org/10.1007/s11356-017-8598-0

Lucheta F., Mossmann Koch N., Käffer M. I., Plangg Riegel R., Martins S., Schmitt J. L., Koch N., Isabel M. & Plangg R. 2019. — Lichens as indicators of environmental quality in southern Brazil: An integrative approach based on community composition and functional parameters. *Ecological Indicators* 107: 105587. https://doi.org/10.1016/j.ecolind.2019.105587

Lücking R., Villaseñor J. L., Herrera-Campos M. A., Pérez-Pérez R. E., Egan R. S., Esslinger T. L. & Nash III T. H. 2016a. — Phylogenetic structure of metacommunities in Mexican Parmeliaceae (lichenized Ascomycota: Lecanorales). *Bibliotheca Lichenologica* 110: 27-54

Lücking R., Hodkinson B. P. & Leavitt S. 2016b. — The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota-Approaching one thousand genera. *The Bryologist* 119 (4): 361-416. https://doi.org/10.1639/0007-2745-119.4.361

Lücking R., Leavitt S. & Hawksworth D. L. 2021. — Species in lichen-forming fungi: balancing between conceptual and practical considerations, and between phenotype and phylogenomics. *Fungal Diversity* 109: 99-154. https://doi.org/10.1007/s13225-021-00477-7

Marini L., Nascimbene J., Nimis P. L., Luigi P. & Nimis P. L. 2011. — Large-scale patterns of epiphytic lichen species richness: Photobiont-dependent response to climate and forest structure. *Science of the Total Environment* 409 (20): 4381-4386. https://doi.org/https://doi.org/10.1016/j.scitotenv.2011.07.010

Martínez-Calderón V., Siqueiros-Delgado M. & Martínez-Ramírez J. 2017. — Checklist of the genus *Quercus* (Fagaceae) of Aguascalientes, México. *Check List* 13 (1): 1-22. https://doi.org/10.15560/13.1.2045

Marmor L., Tõrra T., Saag L. & Randlane T. 2011. — Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. *Ecological Indicators* 11 (5): 1270-1276. https://doi.org/10.1016/j.ecolind.2011.01.009

Matos P., Pinho P., Aragón G., Martínez I., Nunes A., Soares A. M., Branquinho C., Amadeu S. & Branquinho C. 2015. — Lichen traits responding to aridity. *Journal of Ecology* 103 (2): 451-458. https://doi.org/10.1111/1365-2745.12364

Matos P., Vieira J., Rocha B., Branquinho C. & Pinho P. 2019. — Modeling the provision of air-quality regulation ecosystem service provided by urban green spaces using lichens as ecological indicators. *Science of the Total Environment* 665: 521-530. https://doi.org/https://doi.org/10.1016/j.scitotenv.2019.02.023

McCune B. 2000. — Lichen communities as indicators of forest health. *The Bryologist* 103 (2): 353-356. https://doi.org/10.1639/0007-2745(2000)103[0353:LCAIOF]2.0.CO;2

McCune B. 2015. — The front door to the fourth corner: variations on the sample unit × trait matrix in community ecology. *Community Ecology* 16 (2): 267-271. https://doi.org/10.1556/168.2015.16.2.14

McCune B. & Mefford M. J. 2018. — PC-ORD. Multivariate Analysis of Ecological Data. Version 7.08. MJM Software, Gleneden Beach.

Miguel-Vázquez M., Simijaca D., Pérez-Pérez R. E. & Ocampo G. 2021. — Lichenized fungi of the arid zones of central Mexico: new records for the country and the state of Aguascalientes. *Sydowia* 74: 15-31. https://doi.org/10.12905/0380.sydowia74-2021-0015

Miranda-González R. & McCune B. 2020. — The weight of the crust: Biomass of crustose lichens in tropical dry forest represents more than half of foliar biomass. *Biotropica* 52 (6): 1298-1308. https://doi.org/10.1111/btp.12837

Moncada B., Coca L. F., Díaz-Escandón D., Jaramillo-Ciro M., Simijaca D., Soto-Medina E. & Lücking R. 2022. — Diversity, ecogeography, and importance of lichens of Colombia, *in* de Almeida R. F., Lücking R., Vasco-Palacios A., Gaya E. & Diazgranados M. (eds), *Catalogue of Fungi of Colombia*. Kew Publishing, Royal Botanic Gardens, Kew, London: 77-91.

Mongkolsuk P., Meesim S., Poengsungnoen V., Buaruang K., Schumm F. & Kalb K. 2015. — The lichen family Physciaceae in Thailand – II. Contributions to the genus *Heterodermia sensu lato*. *Phytotaxa* 235: 1-66. https://doi.org/10.11646/phytotaxa.235.1.1

Murtagh G. J., Dyer P. S. & Crittenden P. D. 2000. — Sex and the single lichen. *Nature* 404: 564. https://doi.org/10.1038/35007142

Nascimbene J., Benesperi R., Brunialti G., Catalano I., Vedove M. D., Grillo M., Isocrono D., Matteucci E., Potenza G., Puntillo D., Puntillo M., Ravera S., Rizzi G. & Giordani P. 2013. — Patterns and drivers of β-diversity and similarity of *Lobaria pulmonaria* communities in Italian forests. *Journal of Ecology* 101 (2): 493-505. https://doi.org/10.1111/1365-2745.12050

Nascimbene J. & Marini L. 2015. — Epiphytic lichen diversity along elevational gradients: biological traits reveal a complex response to water and energy. *Journal of Biogeography* 42 (7): 1222-1232. https://doi.org/10.1111/jbi.12493

Nascimbene J. & Spitale D. 2017. — Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario. *Biological Conservation* 216: 26-32. https://doi.org/10.1016/j.biocon.2017.09.021

Nascimento E., Maia L. C., Cáceres M. & Lücking R. 2021. — Phylogenetic structure of lichen metacommunities in Amazonian and Northeast Brazil. *Ecological Research* 36 (3): 440-463. https://doi.org/10.1111/1440-1703.12206

Nash III T., Ryan B., Gries C. & Bungartz F. 2002. — *Lichen flora of the greater Sonoran desert region*. Vol. 1. Lichens Unlimited, Arizona State University, Tempe.

Nash III T., Ryan B., Diederich P., Gries C. & Bungartz F. 2004. — *Lichen flora of the greather Sonoran desert region*. Vol. 2. Lichens Unlimited, Arizona State University, Tempe.

Nash III T., Ryan B., Diederich P., Gries C. & Bungartz F. 2007. — *Lichen flora of the greater Sonoran desert region*. Vol. 3. Lichens Unlimited, Arizona State University, Tempe.

Nelsen M. P., Lücking R., Boyce C. K., Lumbsch H. T. & Ree R. H. 2020. — The macroevolutionary dynamics of symbiotic and phenotypic diversification in lichens. *Proceedings of the National Academy of Sciences of the United States of America* 117 (35): 21495-21503. https://doi.org/10.1073/pnas.2001913117

Nelson P. R., McCune B., Roland C. & Stehn S. 2015a. — Nonparametric methods reveal non-linear functional trait variation of lichens along environmental and fire age gradients. *Journal of Vegetation Science* 26 (5): 848-865. https://doi.org/10.1111/jvs.12286

Nelson P. R., McCune B. & Swanson D. K. 2015b. — Lichen traits and species as indicators of vegetation and environment. *The Bryologist* 118 (3): 252-263. https://doi.org/10.1639/0007-2745-118.3.252

Nimis P. L., Scheidegger C. & Wolseley P. A. 2002. — *Monitoring with Lichens – Monitoring Lichens*. Springer, Dordrecht, 408 p.

Nordén B., Paltto H., Claesson C. & Götmark F. 2012. — Partial cutting can enhance epiphyte conservation in temperate oak-rich forests. *Forest Ecology and Management* 270: 35-44. https://doi.org/10.1016/j.foreco.2012.01.014

Nualart N., Ibáñez N., Soriano I. & López-Pujol J. 2017. — Assessing the relevance of herbarium collections as tools for conservation biology. *The Botanical Review* 83 (3): 303-325. https://doi.org/10.1007/s12229-017-9188-z

Otálora M., Jørgensen P. & Wedin M. 2014. — A revised generic classification of the jelly lichens, Collemataceae. *Fungal Diversity* 64 (1): 275-293. https://doi.org/10.1007/s13225-013-0266-1

Palmqvist K. & Sundberg B. 2000. — Light use efficiency of dry matter gain in five macro-lichens: Relative impact of microclimate conditions and species-specific traits. *Plant Cell and Environment* 23 (1): 1-14. https://doi.org/10.1046/j.1365-3040.2000.00529.x

Pérez-Pérez R. E. 2005. — *Impacto del manejo forestal en los macrolíquenes cortícolas de* Pinus patula *(Sclh. & Cham) en la Sierra de Juárez, Oaxaca*. Tesis Doctoral, Doctorado en Recursos Bióticos, Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos, 97 p.

Pérez-Pérez R. E., Miramontes-Rojas N. & Aguilar-Rosales J. 2008. — Macrolíquenes cortícolas en dos especies de coníferas del Parque Nacional Lagunas de Zempoala. *Acta Universitaria* 18 (2): 33-39. https://doi.org/10.15174/au.2008.147

Pérez-Pérez R. E., Quiroz H., Herrera-Campos M. & Garcia R. 2011. — Scale-dependent effects of management on the richness and composition of corticolous macrolichens in pine-oak forests of Sierra de Juárez, Oaxaca, Mexico. *Bibliotheca Lichenologica* 106: 243-258

Pérez-Pérez R. E. & Guzmán G. 2015. — Especies de Parmotrema en un bosque mesófilo de montaña convertido en zona urbana en Xalapa, Veracruz, México. Bosque 36 (3): 357-362. https://doi.org/10.4067/S0717-92002015000300003

Pérez-Pérez R. E., Castillo-Campos G. & Cáceres M. 2015. — Diversity of corticolous lichens in Cloud Forest remnants in La Cortadura, Coatepec, Veracruz, México in relation to phorophytes and habitat fragmentation. *Cryptogamie, Mycologie* 36 (1): 79-92. https://doi.org/10.7872/crym.v36.iss1.2015.79

Petřík P., Pergl J. & Wild J. 2010. — Recording effort biases the species richness cited in plant distribution atlases. *Perspectives in Plant Ecology, Evolution and Systematics* 12 (1): 57-65.

Pinho P., Dias T., Cruz C., Sim Tang Y., Sutton M. A., Martins-Loução M.-A., Máguas C. & Branquinho C. 2011. — Using lichen functional diversity to assess the effects of atmospheric ammonia in Mediterranean woodlands. *Journal of Applied Ecology* 48 (5): 1107-1116. https://doi.org/10.1111/j.1365-2664.2011.02033.x

Prieto M., Martínez I., Aragón G. & Verdú M. 2017. — Phylogenetic and functional structure of lichen communities under contrasting environmental conditions. *Journal of Vegetation Science* 28 (4): 871-881. https://doi.org/10.1111/jvs.12544

Qgis development team 2016. — QGIS geographic information system. Open source geospatial Foundation Project.

Ramírez-Morán N. A., León-Gómez M. & Lücking R. 2016. — Uso de biotipos de líquenes como bioindicadores de perturbación en fragmentos de bosque altoandino (Reserva Biológica “Encenillo”, Colombia). *Caldasia* 38 (1): 31-52. https://doi.org/10.15446/caldasia.v38n1.57821

Ramírez-Peña D. A. 2019. — *Diversidad y distribución vertical de los líquenes cortícolas de* Alnus acuminata *subsp.* arguta *en la reserva ecológica La Cortadura, Coatepec, Veracruz, México*. Tesis de Maestría. INECOL, A.C., Xalapa, 51 p.

Rapai S. B., McMullin R. T. & Newmaster S. G. 2012. — The importance of macrolichen traits and phylogeny in forest community assemblage along a high elevation gradient in southwestern British Columbia. *Forest Ecology and Management* 274: 231-240. https://doi.org/https://doi.org/10.1016/j.foreco.2012.02.018

Rivas-Plata E., Lücking R. & Lumbsch H. T. 2008. — When family matters: an analysis of Thelotremataceae (Lichenized Ascomycota: Ostropales) as bioindicators of ecological continuity in tropical forests. *Biodiversity and Conservation* 17 (6): 1319-1351. https://doi.org/10.1007/s10531-007-9289-9

Rosabal D., Burgaz A. R. & Reyes O. J. 2013. — Substrate preferences and phorophyte specificity of corticolous lichens on five tree species of the montane rainforest of Gran Piedra, Santiago de Cuba. *The Bryologist* 116 (2): 113-121. https://doi.org/10.1639/0007-2745-116.2.113

Seymour F. A., Crittenden P. D. & Dyer P. S. 2005. — Sex in the extremes: Lichen-forming fungi. *Mycologist* 19 (2): 51-58. https://doi.org/10.1017/S0269915X05002016

Simijaca D., Moncada B. & Lücking R. 2018. — Bosque de roble o plantación de coníferas, ¿qué prefieren los líquenes epífitos? *Colombia Forestal* 21 (2): 123-141. https://doi.org/10.14483/2256201X.12575

Simijaca D., Pérez-Pérez R. E., Escoto-Moreno J. & Ocampo G. 2023. — Multiple new records of lichenized fungi for Aguascalientes, with the assessment of the conservation status of two endemic species of Mexico. *Botanical Sciences* 101 (2): 544-559. https://doi.org/10.17129/botsci.3179

Sipman H. J. M. 1996. — Corticolous lichens, *in* Gradstein S. R., Hietz P., Lücking R., Lücking A., Sipman H. J. M., Vester H. F. M., Wolf J. H. D. & Gardette E. (eds), How to sample the epiphytic diversity of tropical rainforests. *Ecotropica* 2: 66-67.

Siqueiros-Delgado M. E., Rodríguez-Avalos J. A., Martínez-Ramírez J. & Sierra-Muñoz J. C. 2016. — Situación actual de la vegetación del estado de Aguascalientes, México. *Botanical Sciences* 94 (3): 455-470. https://doi.org/10.17129/botsci.466

Siqueiros-Delgado M., Rodríguez-Avalos J., Martínez-Ramírez J., Sierra-Muñoz J. C. & García-Regalado G. 2017. — *Vegetación del estado de Aguascalientes*. Aguascalientes, México, Universidad Autónoma de Aguascalientes, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 370 p. Available from https://editorial.uaa.mx/docs/ve_vegetacion_aguascalientes.pdf.

Soto-Medina E., Lücking R., Silverstone-Sopkin P. A. & Torres A. M. 2019. — Changes in functional and taxonomic diversity and composition of corticolous lichens in an altitudinal gradient in Colombia. *Cryptogamie, Mycologie* 40 (6): 97-115. https://doi.org/10.5252/cryptogamie-mycologie2019v40a6

Toledo V. & Ordoñez J. 2009. — Zonas ecológicas de México, Escala: 1:1000000. Available from http://www.conabio.gob.mx/informacion/gis/ (accessed on 12 June 2022).

Tripp E. A., Lendemer J. C., Barberán A., Dunn R. R. & Fierer N. 2016. — Biodiversity gradients in obligate symbiotic organisms: exploring the diversity and traits of lichen propagules across the United States. *Journal of Biogeography* 43 (8): 1667-1678. https://doi.org/10.1111/jbi.12746

Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I. & Garnier E. 2007. — Let the concept of trait be functional! *Oikos* 116 (5): 882-892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Wickham H. 2011. — ggplot2. *WIREs Computational Statistics* 3 (2): 180-185. https://doi.org/https://doi.org/10.1002/wics.147

Wolf J. 1993. — Diversity paterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annals of the Missouri Botanical Garden* 80 (4): 928-960. https://doi.org/10.2307/2399938

Wolf J. H. D. 1994. — Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112 (1): 15-28. https://doi.org/10.1007/BF00045096

Zambrano A., Nash T. H. & Herrera-Campos M. 2000. — Lichen Decline in Desierto de los Leones (Mexico City). *The Bryologist* 103 (3): 428-441. https://doi.org/10.1639/0007-2745(2000)103[0428:LDIDDL]2.0.CO;2

Zárate-Arias N., Moreno-Palacios M. & Torres-Benítez A. 2019. — Diversity, phorophyte specificity and microenvironmental preferences of corticolous lichens in a sub-Andean forest in the Centro region of Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 43 (169): 737-745. https://doi.org/10.18257/raccefyn.886

Zhou Y., Chen S., Hu G., Mwachala G., Yan X. & Wang Q. 2018. — Species richness and phylogenetic diversity of seed plants across vegetation zones of Mount Kenya, East Africa. *Ecology and Evolution* 8 (17): 8930-8939.

Submitted on 9 February 2023;
accepted on 16 May 2023;
published on 26 July 2023.

APPENDIX

APPENDIX 1. — Frequency of species on the different vegetation types and presence/absence of their functional traits.

Identification	**Dry shrubland**	**Quercus forest**	**Subtropical shrubland**	**Crustose**	**Dimorphic**	**Squamulose**	**Foliose Wide**	**Foliose Narrow**	**Fruticose**	**Jelly**	**Chlorophyta**	**Cyanophyta**	**Apothecia**	**Perithecia**	**Isidia**	**Lobulae**	**Soralia**	**Dual**	**Absent**	**Epiphyte**	**Saxicolous**	**Edaphic**	**Multiple**
Acarospora bullata	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Acarospora chrysops	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Acarospora strigata	2	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Acarospora succedens	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Acarospora veronensis	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Anzia americana	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Aspicilia sp.	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Athallia pyracea	1	2	6	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Athallia vitellinula	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Buellia arborea	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Buellia dispersa	3	1	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Buellia erubescens	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Buellia maritima	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Buellia nashii	0	0	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Buellia stellulata	2	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Buellia tyrolensis	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Caloplaca aff cerina	0	0	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Caloplaca eugyra	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Caloplaca microphyllina	5	7	9	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0
Caloplaca saxicola	6	2	2	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Candelaria concolor	3	2	7	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Candelariella citrina	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Candelina mexicana	3	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Candelina submexicana	9	0	4	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Canoparmelia cryptochlorophaea	0	2	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Canoparmelia texana	0	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Chrysothrix insulizans	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Circinaria contorta	7	0	3	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Cladonia caespiticia	0	3	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
Cladonia chlorophaea	1	2	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
Cladonia furcata	0	5	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Cladonia jaliscana	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Cladonia multiformis	0	2	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Cladonia ochrochlora	0	2	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0
Cladonia pyxidata	0	2	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Cladonia sp.	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Cladonia subcariosa	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Cladonia verticillata	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Clavascidium lacinulatum	4	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Coccocarpia erythroxyli	0	2	2	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
Coccocarpia palmicola	3	4	4	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1
Collema subflaccidum	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Dermatocarpon dolomiticum	2	2	3	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Dermatocarpon miniatum	4	0	2	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Dermatocarpon moulinsii	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Dermatocarpon reticulatum	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Dimelaena oreina	3	3	2	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Diploschistes actinostomus	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Diploschistes dicapsis	1	3	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Diploschistes gypsaceus	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Diploschistes scruposus	0	2	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Enchylium cocophorum	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0
Enchylium conglomeratum	0	0	10	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1
Enchylium polycarpon	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0
Endocarpon pusilum	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Flavoparmelia leucoxantha	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Flavopunctelia borrerioides	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Flavopunctelia flaventior	0	6	12	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0

APPENDIX 1. — Continuation.

Identification	Dry shrubland	Quercus forest	Subtropical shrubland	Crustose	Dimorphic	Squamulose	Foliose Wide	Foliose Narrow	Fruticose	Jelly	Chlorophyta	Cyanophyta	Apothecia	Perithecia	Isidia	Lobulae	Soralia	Dual	Absent	Epiphyte	Saxicolous	Edaphic	Multiple
Flavopunctelia praesignis	0	4	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Flavopunctelia soredica	7	8	17	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Fuscidea mollis	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Gyalolechia flavorubescens	0	0	6	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Gyalolechia stipitata	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Haematomma fenzlianum	2	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Haematomma flexuosum	0	4	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Heppia lutosa	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Hertelidea botryosa	0	0	5	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Heterodermia albicans	3	2	10	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Heterodermia antillarum	0	11	2	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Heterodermia comosa	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
Heterodermia diademata	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Heterodermia dissecta	0	2	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Heterodermia granulifera	0	3	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Heterodermia isidiophora	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Heterodermia obscurata	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Heterodermia rugulosa	2	3	15	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Heterodermia speciosa	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Heterodermia tremulans	1	1	9	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Heterodermia tropica	0	3	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Heteroplacidium compactum	4	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Hyperphyscia adglutinata	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Hyperphyscia minor	1	0	3	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Hyperphyscia syncolla	1	0	2	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Hypotrachyna citrella	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Hypotrachyna horrescens	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Lasallia papulosa	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Lathagrium cristatum	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Lecanora allophana	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Lecanora caesiorubella	0	3	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Lecanora helva	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Lecanora horiza	0	5	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Lecanora sp.	0	2	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Lecidella stigmatea	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Lempholemma chalazanum	1	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0
Lempholemma sp.	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0
Lepra ophthalmiza	0	2	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Lepraria sp.	2	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Leptochidium albociliatum	0	2	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0
Leptogium austroamericanum	0	7	5	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0
Leptogium chloromelum	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Leptogium coralloideum	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Leptogium isidiosellum	0	2	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0
Leptogium joergensenii	2	3	11	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Leptogium megapotamicum	0	2	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0
Leptogium milligranum	0	4	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0
Leptogium pseudofurfuraceum	0	6	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0
Leptogium rugosum	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Leucodermia appalachiensis	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Nephroma parile	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0
Normandina pulchella	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0
Ochrolechia mexicana	0	8	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Parmeliella triptophylla	0	3	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Parmelina tiliaceaea	0	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Parmelinella salacinifera	0	0	3	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Parmelinella versiformis	0	3	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Parmotrema acutatum	0	7	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Parmotrema arnoldii	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Parmotrema cetratum	1	3	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Parmotrema hababianum	1	2	3	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0

Appendix 1. — Continuation.

Identification	Dry shrubland	Quercus forest	Subtropical shrubland	Crustose	Dimorphic	Squamulose	Foliose Wide	Foliose Narrow	Fruticose	Jelly	Chlorophyta	Cyanophyta	Apothecia	Perithecia	Isidia	Lobulae	Soralia	Dual	Absent	Epiphyte	Saxicolous	Edaphic	Multiple
Parmotrema hypoleucinum	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Parmotrema latissimum	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Parmotrema margaritatum	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Parmotrema paramoreliense	0	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Parmotrema praesorediosum	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Parmotrema pseudocrinitum	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Parmotrema reticulatum	2	10	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Parmotrema sp.	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Parmotrema stupenum	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Parmotrema subisidiosum	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
Parmotrema subtinctorium	0	7	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Peltigera leucophlebia	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Peltigera praetextata	0	7	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
Peltula euploca	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
Peltula farinosa	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0
Peltula hassei	2	0	2	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
Peltula patellata	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0
Pertusaria moreliensis	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Pertusaria pustulata	0	3	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Pertusaria sp.	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Pertusaria tejocotensis	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
Phaeophyscia hirsuta	8	0	7	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1
Phaeophyscia hirtella	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Phaeophyscia nashii	1	0	42	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Phaeophyscia nigricans	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Phaeophyscia orbicularis	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Phaeophyscia pusilloides	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Phaeophyscia sonorae	0	0	12	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Physcia aipolia	2	0	6	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0
Physcia atrostriata	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Physcia biziana	2	1	27	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Physcia crispa	1	1	3	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Physcia halei	0	1	2	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Physcia phaea	2	2	2	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Physcia stellaris	0	0	18	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Physcia tribacia	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Physcia undulata	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Physconia isidiomuscigena	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Placidium squamulosum	2	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1
Placidium acarosporoides	3	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0
Pleopsidium oxytonum	7	2	7	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Polyblastidium fragilissimum	0	2	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Polyblastidium hypoleucum	0	4	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Polyblastidium japonicum	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Polyblastidium propaguliferum	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Polycaulonia impolita	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Protoparmeliopsis muralis	3	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0
Pseudoevernia consocians	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Psora cerebriformis	2	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Psora crenata	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0
Psora icterica	2	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Psora pseudorussellii	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Psorula rufonigra	2	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Punctelia caseana	0	4	5	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Punctelia hypoleucites	1	0	5	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Punctelia jeckeri	0	3	4	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Punctelia missouriensis	0	4	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Punctelia perreticulata	0	7	8	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Pyxine petricola	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Pyxine subcinerea	0	1	2	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Ramalina roesleri	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0

APPENDIX 1. — Continuation.

Identification	**Dry shrubland**	**Quercus forest**	**Subtropical shrubland**	**Crustose**	**Dimorphic**	**Squamulose**	**Foliose Wide**	**Foliose Narrow**	**Fruticose**	**Jelly**	**Chlorophyta**	**Cyanophyta**	**Apothecia**	**Perithecia**	**Isidia**	**Lobulae**	**Soralia**	**Dual**	**Absent**	**Epiphyte**	**Saxicolous**	**Edaphic**	**Multiple**
Rhizocarpon infernulum	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Sarcogyne novomexicana	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Sculptolumina japonica	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Scytinium lichenoides	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Scytinium subaridum	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Squamulea squamosa	3	2	3	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Squamulea subsoluta	4	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Staurothele monicae	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Sticta aff sylvatica	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Sticta beauvoisii	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Sticta fuliginosa	0	2	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Sticta weigelii	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Tephromella atra	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Tetramelas chloroleucus	0	3	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Trapelia sp.	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Umbilicaria sp.	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Usnea amblyoclada	0	3	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Usnea arbusculiformis	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Usnea dasopoga	0	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1
Usnea florida	0	3	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Usnea praetevisa	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Usnea strigosa	0	2	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Usnea subfloridana	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Usnea subfusca	0	3	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0
Verrucaria inficiens	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Wetmoreana brouardii	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Xanthoparmelia ahtii	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Xanthoparmelia amableana	0	0	2	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Xanthoparmelia californica	0	2	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Xanthoparmelia cumberlandia	5	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Xanthoparmelia lavicola	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Xanthoparmelia lineola	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Xanthoparmelia mexicana	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Xanthoparmelia moctezumensis	2	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Xanthoparmelia novomexicana	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
Xanthoparmelia plitti	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Xanthoparmelia subcumberlandia	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0
Xanthoparmelia subtasmanica	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0