

Diversity begets diversity: Phorophyte and microsite relations of foliicolous lichens in the lowland rain forest at Los Tuxtlas Biosphere Reserve (Veracruz, Mexico)

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Abstract

We analyzed the structure of foliicolous lichen communities in the northernmost lowland forest of the Neotropics, Los Tuxtlas Tropical Biology Station in Veracruz, Mexico, and its dependence on phorophyte and microclimate. Along a 420-m long transect with 15 equidistant sampling points, within a 10 m radius of each point, we sampled a total 137 phorophytes and 411 leaves. The phorophytes represented 13 species, with diverse leaf traits regarding size, texture, presence of hairs and/or glands, and longevity, including: *Astrocaryum mexicanum* (Arecaceae), *Chamaedorea ernesti-augustii* (Arecaceae), *Costus scaber* (Costaceae), *Guarea glabra* (Meliaceae), *Heliconia latispatha* (Heliconiaceae), *Monstera acuminata* (Araceae), *Myriocarpa longipes* (Urticaceae), *Piper hispidum* (Piperaceae), *Poulsenia armata* (Moraceae), *Pseudolmedia oxyphyllaria* (Moraceae), *Salacia megistophylla* (Celastraceae), *Siparuna thecaphora* (Siparunaceae) and *Syngonium podophyllum* (Araceae). NDMS ordination and cluster analysis grouped the phorophytes into hierarchically structured clusters variously correlated with microsite, phorophyte species and foliicolous lichen species richness. Indicator species analysis revealed statistically significant foliicolous lichen species characteristic for terminal clusters and for phorophyte species. We conclude that the principle of “diversity begets diversity” may apply, in that phorophyte diversity influences the diversity of foliicolous lichen communities through the manifestation of subtle phorophyte preferences, best seen in well-developed communities on leaves with higher longevity. Thus, well-preserved forest ecosystems, with a higher diversity of suitable phorophytes, will support a higher diversity of foliicolous lichens, a phenomenon that extends to epiphytes in general.

KEYWORDS

biodiversity maintenance, environmental monitoring, epiphyte diversity, phyllosphere, tropical rainforest

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1 | INTRODUCTION

Leaf-dwelling or foliicolous lichens inhabit tropical and subtropical humid to wet forests (Herrera-Campos et al., 2004; Lücking, 2001a, 2008; Pinokiyo, Singh, & Singh, 2006; Santesson, 1952). Currently more than 800 species are known worldwide, more than 600 of which are found in the Neotropics (Lücking, 2008). Foliicolous lichens exhibit striking patterns of small-scale diversity, with up to 50 species found on a single leaf, equivalent to 5% of known species, and up to 300 species at a single site (Lücking, 1999a, 2001b, 2008; Lücking & Matzer, 2001).

The maintenance of such high levels of diversity is ascribed to the dynamics of leaf shedding and replacement in tropical forests, which requires foliicolous lichens to continuously establish *de novo* microcommunities on individual leaves, thus preventing competitive exclusion (Cáceres & Lücking, 2006; Lücking, 2001a, 2008; Mežaka, Bader, Salazar-Allen, & Mendieta-Leiva, 2020; Rogers, 1989; Rogers & Barnes, 1986). This mechanism can be compared to the concept of intermediate disturbances fostering tree diversity in tropical forests (Connell, 1978; Molino & Sabatier, 2001), the intermediate disturbances provided by stochastically distributed tree fall gaps resulting in a mosaic of successional stages. The intermediate disturbance hypothesis has been challenged (Fox, 2013), although it is based on straightforward assumptions. While an undisturbed community would go through various successional stages in its entirety, one of the stages exhibiting the highest level of diversity, intermediate disturbances within a community result in the simultaneous maintenance of different successional stages in a stochastic spatial arrangement, thus exhibiting a higher diversity than any of its individual successional stages. The reason is because undisturbed community development leads to local extinction of species characteristic of early and intermediate successional stages, whereas a successional mosaic maintains these species in a patchy pattern.

The successional dynamics of foliage in tropical rain forests, with leaf longevity mostly not exceeding 3 years (Bentley, 1979; Hegarty, 1990; Kikuzawa, 1996; Rogers & Clifford, 1993; Shiodera, Rahajoe, & Kohyama, 2008; Williams, Field, & Mooney, 1989; Xu et al., 2017), precisely exhibits this dynamic pattern: while the leaf substrate is permanently available, it undergoes substantial, continuous, individual turnover. As a result, foliicolous lichens and other organisms, including bryophytes (mostly liverworts), fungi, algae, cyanobacteria and invertebrates, have evolved complex and highly diverse microcommunities, in what has been dubbed the “phyllosphere” (Coley & Kursar, 1996; Freiberg, 1998;

Lücking, 2001a; Lücking & Bernecker-Lücking, 2000; Ruinen, 1961; Sonnleitner, Dullinger, Wanek, & Zechmeister, 2009).

Microhabitat preferences of foliicolous lichens largely depend on microclimate, but also on phorophyte features (Lücking, 1998a, 1998b, 1999b, 1999c, 2001a, 2008; Pinokiyo et al., 2006). Three macrocommunities can be distinguished in the shady understory, in smaller light gaps, and in the exposed canopy, with distinct species composition (Lücking, 1995a, 1999a, 1999c; Sipman, 1997). In disturbed habitats, foliicolous lichen communities generally become depauperate or disappear (Cáceres, Maia, & Lücking, 2000; Lücking, 1995b; Pinokiyo et al., 2006), although rich communities can develop on non-native phorophytes when environmental conditions remain highly favorable (Sanders & Llop, 2020). Due to their sensitivity to environmental parameters, foliicolous lichens are thus excellent indicators of ecosystem health (Coley & Kursar, 1996; Hawksworth, Iturriaga, & Crespo, 2005; Lücking, 1997; Pinokiyo et al., 2006; Seaward, 1996). Unfortunately, tropical forests are increasingly replaced by other forms of land use, and Mexico is no exception: deforestation has caused the loss of approximately 90% of the tropical forest, including in the Los Tuxtlas Biosphere Reserve, which represents the northern limit of tropical wet forest in the Neotropics (Arroyo-Rodríguez, Dunn, Benitez-Malvido, & Mandujano, 2009; Dirzo & Garcia, 1992; Durand & Lazos, 2008). Clear-cutting, selective logging and managed regrowth lead to a decrease in phorophytes suitable to support rich epiphyte communities, including foliicolous lichens, thus decreasing the functional diversity of forest ecosystems and their potential for ecosystem services.

In the present study, we assessed the role of phorophytes as microniches driving the diversity of foliicolous lichen communities. This approach was based on the hypothesis that “diversity begets diversity” (Palmer & Maurer, 1997; Whittaker, 1975), a concept that can be applied to different situations, including host–parasite interactions (Janz, Nylin, & Wahlberg, 2006), environmental heterogeneity (Stevens & Tello, 2011) and functional diversity (Maynard et al., 2017). In the case of epiphyte–phorophyte relationships, one could interpret phorophyte composition and diversity as environmental heterogeneity, as phorophytes provide a micro-environment for epiphytes; therefore, phorophyte diversity should “beget” epiphyte diversity (Benavides, Vasco, Duque, & Duivenvoorden, 2011; Köster, Nieder, & Barthlott, 2011; Nieder, Engwald, & Barthlott, 1999; Sáyo et al., 2013). Limited studies suggest the diversity of bark-dwelling lichens does depend on phorophyte diversity (Cáceres,

Lücking, & Rambold, 2007; Cornelissen & Ter Steege, 1989; Rosabal, Burgaz, & Reyes, 2013; Soto-Medina, Lücking, & Bolaños-Rojas, 2012). As a consequence, one would postulate that anthropogenic alterations that reduce phorophyte diversity also reduce epiphyte diversity, a hypothesis supported by studies on vascular epiphytes and lichens (Ardila-Ríos, Moncada, & Lücking, 2015; Merwin, Rentmeester, & Nadkarni, 2003). For foliicolous lichens in a Costa Rican rain forest, Lücking (1998b) found subtle phorophyte preferences, and lichen community patterns were correlated with phorophyte species when microclimatic parameters were comparable. However, an assessment of phorophyte composition as driver of foliicolous lichen community structure within a microclimatic gradient has not yet been made. To that end, we sampled foliicolous lichen communities on 13 phorophyte species in a lowland rain forest in Los Tuxtlas Biosphere Reserve, representing a broad range of leaf characteristics, testing the null hypothesis that phorophyte species have no influence on foliicolous lichen community structure and diversity.

2 | MATERIAL AND METHODS

2.1 | Study site

The study was carried out in the state of Veracruz, Mexico, at the Estación de Biología Tropical “Los Tuxtlas” (Los Tuxtlas Tropical Biology Station), administrated by the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM; Dirzo, González-Soriano, & Vogt, 1997; Estrada, Coates-Estrada, & Martínez-Ramos, 1985). The station forms part of the Los Tuxtlas Biosphere Reserve and is located on the eastern slope of San Martín Tuxtlas Volcano, along the coastal plain of the Gulf of Mexico, between 18°34' and 18°36' N and 95°04' and 95°09' W (Figure 1). The area covers an altitudinal range between 150 and 700 m (Campos, Kelly, & Delgado, 2004; Cedillo & Durand, 2004; Estrada et al., 1985). The climate is warm-humid, with an annual average temperature of 27°C, although at higher elevations the mean temperature drops to 18°C. Annual rainfall amounts to almost 5,000 mm, with a drier season from March to May. From September to February, the

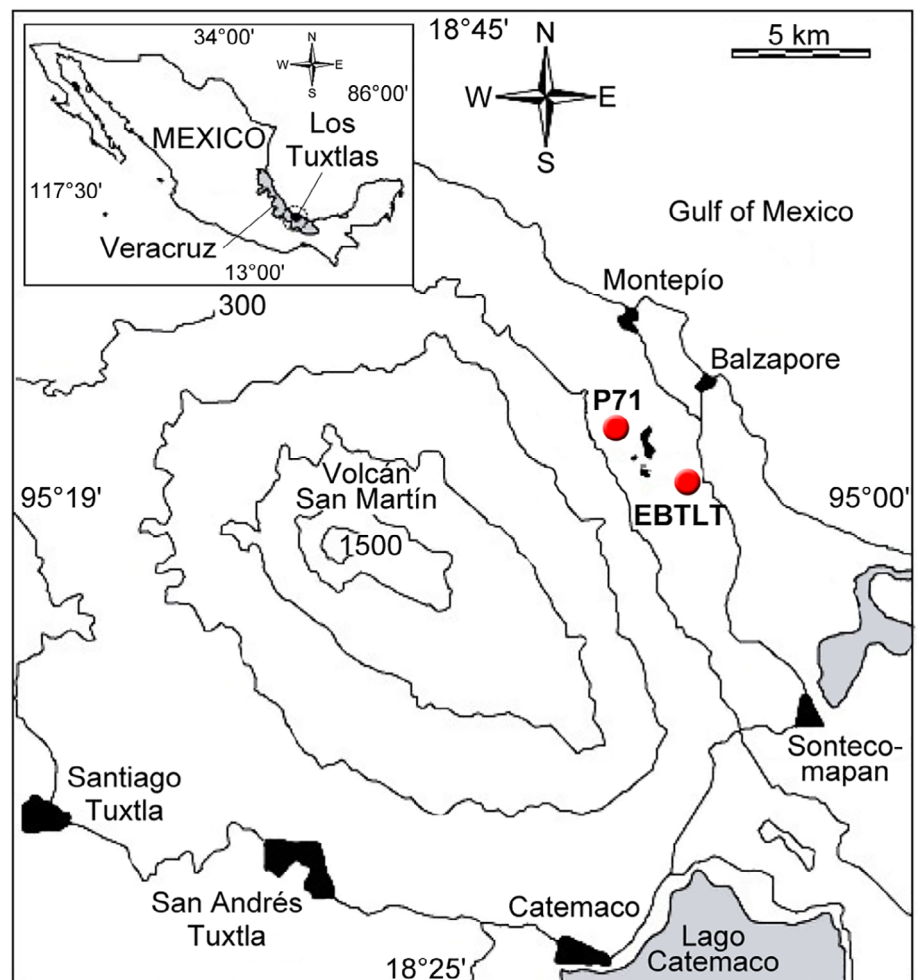


FIGURE 1 Map of the study area and its location in Mexico. EBTLT, Estación Biológica Tropical “Los Tuxtlas”; P71, Parcela 71 (study site). Coordinates indicate (clockwise) N, E, S, W [Color figure can be viewed at wileyonlinelibrary.com]

area is affected by the displacement of cold and humid air masses from the north (Lot-Helgueras, 1976; Soto & Gama, 1997).

Los Tuxtlas represents the northernmost extension of neotropical lowland rain forest and includes a diversity of vegetation types, such as (semi-) evergreen lowland rain forest (*selva alta perennifolia*, *selva mediana subperennifolia*), mountain and pine mesophilic forest (*selva mesófila*), deciduous lowland forest (*selva mediana caducifolia*), as well as mangroves, coastal oak, and induced and cultivated pasture, resulting in a diversity of habitats, such as lakes, streams, waterfalls, wetlands, lagoons and rivers (Bongers, Popma, Del Castillo, & Carabias, 1988; Ibarra-Manríquez, Martínez-Ramos, Dirzo, & Núñez-Farfán, 1997; Vázquez, Campos, Armenta, Carvajal, & I, 2010). Like many other regions in Mexico and the Neotropics, Los Tuxtlas faces pressure through urbanization, expansion of agricultural and livestock areas, introduction of exotic and invasive species and exploitation such as mining, hunting and selective logging (Dirzo & Mendoza, 2004; Guevara, Laborde, & Sánchez, 2000; Guevara, Meave, & Castillo, 1994; Siemens, 2009; Vázquez et al., 2010). Several new species of foliicolous lichens were discovered in this reserve (Herrera-Campos & Lücking, 2002; Herrera-Campos, Martínez-Colín, Bárcenas-Peña, & Lücking, 2004).

2.2 | Sampling

The study was performed in a portion of largely undisturbed evergreen rain forest (“*selva alta perennifolia*”), located at 18°35'86" N and 95°06'14" W, in the so-called “parcela 71”, passing the Rubén Sánchez ranch. We marked a 420-m long transect with 15 sampling points, set apart in equal distance of 30 m each. At each point, a circle with a radius of 10 m was drawn and all phorophytes belonging to 13 pre-selected species (Table 1) were sampled, randomly selecting three mature leaves from different branches of each phorophyte. For palm leaves (*Astrocaryum*, *Chamaedorea*), we randomly selected three leaflets, and for *Heliconia* leaves, we collected a single blade and subsequently randomly cut out three 10 cm × 10 cm sections for study. Pre-selection of phorophytes was necessary to allow for meaningful statistical analysis of phorophyte type, since an entirely random approach would result in most samples representing unique phorophytes sampled only once.

The phorophyte species were pre-selected based on the following criteria: (a) sufficient abundance to allow for repeated sampling at the 15 transect points; (b) sufficient coverage of foliicolous lichens on mature leaves and (c) between-species variation of phorophyte features such as leaf size, surface texture, presence of

TABLE 1 Pre-selected phorophyte species sampled along a transect of 420 m, indicating growth form and frequency of sampled individuals

Phorophyte species (family)	Growth type	Individuals sampled	Leaves sampled ^a
<i>Astrocaryum mexicanum</i> Liebm. ex Mart. (Arecaceae)	Palm	11	33
<i>Chamaedorea ernesti-augusti</i> H. Wendl. (Arecaceae)	Palm	15	45
<i>Costus scaber</i> Ruiz & Pav. (Costaceae)	Herb	11	33
<i>Guarea glabra</i> Vahl (Meliaceae)	Tree	5	15
<i>Heliconia latispatha</i> Benth. (Heliconiaceae)	Herb	4	12
<i>Monstera acuminata</i> K. Koch (Araceae)	Climber	14	42
<i>Myriocarpa longipes</i> Liebm. (Urticaceae)	Treelet	13	39
<i>Piper hispidum</i> Sw. (Piperaceae)	Tree	14	42
<i>Poulsenia armata</i> (Miq.) Standl. (Moraceae)	Tree	9	27
<i>Pseudolmedia oxyphyllaria</i> J.D. Smith (Moraceae)	Tree	12	36
<i>Salacia megistophylla</i> Standl. (Celastraceae)	Treelet	11	33
<i>Siparuna thecaphora</i> (Poepp. & Endl.) A. DC. (Siparunaceae)	Tree	7	21
<i>Syngonium podophyllum</i> Schott (Araceae)	Climber	11	33
Total		137	411

^aLeaves sampled also refers to leaflets in case of palms and 10 cm × 10 cm portions in case of *Heliconia* leaves.

hairs and/or glands, leaf longevity (Conran, 1997; Lücking, 1998a, 1998b). Phorophytes with sufficient coverage of foliicolous lichens were preferred as only these allowed to discern subtle differences in phorophyte preferences, given that low-diversity phorophytes typically support only early successional stages of foliicolous lichen communities, encompassing the same set of species (Lücking, 1998b). Given the individual distribution and abundance of each phorophyte species along the transect points, this resulted in a total of 137 sampled phorophytes, representing 411 leaves or leaf portions, with between four and 15 sampled phorophytes (between 12 and 45 leaves or leaf samples) per phorophyte species (Table 1).

Following Lücking (1998a, 1999c), we used relative light intensity as proxy to characterize microsite. Each of the 15 transect points was considered a separate measuring point. Relative light intensity was determined using an EXTECH INSTRUMENTS 4010 luxmeter. Measurements were made under conditions of diffuse light (homogeneous cloud cover), by measuring each of the sampling points three times at different times in relation to the light intensity under free sky. In addition to determining relative light intensity as percentage values, the resulting mean values were also transformed into five categories of relative light intensity, in order to allow comparison with the microsite indices proposed by Lücking (1997) (Table 2). This approach is largely analogous to the analysis of hemisphere photographs and results in a level of resolution appropriate for microsite characterization at community level.

2.3 | Processing and identification of foliicolous lichen material

The collected leaves were pressed and air-dried at room temperature until completely dry. Subsequently, the lichens present on each leaf were identified using the monograph of Lücking (2008) and the world-wide rapid color guides of foliicolous lichens (Lücking & Martínez-Colín, 2004). In order to observe morphological features,

we employed an OLYMPUS SZ-STU1 stereomicroscope, and for anatomical characters based on thin sections, we used an OLYMPUS BH-2 compound microscope. When applicable, for spot tests, we applied 10% KOH and Lugol's solutions. Only thalli with structures allowing their identification were studied; however, since single leaves usually support hundreds of individuals (Lücking & Matzer, 2001), in most cases unidentifiable thalli represented taxa present on the same leaves with identifiable individuals. As a result, a total of 4,431 occurrences of species on individual leaves were recorded. All determination work was performed in the lichen laboratory at the Instituto de Biología, UNAM.

2.4 | Data analysis

Based on the results of the taxonomic identifications, we established a primary matrix of foliicolous lichen species versus 137 phorophyte samples, using the number of leaves per phorophyte on which a species was found (between 0 and 3) as proxy for abundance (Table S1). In a secondary matrix of parameters versus 137 phorophyte samples (Table S2), we recorded the following three parameters: (a) phorophyte species, (b) mean relative light intensity and (b) microsite index (according to Table 2).

To visualize foliicolous lichen community structure based on species abundance data, we performed non-metric multidimensional scaling (NMDS) ordination and cluster analysis, using the Sørensen distance measure in both approaches and flexible beta (set to -0.25) as clustering algorithm (McCune, Grace, & Urban, 2002; McCune & Mefford, 1999). For comparisons of microsite parameters and foliicolous lichen species richness between groups formed in the NMDS and cluster dendrogram and between phorophyte species, we employed Kruskal-Wallis nonparametric ANOVA (H test), as well as a Chi Square test for phorophyte species composition and a randomized Monte Carlo indicator species analysis for foliicolous lichen species composition. In order to compare the microsite categories derived from our study

TABLE 2 Transformation of mean relative light intensities measured at the sampling points into microsite categories proposed by Lücking (1997)

Range of measured mean values	Microsite index	Microsite classification	Corresponding site classification
0–2%	1	Shady understory	Closed forest
2–5%	2	Transition toward light gaps	
5–10%	3	Light gaps	Transition toward open vegetation
10–30%	4	Transition toward canopy	
30–100%	5	Canopy	Open vegetation

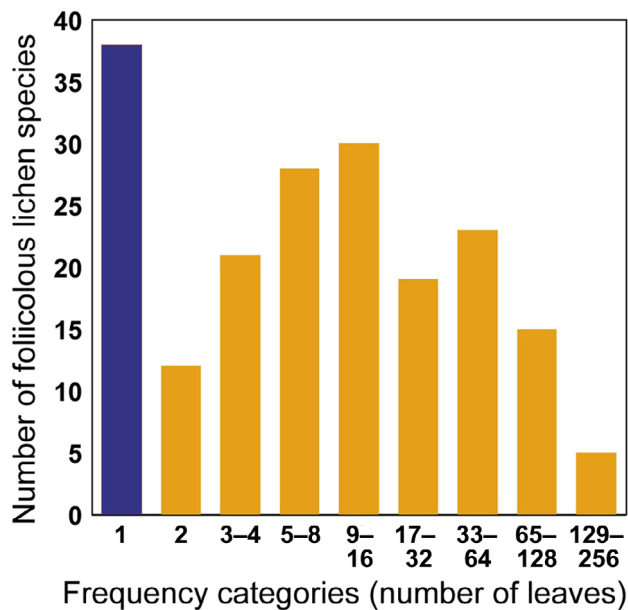


FIGURE 2 Frequency histogram of foliicolous lichen species found on the studied phorophytes, based on the number of leaves on which each species was encountered [Color figure can be viewed at wileyonlinelibrary.com]

data with those previously established for the same foliicolous lichen species by Lücking (1997), we performed non-parametric Spearman rank correlation.

Multivariate and statistical analyzes were performed in PC-Ord 6.0 (McCune & Mefford, 1999) and Statistica™ 6.0 (StatSoft, Tulsa; TIBCO Software).

3 | RESULTS

3.1 | Biotic inventory

We identified a total of 191 species of foliicolous lichens on the 137 studied phorophytes (Table S3), corresponding to those reported earlier from the study area (Herrera-Campos, Lücking, et al., 2004). The 191 species represented 40 genera, 15 families and eight orders according to current classification schemes (Lücking, 2008; Lücking, Hodkinson, & Leavitt, 2017). The highest number of genera and species was found in the families Gomphillaceae, Pilocarpaceae and Strigulaceae, respectively. The most diverse genera were *Porina* (27 species), *Strigula* (18), *Fellhanera* (10) and *Tricharia* (7).

Based on the number of leaves on which each species was found, the frequency histogram showed a log-normal shape, except for the lowest category (one leaf), which could not be further subdivided (Figure 2). The most abundant species was *Porina karnatakensis*, the only taxon found on more than half of the studied leaves. Nine further species were

TABLE 3 The 25 most frequent foliicolous lichen species found in this study

Species	Leaves	[%]
<i>Porina karnatakensis</i>	214	54
<i>Gyalectidium filicinum</i>	189	47
<i>Porina alba</i>	186	47
<i>Strigula smaragdula</i>	152	38
<i>Porina epiphylla</i>	144	36
<i>Sporopodium lepreurii</i>	123	31
<i>Porina rubentior</i>	120	30
<i>Tricharia vainioi</i>	114	29
<i>Mazosia rotula</i>	108	27
<i>Anisomeridium foliicola</i>	103	26
<i>Phyllobathelium firmum</i>	85	21
<i>Arthonia leptosperma</i>	84	21
<i>Porina atrocoerulea</i>	82	21
<i>Tricharia urceolata</i>	81	20
<i>Trichothelium minus</i>	81	20
<i>Coenogonium subluteum</i>	78	20
<i>Fouragea filicina</i>	78	20
<i>Trichothelium epiphyllum</i>	78	20
<i>Mazosia melanophthalma</i>	77	19
<i>Aulaxina minuta</i>	67	17
<i>Strigula phylogena</i>	64	16
<i>Gyalectidium imperfectum</i>	61	15
<i>Porina pseudoapplanata</i>	60	15
<i>Porina rufula</i>	60	15
<i>Strigula nemator</i>	57	14

Note: [%] refers to the relative proportion among all 411 leaves.

found on at least 25% of all leaves, including the common and widespread *Gyalectidium filicinum*, *Porina alba*, *Strigula smaragdula* and *Porina epiphylla* (Table 3). A total of 71 species were found on four or fewer leaves (i.e., less than 1% of all leaves), including 38 on a single leaf only (Table S1). In terms of the number of phorophytes with a given species present, *Gyalectidium filicinum* was the most frequent (95 out of 137 phorophytes), followed by *P. alba* (94), *P. karnatakensis* (91), *P. epiphylla* (76) and *Strigula smaragdula* (69). This suggests differentiated population structures between species, with some frequent species more dispersed and others more clustered on individual phorophytes.

3.2 | Community structure

NMDS ordination showed no clear clustering of the 137 studied phorophytes but distinctive patterns

regarding the distribution of particular phorophyte species (Figure 3). Most phorophytes were concentrated in one or two of the quadrants, which was particularly obvious for *Salacia*. We found significant axis correlations for relative light intensity and microsite, the left portion of the diagram representing phorophytes in more illuminated microsites. Both correlations were almost identical, suggesting that microsite is an appropriate proxy for relative light intensity. There was also a significant correlation with foliicolous lichen species richness per phorophyte toward the lower right quadrant, paralleled by a significant correlation with *Salacia* phorophytes concentrated in that quadrant. Relative light intensity and microsite category were not correlated with phorophyte species (Kruskal-Wallis ANOVA: $H = 11.01$, $p = .5279$; $H = 10.78$, $p = .5476$). However, lichen species richness was strongly correlated with phorophyte species (Kruskal-Wallis ANOVA: $H = 38.72$, $p = .0001$), with *Astrocaryum*, *Poulsenia*, *Pseudolmedia* and *Salacia* distinctly above and *Chamaedorea*, *Siparuna* and *Syngonium* distinctly below average.

Indicator species analysis using phorophyte species as grouping variable revealed statistically significant preferences for 59 out of the 191 foliicolous lichen species,

involving 10 of the 13 phorophyte species (Table 4). Most of these (50) were concentrated among four phorophyte species, *Astrocaryum* (10 species), *Heliconia* (14), *Poulsenia* (7) and *Salacia* (19). There was a notable concentration of certain genera on certain phorophyte species, such as *Fellhanera* on *Heliconia* and *Strigula* on *Salacia*.

Cluster analysis, in combination with the NMDS ordination, arranged the 137 phorophytes into six main clusters (A–F), with super- and subdivisions at up to six hierarchical levels, most of them in Cluster A (Figure 4). Two of the final subclusters, B01 and C02, consisted exclusively of a single phorophyte species each, *Astrocaryum* and *Salacia*, respectively. Several other subclusters had a predominant phorophyte species, whereas others were more diverse.

The cluster dendrogram exhibited significant hierarchical structure in terms of phorophyte species and microsite (relative light intensity), as well as correlation with species richness per phorophyte (Figure 5; Table S4). Relative light intensity correlated with superdivisions and the main cluster divisions, plus one final subdivision in Cluster A (Figure 5a). A similar pattern was observed for foliicolous lichen species richness, with

FIGURE 3 NMDS ordination of the 137 phorophytes based on foliicolous lichen species abundance. The 13 different phorophyte species are indicated by different symbols. The arrows indicate axis correlations as follows: L, mean relative light intensity; M, microsite index; R, foliicolous lichen species richness per phorophyte; S, *Salacia* [Color figure can be viewed at wileyonlinelibrary.com]

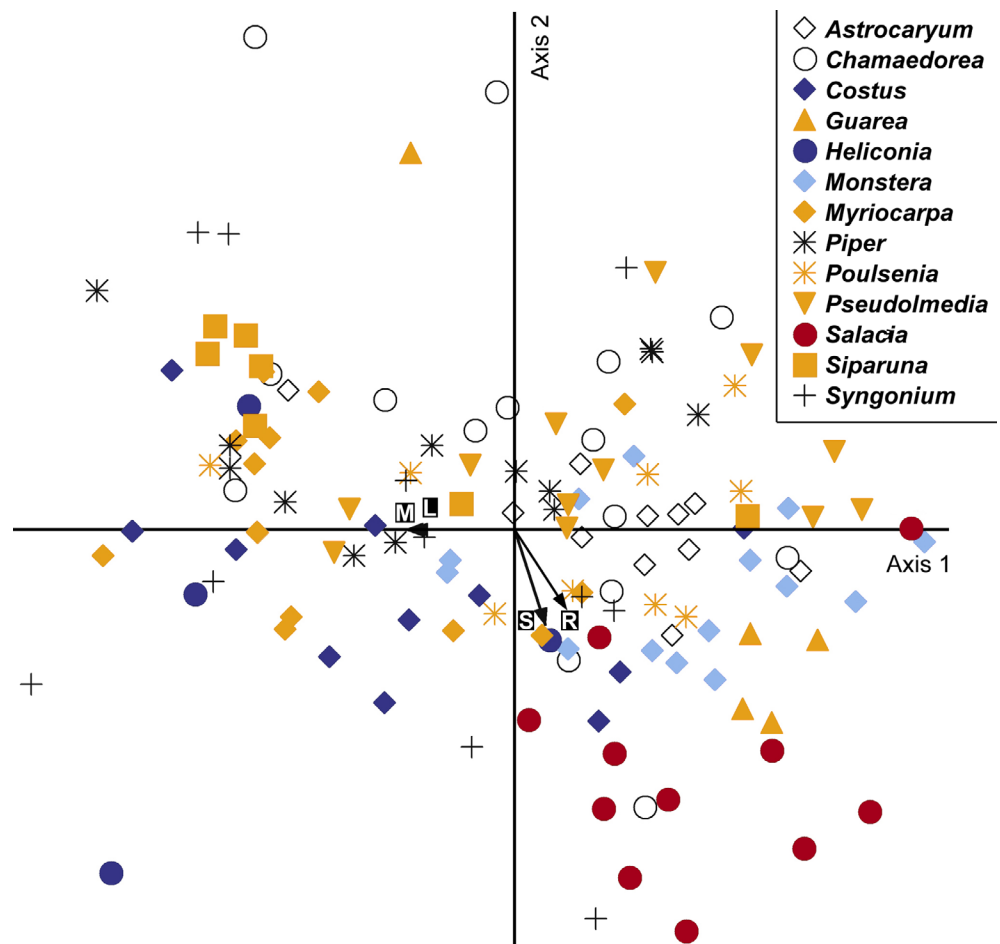


TABLE 4 List of foliicolous lichen species with statistically significant preferences for a given phorophyte species based on indicator species analysis

Species	Phorophyte	p-value	Species	Phorophyte	p-value
<i>Arthonia accolens</i>	<i>Astrocaryum</i>	0.0010	<i>Lyromma palmae</i>	<i>Piper</i>	0.0190
<i>Echinoplaca diffluens</i>	<i>Astrocaryum</i>	0.0050	<i>Caprettia confusa</i>	<i>Poulsenia</i>	0.0020
<i>Aulaxina quadrangula</i>	<i>Astrocaryum</i>	0.0090	<i>Strigula nematora</i>	<i>Poulsenia</i>	0.0040
<i>Opegrapha filicina</i>	<i>Astrocaryum</i>	0.0110	<i>Byssoloma leucoblepharum</i>	<i>Poulsenia</i>	0.0120
<i>Arthonia mira</i>	<i>Astrocaryum</i>	0.0160	<i>Strigula antillarum</i>	<i>Poulsenia</i>	0.0160
<i>Mazosia melanophthalma</i>	<i>Astrocaryum</i>	0.0200	<i>Chroodiscus australiensis</i>	<i>Poulsenia</i>	0.0170
<i>Porina pseudoapplanata</i>	<i>Astrocaryum</i>	0.0230	<i>Porina alba</i>	<i>Poulsenia</i>	0.0320
<i>Porina vezdae</i>	<i>Astrocaryum</i>	0.0330	<i>Byssolecania variabilis</i>	<i>Poulsenia</i>	0.0410
<i>Trichothelium epiphyllum</i>	<i>Astrocaryum</i>	0.0330	<i>Trichothelium minus</i>	<i>Pseudolmedia</i>	0.0390
<i>Sporopodium citrinum</i>	<i>Astrocaryum</i>	0.0380	<i>Bacidina hypophylla</i>	<i>Salacia</i>	0.0010
<i>Porina atriceps</i>	<i>Costus</i>	0.0300	<i>Porina leptospermoides</i>	<i>Salacia</i>	0.0010
<i>Microtheliopsis uleana</i>	<i>Guarea</i>	0.0020	<i>Strigula janeirensis</i>	<i>Salacia</i>	0.0010
<i>Porina rubescens</i>	<i>Guarea</i>	0.0020	<i>Strigula prasina</i>	<i>Salacia</i>	0.0010
<i>Mazosia dispersa</i>	<i>Guarea</i>	0.0450	<i>Arthonia leptosperma</i>	<i>Salacia</i>	0.0020
<i>Asterothyrium atomarginatum</i>	<i>Heliconia</i>	0.0010	<i>Coenogonium hypophyllum</i>	<i>Salacia</i>	0.0030
<i>Gyalectidium catenulatum</i>	<i>Heliconia</i>	0.0030	<i>Porina imitatrix</i>	<i>Salacia</i>	0.0030
<i>Trichothelium alboatrum</i>	<i>Heliconia</i>	0.0060	<i>Strigula microspora</i>	<i>Salacia</i>	0.0030
<i>Fellhanera bouteillei</i>	<i>Heliconia</i>	0.0160	<i>Byssolecania deplanata</i>	<i>Salacia</i>	0.0040
<i>Fellhanera rhapsidophylli</i>	<i>Heliconia</i>	0.0160	<i>Porina leptosperma</i>	<i>Salacia</i>	0.0040
<i>Fellhanera subfuscata</i>	<i>Heliconia</i>	0.0180	<i>Bapalmuia palmularis</i>	<i>Salacia</i>	0.0060
<i>Porina thaxteri</i>	<i>Heliconia</i>	0.0180	<i>Strigula phyllogena</i>	<i>Salacia</i>	0.0070
<i>Vezdaea foliicola</i>	<i>Heliconia</i>	0.0180	<i>Porina karnatakensis</i>	<i>Salacia</i>	0.0100
<i>Gyalectidium caucasicum</i>	<i>Heliconia</i>	0.0290	<i>Psoroglaena epiphylla</i>	<i>Salacia</i>	0.0110
<i>Bacidina scutellifera</i>	<i>Heliconia</i>	0.0350	<i>Byssolecania fumosonigricans</i>	<i>Salacia</i>	0.0190
<i>Byssoloma chlorinum</i>	<i>Heliconia</i>	0.0350	<i>Strigula macrocarpa</i>	<i>Salacia</i>	0.0200
<i>Cryptothecia candida</i>	<i>Heliconia</i>	0.0350	<i>Strigula viridis</i>	<i>Salacia</i>	0.0290
<i>Asterothyrium monosporum</i>	<i>Heliconia</i>	0.0400	<i>Anisomeridium foliicola</i>	<i>Salacia</i>	0.0420
<i>Sporopodium leprieurii</i>	<i>Heliconia</i>	0.0430	<i>Coenogonium labyrinthicum</i>	<i>Salacia</i>	0.0480
<i>Porina octomera</i>	<i>Monstera</i>	0.0190	<i>Coenogonium subluteum</i>	<i>Siparuna</i>	0.0050
			<i>Gyalectidium filicinum</i>	<i>Siparuna</i>	0.0110

Note: For full table including IV values, mean and standard deviation, see Table S5.

further correlations with final subdivisions in Clusters A, E and F (Figure 5b). In contrast, the relative frequency of phorophyte species was more strongly correlated with divisions throughout all levels, being absent at those lower levels where the main factors for cluster subdivisions were relative light intensity and/or lichen species richness (Figure 5c). Ten of the 13 phorophyte species were correlated at some level with cluster and/or sub-cluster formation, in final subclusters particularly *Astrocaryum*, *Chamaedorea*, *Guarea*, *Monstera*, *Piper* and *Salacia* (Figures 4 and 5c).

Based on indicator species analysis, foliicolous lichen species discriminated between clusters at almost all hierarchical levels (Figure 6). The highest number of statistically significant, discriminant species was found for the higher-level Clusters B (B01+B02), C (C01+C02+S), and D+E (D01+E01+E02), and for the terminal Clusters A04, B01, B02, C01, C02, D01 and F03 (Figure 6). Two of the three higher-level clusters (B01+B02, C01+C02+S) correlate with relative light intensity (medium to high) and species richness (moderate to high), whereas only one of the terminal clusters (D01) correlates with relative light

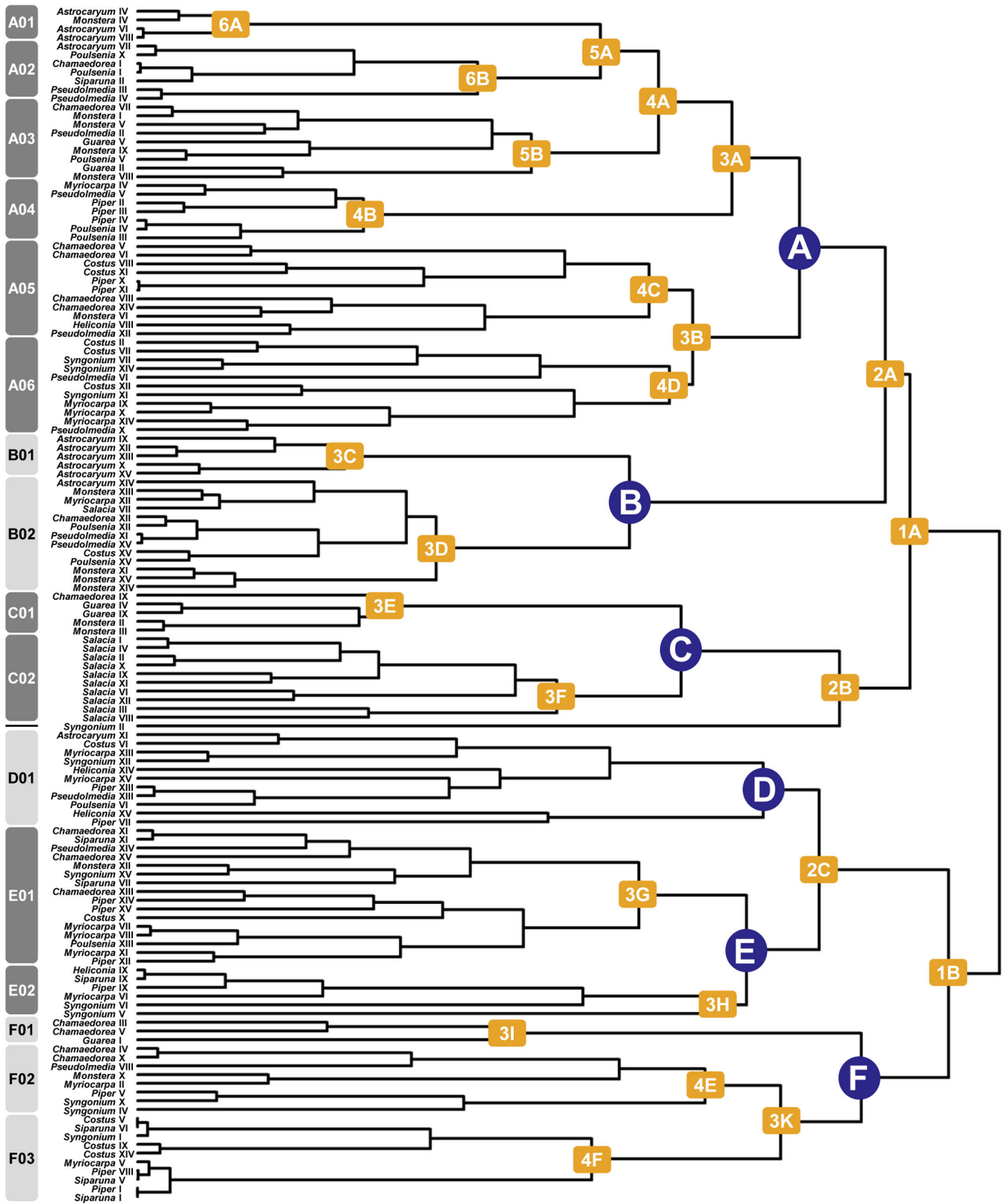


FIGURE 4 Cluster dendrogram of the 137 phorophytes based on foliicolous lichen species abundance. The hierarchical levels are indicated by number/letter combinations (orange), with the main clusters in blue and the terminal clusters in shades of gray [Color figure can be viewed at wileyonlinelibrary.com]

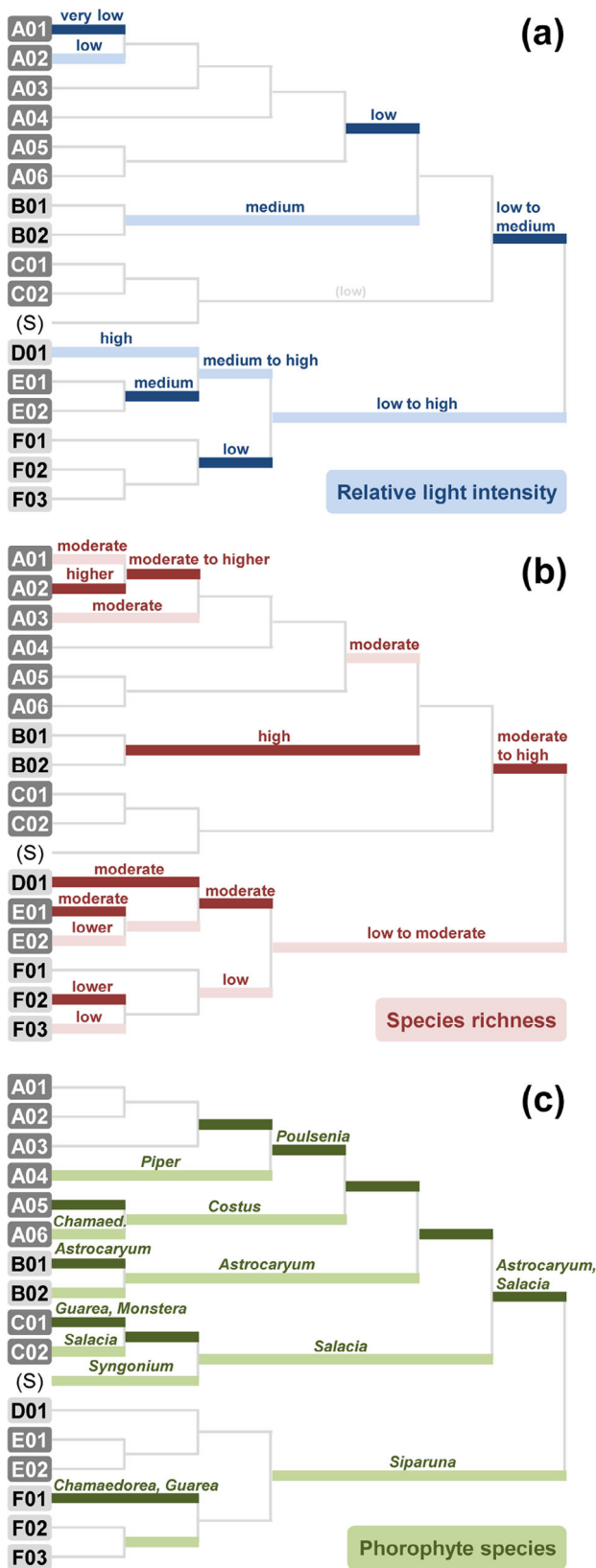


FIGURE 5 (a–c) Correlation of the major and terminal clusters of the cluster dendrogram (Figure 4) with three microenvironmental and community parameters as based on statistical group comparisons (see also Table S4) [Color figure can be viewed at wileyonlinelibrary.com]

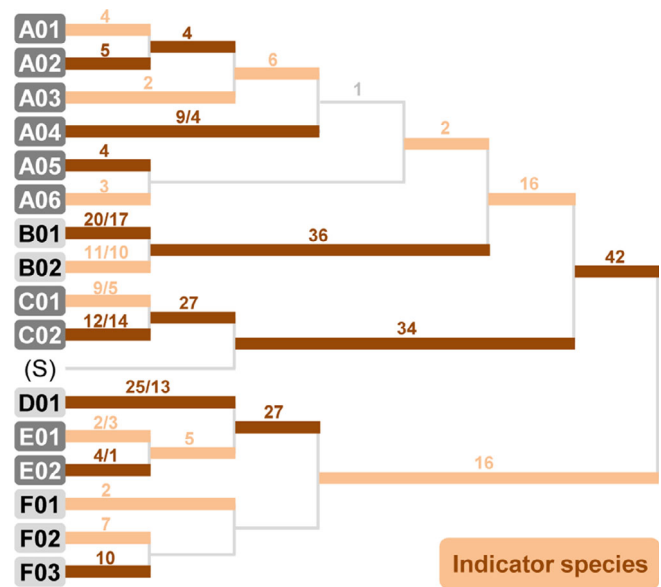


FIGURE 6 Correlation of the major and terminal clusters of the cluster dendrogram (Figure 4) with the number of statistically significant indicator species per cluster (see also Table S5) [Color figure can be viewed at wileyonlinelibrary.com]

intensity (high) and two (D01, F03) with species richness (moderate to low; Figure 5a,b). On the other hand, two of the higher-level and four of the terminal clusters correlate with phorophyte: B01+B02 with *Astrocaryum*, C01+C02+S with *Salacia*, A04 with *Piper*, B01 with *Astrocaryum*, C01 with *Guarea* and *Monstera* and C02 with *Salacia* (Figure 5c). Foliicolous lichen species composition therefore appears to be driven primarily by phorophyte, particularly in terminal clusters, and secondarily by microclimate, in higher-level clusters.

The discriminant species of higher-level Cluster B represented a diverse taxonomic array, representing 19 genera in 10 families, whereas in cluster C, nine genera and eight families were present, and in Cluster D+E, 17 genera and six families (Table S5). Three terminal clusters were largely characterized by different species of Gomphillaceae: B01 (*Aulaxina*, *Echinoplaca*, *Tricharia*), F03 (*Gyalectidium*, *Tricharia*) and D01 (*Asterothyrium*, *Echinoplaca*, *Tricharia*). D01 and A04 also including discriminant species of Pilocarpaceae (*Fellhanera*, *Byssoloma*), as did C02 (*Bapalmuia*, *Byssolecania*). The latter, as well as B02 and C01 featured Porinaceae (*Porina*), and C01 also Roccellaceae (*Mazosia*) and C02 Strigulaceae (*Strigula*).

Of the 191 species of foliicolous lichens found in this study, 141 have published microsite indices (Lücking, 1997). Comparing the microsite categories inferred for these species from the data on relative light intensity in this study (mean per species) resulted in a statistically highly significant linear correlation

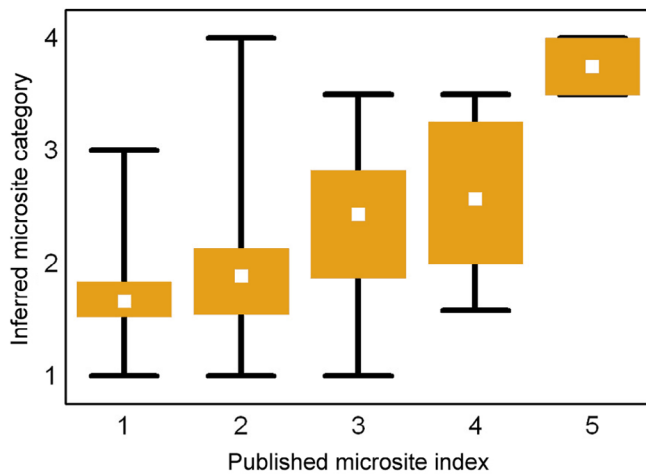


FIGURE 7 Variation of inferred microsite category based on relative light intensity for species with previously published microsite indices (Lücking, 1997). Boxplot indicates mean, 25% quartile and minimum/maximum [Color figure can be viewed at wileyonlinelibrary.com]

($R_{\text{Spearman}} = .54, p < .001$). However, we observed a less pronounced slope in the inferred microsite categories, with species with a published index of one oscillating between 1.5 and 2 in the inferred categories and species with indices between three and five oscillating between 2.5 and 4 in the inferred categories (Figure 7).

4 | DISCUSSION

This work is one of few investigating the community structure of foliicolous lichens in wet tropical forest. Previous studies were carried out in Australia (Conran, 1997; Conran & Rogers, 1983; Rogers & Barnes, 1986), Guatemala (Barillas, Lücking, & Winkler, 1993), Costa Rica (Lücking, 1998a, 1998b; Lücking, 1999a, 1999b, 1999c) and Brazil (Cáceres et al., 2000). However, this is the first study to simultaneously analyze the influence of microsite and phorophyte species on foliicolous lichen community structure based on a stochastic sample representing a microclimatic gradient.

The total of 191 species found in this work is one of the highest numbers reported at a global level. Higher numbers are only known from La Selva Biological Station in Costa Rica (293 species; Lücking, 1999a, 2001b), Jatun Satcha Biological Station in Ecuador (232; Lücking, 1999d) and the Botarrama trail in Braulio Carrillo National Park in Costa Rica (217; Lücking, 1999b). The somewhat lower richness documented for Los Tuxtlas Biological Station is likely due to this region representing the northern limit of the

neotropical lowland rain forest, with certain species not found at these higher latitudes (Herrera-Campos, Lücking, et al., 2004).

Composition and community structure of foliicolous lichens at Las Tuxtlas were overall similar to those found at the aforementioned sites in Costa Rica and Ecuador (Lücking, 1998a, 1998b, 1999a, 1999b, 1999d). The most abundant species were shared between these localities, including *Gyalectidium filicinum*, *Porina alba*, *P. epiphylla*, *P. karnatakensis* and *Strigula smaragdula*, suggesting that our findings can be generalized within broader area in the Neotropics. Santos, Cáceres, and Lücking (2020) demonstrated that the foliicolous lichen biota of Mexico is part of a larger biogeographic region encompassing all of Central America and northwestern South American (Chocó). The significant correlation between published microsite indices for foliicolous lichens (Lücking, 1997) and the microsite categories derived from mean relative light intensity measurements in the present work also demonstrates that microsite preferences of these lichens are consistent across their distribution range.

Foliicolous lichen communities in tropical rain forests are largely structured by three factors: (a) microclimatic parameters such as relative light intensity and humidity, (b) phorophyte features such as leaf surface structure and leaf longevity and (c) primary succession (Lücking, 1998a, 1998b, 1999b, 1999c; Mežaka et al., 2020). In terms of community parameters, these factors are reflected in species composition (microclimate, phorophyte) and species richness (phorophyte, succession). The phorophyte species thereby influences both species composition, through leaf surface characteristics, and species richness, through leaf longevity. The latter primarily determines how far primary succession develops and how many species accumulate in an individual community (Conran & Rogers, 1983; Lücking, 1998a, 1998b, 1999b; Rogers, 1989; Rogers & Barnes, 1986).

Our analysis allowed us to discern the influence of the three main factors on community structure at various hierarchical levels. Relative light intensity (microsite) was correlated with the formation of community clusters at high and intermediate levels, dividing the clusters into groups corresponding to the shady understory (low light levels; Groups A, F), to small light gaps (medium light levels; Groups B, E) and to the transition to canopy (high light levels; Group D). In contrast, phorophyte species was largely correlated with the formation of terminal community clusters, particularly in Groups B and C, but also A and F, although this effect was discernable at higher-level clusters as well. The distribution of species richness among clusters indicated a potential influence of

leaf longevity. Although precise data on leaf longevity are not available for most of the phorophytes studied here, some conclusions can be made from the literature. Thus, species of *Astrocaryum*, *Monstera* and *Salacia* are usually associated with high (> 50 months), those of *Guarea*, *Heliconia*, *Pseudolmedia* and *Syngonium* with medium (30–50 months), those of *Chamaedorea* and *Piper* with medium to low (15–30 months) and those of *Costus* and *Siparuna* with low (< 15 months) leaf longevity (Ataroff & Schwarzkopf, 1992; Bentley, 1979; Bongers et al., 1988; Dirzo, Gomez-Vázquez, & Castelan-Sanchez, 1997; Hartshorn, 1991; Lücking, 1998a; Nicotra, 1999; Nicotra, Chazdon, & Montgomery, 2003; Piñero, Martínez-Ramos, Mendoza, Álvarez-Buylla, & Sarukhan, 1986; Piñero, Martínez-Ramos, & Sarukhan, 1984; Piñero, Sarukhan, & González, 1977; Poorter, Van de Plassche, Willems, & Boot, 2004; Reich, Uhl, Walters, & Ellsworth, 1991; Rogers & Clifford, 1993; Steingraeber & Fisher, 1986; Williams et al., 1989). Accordingly, community clusters with (moderate to) high species richness were statistically associated with *Astrocaryum*, *Guarea*, *Monstera*, and *Salacia* (Groups B, C), with up to 51 species on individual phorophytes of *Astrocaryum* and *Salacia* and up to 46 on *Monstera*. In turn, the only cluster with low species richness (group F) included largely phorophytes representing *Chamaedorea*, *Costus*, *Piper* and *Siparuna* (11 out of 21), although this was not statistically significant. Notably, the terminal Cluster F03 had the lowest mean foliicolous species richness, along with a high proportion of *Costus* and *Siparuna* phorophytes (six out of 10). Common species in this cluster were *Coenogonium subluteum*, *Gyalectidium filicinum*, *Porina alba* and *Strigula smaragdula*. While not statistically significant for the cluster itself, two of these species, *C. subluteum* and *G. filicinum*, were statistically more frequent on leaves of *Siparuna*, one of the two dominant phorophyte species in cluster F03. This supports earlier findings that leaf longevity drives community richness, through the simple mechanism that communities reaching early successional stages mostly consist of few pioneer species adapted to rapid colonization and establishment, including species such as *Coenogonium subluteum*, *Porina alba* and *Gyalectidium filicinum* (Conran & Rogers, 1983; Lücking, 1998a, 1998b, 1999b, 2001a, 2001b, 2008; Lücking & Bernecker-Lücking, 2002).

Our results indicate that phorophyte preferences manifest themselves largely on phorophytes with long leaf longevity, allowing individual lichen communities to develop phorophyte-dependent patterns of secondary succession, with the establishment of taxa exhibiting preferences for certain leaf characteristics. Indeed, statistically significant differences in the composition of

phorophytes between clusters that were not correlated with foliicolous lichen species richness, and so not explained by leaf longevity, were concentrated in Groups B and C, mostly composed of *Astrocaryum*, *Guarea*, *Monstera* and *Salacia*, with medium to high leaf longevity. Most notable were terminal clusters consisting of single phorophyte species, such as B01 (5× *Astrocaryum*), part of B02 (3× *Monstera*) and particularly C02 (10× *Salacia*). These phorophyte-based clusters were not caused through spatial autocorrelation, given that the individual phorophytes in each cluster were not spatially associated but dispersed along the transect. The formation of these clusters was thereby not only correlated with statistically significant indicator species but also by with rare species limited to certain clusters. The *Salacia* cluster (C02) was characterized by species of the genera *Bapalmuia*, *Malmidea*, *Psoroglaena*, and particularly *Strigula*, rare or absent on other phorophytes, whereas the *Astrocaryum* cluster (B01) featured species of *Aulaxina*, *Chroodiscus*, *Opegrapha* and *Tricharia*. The preferred association of various species of *Strigula* with leaves of *Salacia* was notable. Most of these lichens grow below the leaf cuticle and are particularly susceptible to anatomical leaf characteristics (Chapman, 1976; Lücking, 2001a, 2008; Sérusiaux, 1989), so *Salacia* appears to provide a favorable leaf anatomy for these *Strigula* species to establish.

Our findings suggest that phorophyte diversity positively influences foliicolous lichen species richness in terms of gamma diversity, not because of absolute phorophyte specificity, such as found in parasite–host relationships, but through subtle phorophyte preferences caused by niche characteristics that are only detectable through statistically meaningful sampling. Similar patterns have been found for epiphytes in general, including bark-dwelling (corticolous) lichens (Ardila-Ríos et al., 2015; Cáceres et al., 2007; Cornelissen & Ter Steege, 1989; Rosabal et al., 2013; Soto-Medina et al., 2012), but also bryophytes and vascular epiphytes (Benavides et al., 2011; Köster et al., 2011; Merwin et al., 2003; Nieder et al., 1999; Sáyago et al., 2013). Hence, the notion of “diversity begets diversity” due to environmental heterogeneity (Palmer & Maurer, 1997; Stevens & Tello, 2011; Whittaker, 1975) appears to be supported: phorophyte diversity “begets” diversity of foliicolous lichen communities through subtle phorophyte preferences. While this pattern is generally detectable in epiphyte communities, foliicolous lichens provide a unique model to study this phenomenon, due to the short longevity of the substrate and the fast community development, allowing not only studies in situ but also experimental setups with artificial substrata (Lücking & Bernecker-Lücking, 2002, 2005; Sanders & Lücking, 2002).

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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