

Research

Vertical distribution of epiphytic lichens on *Quercus laurina* Humb. & Bonpl. in a remnant of cloud forest in the state of Veracruz, México

Gonzalo Castillo-Campos, Rosa Emilia Pérez-Pérez, Octavio Córdova-Chávez,
José Guadalupe García-Franco and Marcela Eugenia da Silva Cáceres

G. Castillo Campos (<https://orcid.org/0000-0002-3059-8109>) and O. C. Chávez, Red de Biodiversidad y Sistemática, Inst. de Ecología, Xalapa, Veracruz, México. – R. E. Pérez-Pérez (<https://orcid.org/0000-0001-5874-2849>) ✉ (emilia.perez@correo.buap.mx), Facultad de Ciencias Biológicas, Edificio 1 B10 1, Ciudad Universitaria, Benemérita Universidad Autónoma de Puebla CP. 72570, Puebla, México. – J. G. García-Franco, (<https://orcid.org/0000-0003-0540-6045>), Red de Ecología Funcional, Inst. de Ecología, Xalapa, Veracruz, México. – M. E. da Silva Cáceres, (<https://orcid.org/0000-0002-5612-1309>), Depto de Biociências, Univ. Federal de Sergipe, Itabaiana, Sergipe, Brazil.

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In the tropics, corticolous lichen richness and cover tend to increase from the trunk base to the top of the crown of trees. In this study we calculated the total beta diversity of the lichen community along a vertical gradient on *Quercus laurina* in Mexican cloud forest. By comparing the richness and cover of the lichens by zone, we show that foliose and fruticose lichens are a minor component of the total lichen species richness, but have a higher cover than the crustose lichens. Five zones were identified along each phorophyte (n = 15) with a diameter at breast height >40 cm. A total of 92 species were identified. Of these, 38% were found only in a single zone, 51% were shared between the different zones and 11% occurred across all zones. Species richness and cover increased from the lowest to the highest zones of the phorophytes. Dissimilarity in species composition between the zones could be explained by species replacement. An indicator species analysis revealed that only a few species, e.g. *Hypotrachyna vexans*, *H. cf. sublaevigata* and *Ramalina cf. sinaloensis* prefer a particular zone. The results show that the lichen community associated with *Quercus laurina* phorophytes is highly diverse and suggest that species richness and cover are related to the zone and the various growth forms.

Keywords: beta diversity, corticolous lichens, Neotropical lichens, tropical cloud forest

Introduction

Corticolous lichens are diverse and functionally important organisms in forest ecosystems, where they contribute to biomass and play a key role in water and nutrient cycling. Biomass and nutrients accumulate as lichens grow, to be subsequently released when they die and decompose; hence the importance of lichens in the nitrogen, phosphorus and potassium cycles (Pike 1978, Hölscher et al. 2004, Obregon et al. 2011). Furthermore, lichens provide food and shelter to various aquatic and terrestrial



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invertebrates (gastropods, micro- and macro-arthropods, spiders and dragonflies and other odonates) (Mukherjee et al. 2010, Meyer et al. 2014, Asplund et al. 2015), as well as camouflage and material for nests of vertebrates such as birds (Uliczka and Angelstam 2000).

The presence of corticolous lichens is related to forest type, age, composition and structure, as well as to light and moisture availability (McCune et al. 1997, Campbell and Coxson 2001, Fanning et al. 2007, Johansson et al. 2010, Li et al. 2015), and wind speed and exposure (Armstrong and Welch 2007). At the scale of trees, the vertical distribution of species and the structure of the lichen communities are influenced by their poikilohydric physiology (Komposch and Hafellner 2000, Normann et al. 2010). Lichens respond mainly to light and moisture (Sillet and Rambo 2000, Cleavitt et al. 2009, Li et al. 2015), which vary the base of the trunk to the crown of trees (Freiberg 1997, Freiberg and Freiberg 2000, Komposch and Hafellner 2000, Hauck et al. 2001, Holz et al. 2002, Boch et al. 2013), especially in the tropics (Komposch and Hafellner 2000). Other parameters that affect the lichen community are bark pH and structure (Hauck et al. 2001, Cleavitt et al. 2009), and, within trees of the same species, available space (tree size) and time for colonization (tree age) (Freiberg 1996, Cobanoglu and Sevgi 2009, Boch et al. 2013), as well as potential competition with other epiphytic organisms (Armstrong and Welch 2007, Cleavitt et al. 2009). Owing to this, the distribution of lichens on trees is not homogeneous, as some species live in shady and humid zones, while others thrive in brighter and drier areas, and yet others display a broader range of micro-environmental tolerance (Sporn et al. 2010).

It has been documented that along the vertical gradient of tree trunks, the community of non-vascular epiphytes is dominated by bryophytes in the zone closest to the ground, while macrolichens (cyanolichens, alectoroid and foliose lichens) become progressively more dominant towards the canopy (McCune et al. 1997). Both the host tree species and canopy height are considered to influence the species richness and growth forms of lichens (Fanning et al. 2007, Kiebacher et al. 2016), and it has been suggested that lichen species usually show preference for a certain microhabitat (Peck et al. 2002).

This study was carried out in a remnant of cloud forest in the central part of the state of Veracruz, Mexico. This vegetation type is characterized by an abundance and richness of vascular epiphytes, mainly of the families Orchidaceae, Bromeliaceae and Polypodiaceae (Flores-Palacios and García-Franco 2008). Previous studies also indicate that a key epiphyte component are lichens, as 205 species belonging to 77 genera have been documented inhabiting the trunks of various phorophyte species (Pérez-Pérez et al. 2015) and across the trunk of *Quercus laurina* Humb. & Bonpl. (Córdova-Chávez 2015), but it is not yet known whether there is species turnover along the trunk. The aim of this study was to analyze the turnover of lichen species along the vertical gradient in phorophytes of *Quercus laurina*. We expected that

foliose and fruticose species would be a minor component of the total lichen species richness but would have a higher cover than the crustose lichens (Komposch and Hafellner 2000, Johansson et al. 2010, Normann et al. 2010).

Material and methods

Study site

The study was conducted in the mountainous area at the center of the state of Veracruz, Mexico, specifically in La Cortadura Ecological Reserve located on the Cofre de Perote eastern slopes (19°29'17.6"N, 97°02'25.9"W, at 2000 m a.s.l.) (Fig. 1). The local climate is humid temperate, with a mean temperature of 18°C and a mean annual precipitation of 2500 mm (García-Franco et al. 2008, De la Rosa and Negrete-Yankelevich 2012). The reserve spans across 107 ha, 45 of which correspond to relatively well-preserved cloud forest, and the rest is covered by forest patches under various successional states and pasture areas (De la Rosa and Negrete-Yankelevich 2012). The best represented tree species in the forest are *Parathesis melanosticta* (Schltld.) Hemsl., *Hedyosmum mexicanum* Cordem., *Miconia chryso-neura* Triana, *Alchornea latifolia* Sw., *Miconia glaberrima* (Schltld.) Naudin, *Cyathea fulva* (M. Martens and Galeotti) Fée, *Turpinia occidentalis* (Swartz) G. Don., *Clethra mexicana* DC. and *Quercus laurina* Humb. and Bonpl. (García-Franco et al. 2008), the latter being one of the most frequent species (Pérez-Pérez et al. 2015).

Lichen sampling and taxonomic identification

Lichen sampling was conducted in 15 phorophytes of *Quercus laurina* with a diameter at breast height (DBH) larger than 40 cm; separated by an average distance of 45.17 ± 20.15 m ($1 \pm$ SD; minimum 7.9; 83.9 maximum) (Fig. 1). The trees were located on a hilltop at 2000 m a.s.l. to maximize the likelihood that all trees were exposed to the same environmental conditions. The five Johansson zones were defined in each phorophyte (Gradstein et al. 2003); these zones identify sections of tree trunks that have been associated with different niches for epiphytic plants (Fig. 2). The presence and cover of lichens in each zone were recorded by placing two sample plots of 20×50 cm transparent plastic sheets (0.1 m^2), subdivided in 2×2 cm squares (Kuusinen 1994, Kivistö and Kuusinen 2000, Pérez-Pérez et al. 2011). The data from the two sample plots in each Johansson zone were added up to derive the species richness and their cover per zone, to perform the statistical analysis.

Phorophytes were climbed using the single-rope technique, which is widely used for studying epiphytic plants (Barker and Sutton 1997, Freiberg 1999, Komposch and Hafellner 2000, Barker and Pinard 2001, Gradstein et al. 2003, Holz and Gradstein 2005, Normann et al. 2010, Pos and Slegers 2010, Sporn et al. 2010, Obregon et al. 2011,

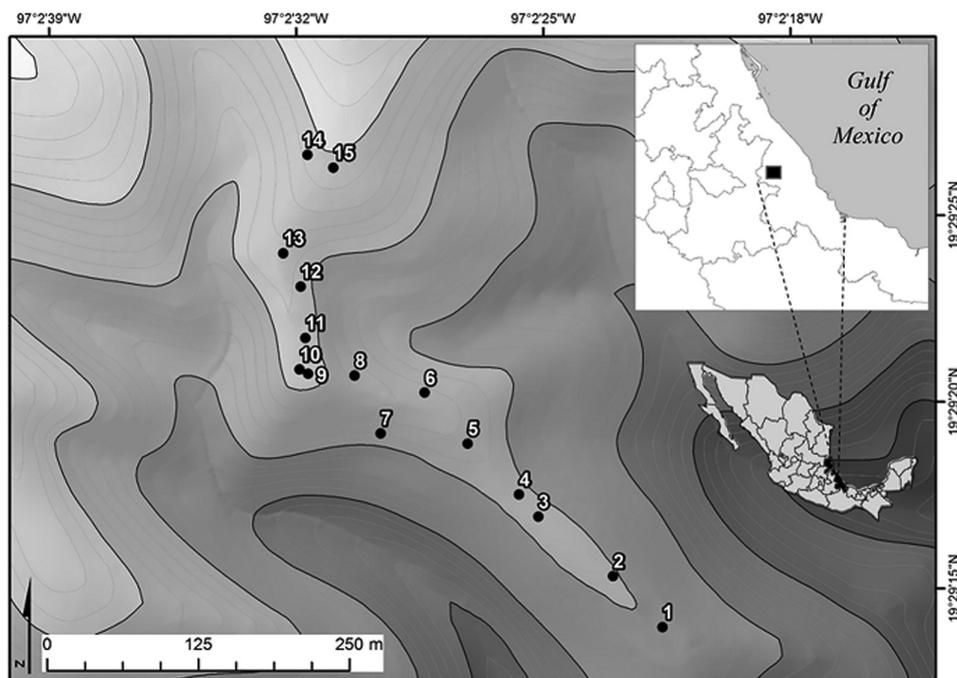


Figure 1. Location of the sampling site and sampled phorophytes at La Cortadura forest, Veracruz, Mexico. Dots and numbers indicate the approximate location of the *Quercus laurina* Humb. & Bonpl. phorophytes sampled.

Boch et al. 2013). In each phorophyte, a rope was placed in the fork of the highest branches (ca 1.5 m from the phorophyte top), provided it ensured safe climbing and sampling. Each Johansson zone was sampled in the central trunk with enough diameter to fit the sampling plot, and the diameter and height of each zone of the phorophyte sampled were measured.

Samples were recorded and collected starting from the tree top down to the trunk base, along the orientation that showed the greatest lichen cover (Pérez-Pérez et al. 2015), to maximize the sampling in those tree sections that were not easily accessible. The cover of each taxon was measured in cm^2 (Kuusinen 1994, Kivistö and Kuusinen 2000, Pérez-Pérez et al. 2011, 2015). The different genera and/or species were identified using specialized keys supported by chemical testing (10% potassium hydroxide (K), sodium hypochlorite (C) and paraphenyldenediamine (P)) (Harris 1984, 1995, Marbach 2000, Staiger 2002, Galloway and Thomas 2004, Kashiwadani and Nash III 2004, Cáceres 2007, Aptroot et al. 2008, Rivas Plata and Lücking 2008, Ertz 2009, Lücking et al. 2009, 2011, Aptroot 2012, Aptroot and Cáceres 2013, 2014, Moncada et al. 2013, Lücking 2014, Nelsen et al. 2014, Breuss and Lücking 2015, Mongkolsuk et al. 2015, Aptroot and Lücking 2016, Herrera-Campos et al. 2016). Specimens lacking reproductive structures were identified to genus only. Backup specimens were deposited in the herbaria XAL (Laboratory of Mycology, Instituto de Ecología, A.C., Mexico), ISE (Laboratory of Lichenology, Universidade Federal de Sergipe campus Itabaiana, Brazil) and BUAP (Laboratory of Plant Biology, Faculty of Biological Sciences, Benemérita Universidad Autónoma de Puebla, Mexico).

Data analysis

We analyzed the dissimilarity in species composition across the different Johansson zones. We calculated total beta diversity ($\beta_{cc} = \frac{b+c}{a+b+c}$), which was further divided into species replacement ($\beta_{-3} = 2x \frac{\min(b,c)}{a+b+c}$) and the difference in species richness between pairs of zones ($\beta_{rich} = \frac{|b-c|}{a+b+c}$); where a is the number of species common to both zones, b is the number of species exclusive to the first zone, c is the number of species exclusive to the second zone and $\min(b, c)$ is the minimum number of exclusive species. The values obtained range from 0 (when all species occur in both zones) to 1 (when no species is shared between zones) (Carvalho et al. 2012, Juárez Ramírez et al. 2015). Error bars were constructed at 100% of richness and cover as a function of the Johansson zones; these were programmed with Fortran. The data on species cover and richness recorded for the Johansson zones were compared using non-parametric Kruskal–Wallis tests followed by Wilcoxon test for pair-wise comparisons (Rosabal et al. 2010, Li et al. 2015, Maceda-Veiga and Gómez-Bolea 2017). An indicator species analysis (ISA) was used for the five Johansson zones in the 15 phorophytes, applying a Monte Carlo test, with zone as the clustering variable; species frequency and cover data were pooled randomly with 4999 replicates to identify any preference of lichens for particular Johansson zones (McCune and Grace 2002). The statistical analyses were conducted using the programs Statistic 7 (StatSoft 2004) and PCord 7.07 (McCune and Mefford 2018).

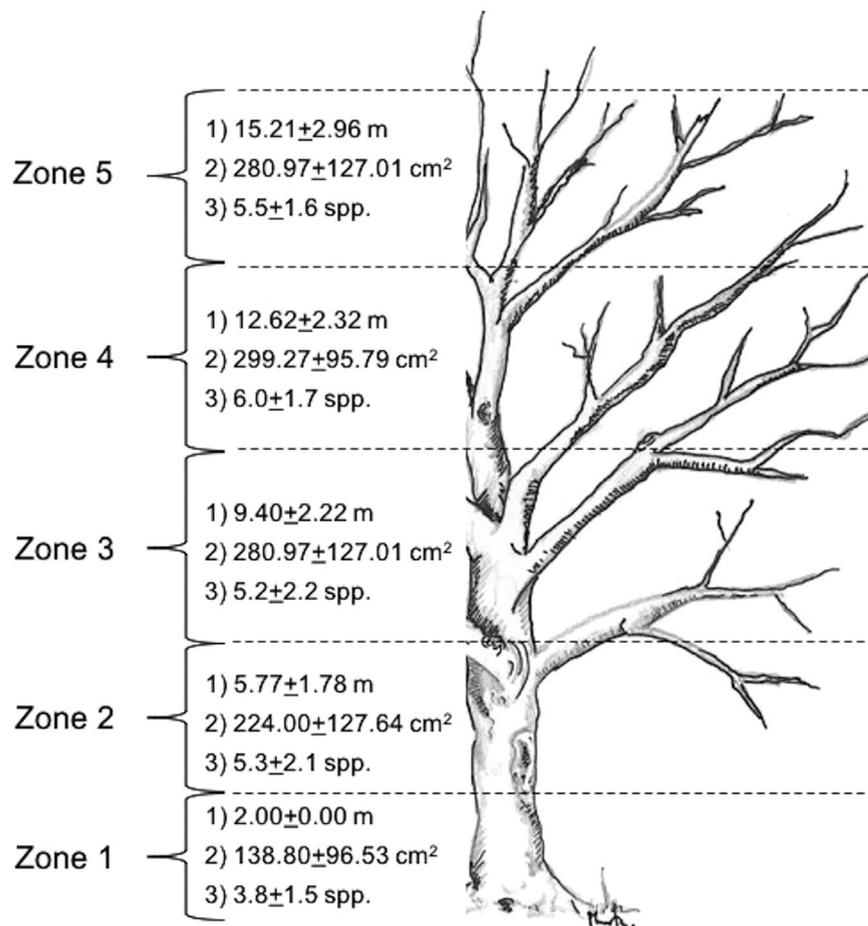


Figure 2. Johansson's zones (as modified by Gradstein et al. 2003): Each zone shows 1) average height, 2) area of trunk available, as calculated from the diameter and length of the trunk segment and 3) average number of lichen species.

Results

The structures in each Johansson zone differed in diameter and showed a gradient of space availability, with zones 1 and 2 (at the trunk base) having the largest diameter (Z1 54.91 + 19.66 cm; Z2 43.72 + 14.18 cm, Z3 35.48 + 11.45 cm, Z4 27.46 + 10.36 cm, Z5 22.46 + 7.54 cm). However, the total available surface area (cm²) was similar, due to the length of the trunk segment in each zone (Fig. 2). The vertical gradient where Johansson zones were located ranged from 2.0 to 15.21 m in height, suggesting broad ranges in the conditions that favor the establishment and growth of lichens.

The 15 phorophytes of *Quercus laurina* hosted a total of 92 lichen species, belonging to 43 genera, 20 families and 7 orders. The families with the highest richness were Parmeliaceae and Graphidaceae, with 30 and 19 species, respectively, while seven families were monospecific (Table 1). Only four families showed cyanobacteria as photobionts: Coccocarpiaceae (one species), Collemataceae (two species), Lobariaceae (three species) and Pannariaceae (one species). On average, 18 ± 3 lichen species were recorded per phorophyte (n = 15).

The analysis of species richness by zone revealed that richness increases from the lowest to the highest zones of the tree (Fig. 3).

Out of the total number of species, 39 (42%) were unique to a single Johansson zone, e.g. *Anzia* cf. *ornata*, *Catinaria* sp., *Lopezaria versicolor*, *Myriotrema* sp. and *Phaeographis* cf. *leio-grammodes*, 44 (48%) were shared between different zones (two to four zones). Nine (10%) species were recorded in all Johansson zones with a relatively high cover; these were *Herpothallon rubrocinctum*, *Parmotrema* sp. 1, *Parmotrema* sp. 2, *Ocellularia* sp., *Usnea* cf. *brasiliensis*, *Usnea* cf. *subfloridana*, *Usnea* cf. *mexicana*, *Pertusaria* sp. and *Punctelia hypoleucites*. *Punctelia hypoleucites* was the species with the highest cover in the entire lichen community (Table 1).

The average number of species per zone was 5.2 ± 1.9 (n = 75) (in Fig. 2, the number 3 of each bracket indicates the average number of species recorded in each zone); these numbers were not significantly different across zones (F = 2.779, p < 0.735). As regards the area available in each zone, averages are lower at the base of phorophytes and increase with height toward the crown (in Fig. 2, the number 2 of each bracket indicates the average area registered in each zone); in spite of this, they were not significantly different because of the broad variation observed. However, the Kruskal–Wallis test indicates significant differences in species richness and cover among the Johansson zones (Fig. 4).

Table 1. Total cover and frequency of lichen species, sorted by orders and families, per Johansson zone on *Quercus laurina* Humb. & Bonpl. phorophytes.

Families	Species	Cover (cm ²)	Frequency by Zona de Johansson					
			Total	Z1	Z2	Z3	Z4	Z5
Arthoniaceae	<i>Cryptothecia lichexanthonica</i> E.L. Lima, Aptroot & M. Cáceres	72	1	0	0	1	0	0
	<i>Cryptothecia</i> sp.	108	5	3	2	0	0	0
	<i>Herpothallon rubrocinctum</i> (Ehrenb.) Aptroot, Lücking & G. Thor	684	25	7	8	6	3	1
Brigantiaaceae	<i>Brigantiaea leucoxantha</i> (Spreng.) R. Sant. & Hafellner	48	1	0	1	0	0	0
Caliciaceae	<i>Cratiria aggreidens</i> (Stirt.) Marbach	36	2	0	0	1	1	0
Coccocarpiaceae	<i>Coccocarpia palmicola</i> (Spreng.) Arv. & D.J. Galloway	4	1	0	0	0	1	0
Collemataceae	<i>Leptogium cyanescens</i> (Pers.) Körb.	8	1	0	0	0	0	1
	<i>Leptogium</i> sp.	52	1	0	0	1	0	0
Graphidaceae	<i>Diorygma</i> sp.	56	3	0	0	1	1	1
	<i>Graphis caesiella</i> Vain.	116	2	0	0	0	1	1
	<i>Graphis</i> cf. <i>distincta</i> Makhija & Adaw.	16	1	0	0	0	1	0
	<i>Graphis mexicana</i> (Hale) Kalb, Lücking & Lumbsch	92	3	1	1	1	0	0
	<i>Graphis</i> cf. <i>streblocarpa</i> (Bél.) Nyl.	56	1	0	0	0	0	1
	<i>Graphis</i> cf. <i>subdisserpens</i> Nyl.	44	1	1	0	0	0	0
	<i>Graphis</i> sp.	68	3	1	0	0	1	1
	<i>Hemithecium</i> sp.	108	3	0	0	1	1	1
	<i>Melanotrema</i> sp.	108	2	0	0	1	1	0
	<i>Myriotrema</i> sp.	32	1	0	1	0	0	0
	<i>Ocellularia albocincta</i> (Hale) Divakar & Mangold	108	1	1	0	0	0	0
	<i>Ocellularia columellata</i> Zahlbr.	48	2	0	0	2	0	0
	<i>Ocellularia</i> sp.	816	14	4	4	2	3	1
	<i>Phaeographis dendritica</i> (Ach.) Müll. Arg.	24	2	0	0	1	0	1
	<i>Phaeographis</i> cf. <i>leiogrammodes</i> (Kremp.) Müll. Arg.	8	1	0	0	0	0	1
	<i>Phaeographis</i> cf. <i>tortuosa</i> (Ach.) Müll. Arg.	60	2	0	0	1	1	0
	<i>Pseudochapsa</i> cf. <i>dilatata</i> (Müll. Arg.) Pammen, Lücking & Lumbsch	24	1	0	0	0	0	1
	<i>Thelotrema conveniens</i> Nyl.	208	6	1	2	1	1	1
	<i>Thelotrema foveolare</i> Müll. Arg.	180	2	1	1	0	0	0
Lecanoraceae	<i>Lecanora tropica</i> Zahlbr.	56	1	0	0	0	0	1
	<i>Lecanora</i> sp.	56	2	2	0	0	0	0
Lobariaceae	<i>Sticta beauvoisii</i> Delise	684	8	0	2	2	1	3
	<i>Sticta</i> aff. <i>cometiella</i> Vain.	140	3	0	1	1	0	1
	<i>Sticta</i> aff. <i>limbata</i> (Sm.) Ach.	24	1	1	0	0	0	0
Malmideaceae	<i>Malmidea hypomelaena</i> (Nyl.) Kalb & Lücking	48	2	0	0	0	0	2
	<i>Malmidea</i> sp.	76	2	1	1	0	0	0
Opegraphaceae	<i>Opegrapha</i> sp.	72	1	1	0	0	0	0
Pannariaceae	<i>Parmeliella clavulifera</i> P.M. Jørg.	16	1	0	0	0	1	0
Parmeliaceae	<i>Anzia americana</i> Yoshim. & Sharp	40	2	0	0	0	1	1
	<i>Anzia</i> cf. <i>ornata</i> (Zahlbr.) Asahina	8	1	1	0	0	0	0
	<i>Flavoparmelia</i> cf. <i>rutidota</i> (Hook. F. & Taylor) Hale	628	8	1	0	0	4	3
	<i>Hypotrachyna</i> cf. <i>brevirhiza</i> (Kurok.) Hale	176	4	0	1	1	1	1
	<i>Hypotrachyna cirrhata</i> (E. Fr.) Divakar, A. Crespo, Sipman, Elix & Lumbsch	20	1	1	0	0	0	0
	<i>Hypotrachyna</i> cf. <i>imbricatula</i> (Zahlbr.) Hale	108	3	0	2	0	1	0
	<i>Hypotrachyna</i> cf. <i>neodissecta</i> (Hale) Hale	116	2	1	0	0	1	0
	<i>Hypotrachyna</i> cf. <i>pseudosinuosa</i> (Asahina) Hale	96	3	0	2	0	1	0
	<i>Hypotrachyna</i> cf. <i>pulvinata</i> (Fée) Hale	112	2	1	0	0	0	1
	<i>Hypotrachyna</i> cf. <i>sublaevigata</i> (Nyl.) Hale	328	9	3	1	1	4	0
	<i>Hypotrachyna vexans</i> (Zahlbr. ex W.L. Culb. & C.F. Culb.)	124	5	4	1	0	0	0
	<i>Hypotrachyna</i> sp.	44	2	1	1	0	0	0
	<i>Parmotrema arnoldii</i> (Du Rietz) Hale	372	8	0	4	1	2	1
	<i>Parmotrema cristiferum</i> (Taylor) Hale	296	2	0	1	0	0	1
	<i>Parmotrema flavescens</i> (Kremp.) Hale	124	1	0	0	0	0	1
<i>Parmotrema</i> cf. <i>grayanum</i> (Hue) Hale	20	1	0	0	0	1	0	
<i>Parmotrema mellissii</i> (C.W. Dodge) Hale	203	3	0	0	0	2	1	

(Continued)

Table 1. Continued.

Families	Species	Cover (cm ²)	Frequency by Zona de Johansson					
			Total	Z1	Z2	Z3	Z4	Z5
	<i>Parmotrema rampoddense</i> (Nyl.) Hale	28	1	0	0	1	0	0
	<i>Parmotrema reticulatum</i> (Taylor) M. Choisy	120	1	0	0	0	0	1
	<i>Parmotrema subsidiosum</i> (Müll. Arg.) Hale	838	12	2	6	0	2	2
	<i>Parmotrema</i> sp. 1	1268	24	4	3	6	4	7
	<i>Parmotrema</i> sp. 2	412	11	3	4	1	2	1
	<i>Punctelia</i> cf. <i>bolliana</i> (Müll. Arg.) Krog	92	2	0	0	0	1	1
	<i>Punctelia hypoleucites</i> (Nyl.) Krog	2260	30	1	2	10	10	7
	<i>Remotrachyna</i> cf. <i>costaricensis</i> (Nyl.) Divakar & A. Crespo	276	4	2	0	1	0	1
	<i>Usnea</i> cf. <i>brasiliensis</i> (Zahlbr.) Motyka	712	18	1	2	6	5	4
	<i>Usnea</i> cf. <i>filipendula</i> Stirt.	268	5	1	1	2	1	0
	<i>Usnea</i> cf. <i>mexicana</i> Vain.	1004	20	1	6	3	5	5
	<i>Usnea</i> cf. <i>subfloridana</i> Stirt.	912	16	1	4	4	3	4
	<i>Usnea</i> sp.	16	1	0	0	0	1	0
Pertusariaceae	<i>Pertusaria</i> cf. <i>dilatata</i> Müll. Arg.	76	2	0	0	0	1	1
	<i>Pertusaria velata</i> (Turner) Nyl.	36	2	0	0	1	0	1
	<i>Pertusaria ventosa</i> Malme	48	3	0	1	0	1	1
	<i>Pertusaria</i> sp.	760	20	1	3	5	8	3
Physciaceae	<i>Heterodermia</i> cf. <i>granulifera</i> (Ach.) W.L. Culb.	68	1	0	0	0	0	1
	<i>Heterodermia</i> cf. <i>tropica</i> (Kurok.) Sipman	64	2	0	0	0	0	2
	<i>Heterodermia</i> sp.	20	1	0	0	0	1	0
	<i>Leucodermia appalachensis</i> (Kurok.) Kalb	140	3	1	1	0	1	0
	<i>Physcia</i> cf. <i>caesia</i> (Hoffm.) Hampe ex Fűrnr.	4	1	0	1	0	0	0
Pilocarpaceae	<i>Eugeniella</i> sp.	72	1	0	0	1	0	0
Pyrenulaceae	<i>Pyrenula dermatodes</i> (Borrer) Schaer.	184	6	0	3	2	1	0
Ramalinaceae	<i>Micarea</i> sp.	40	2	1	0	1	0	0
	<i>Catinaria</i> sp.	8	1	0	0	1	0	0
	<i>Crocynia gossypina</i> (Sw.) A. Massal.	56	1	0	0	0	0	1
	<i>Crocynia pyxinoides</i> Nyl	24	1	0	0	0	1	0
	<i>Lopezaria versicolor</i> (Flot.) Kalb & Hafellner	4	1	0	0	0	1	0
	<i>Phyllopsora</i> cf. <i>ochroxantha</i> (Nyl.) Zahlbr.	92	2	0	1	1	0	0
	<i>Phyllopsora</i> sp.	48	1	0	1	0	0	0
	<i>Ramalina</i> cf. <i>sinaloensis</i> Bowler & Rundel	100	4	0	0	1	0	3
	<i>Ramalina</i> sp.	44	1	0	0	0	0	1
Roccellaceae	<i>Syncesia psaroleuca</i> (Nyl.) Tehler	184	1	0	1	0	0	0
	<i>Syncesia</i> sp.	8	1	1	0	0	0	0
Trypetheliaceae	<i>Astrothelium coccineum</i> Córdova-Chávez, Aptroot & M. Cáceres	58	2	0	0	0	1	1
	<i>Bathelium degenerans</i> (Vain.) R.C. Harris	396	11	0	1	3	3	4
	<i>Polymeridium catapastum</i> (Nyl.) R.C. Harris	80	2	0	0	1	1	0
	<i>Polymeridium sulphurescens</i> (Müll. Arg.) R.C. Harris	36	3	0	1	1	0	1

Likewise, the lower zones (Z1 versus Z2) had lower richness than the higher zones (Z4 versus Z5). In Fig. 5 the species richness between pairs of zones is shown in detail, as well as the percentage of species that corresponds to each of them, as well as the percentage of shared species. Differences in species composition among the five Johansson zones were very high, with total dissimilarity values (β_{cc}) between pairs of zones around 0.60 (60%). Dissimilarity in species composition between zones can be explained by species replacement given that replacement values (β_{-3}) ranged from 50 to 59% (Fig. 6).

The indicator species analysis (ISA) and the Montecarlo test revealed that the species with significant values were *Hypotrachyna vexans* (indicator values: IV = 17; p = 0.02) and *Parmotrema subsidiosum* (IV = 19; p = 0.05), which showed

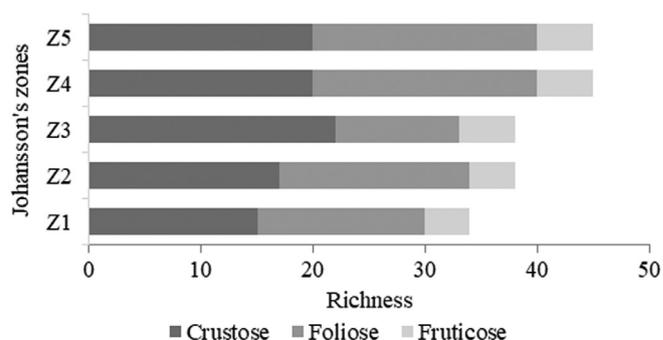


Figure 3. Species richness of lichen species grouped by growth form in each Johansson's zone on *Quercus laurina* Humb. & Bonpl. phorophytes.

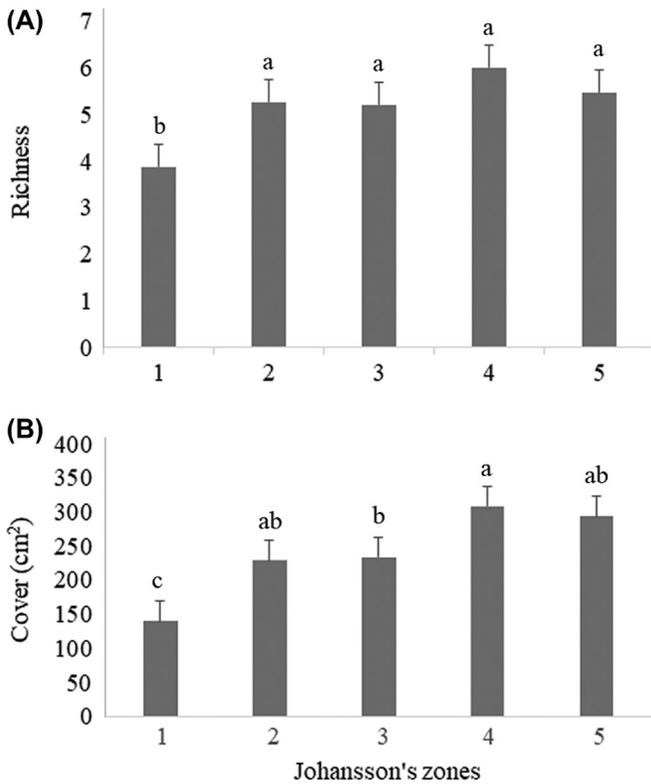


Figure 4. Lichen species richness (A) and cover (B) present in the Johansson's zones (see text to explanation above the zone numbers). Different letters indicate significant differences between zones, after Wilcoxon nonparametric One-way ANOVA: Richness: $\chi^2 = 12.22$, DF 4, $p = 0.0158$; Cover $\chi^2 = 17.91$, DF 4, $p = 0.0013$.

preference for zones 1 and 2, respectively; *Hypotrachyna* cf. *sublaevigata* (IV = 19; $p = 0.04$) and *Pertusaria* sp. (IV = 24; $p = 0.03$) preferred zone 4; and *Ramalina* cf. *sinaloensis* (IV = 16; $p = 0.05$) showed preference for zone 5. However, none of them was unique to a particular zone.

Discussion

There are several factors that determine the vertical distribution of the lichen community, such as microclimate (solar radiation and humidity), exposure time (phorophyte age), habitat quality (bark texture), height above the ground, growth form, reproductive potential of the species and even successional processes (opportunity of colonization and dispersion) (Pirintsos et al. 1993, Campbell and Coxson 2001, Marmor et al. 2012, Merinero et al 2014, Sales et al. 2016). Campbell and Coxson (2001) indicated that the driving factors are light and moisture availability. On the other hand, the time required for colonization has also been considered relevant (Yarranton 1972, Boch et al. 2013), as tree zones are of different ages. Johansson et al. (2010) indicate that in *Quercus* phorophytes, the oldest part of the trunk is at 2 m height; it is in the oldest parts of the phorophyte that succession processes can take place (Freiberg 1996).

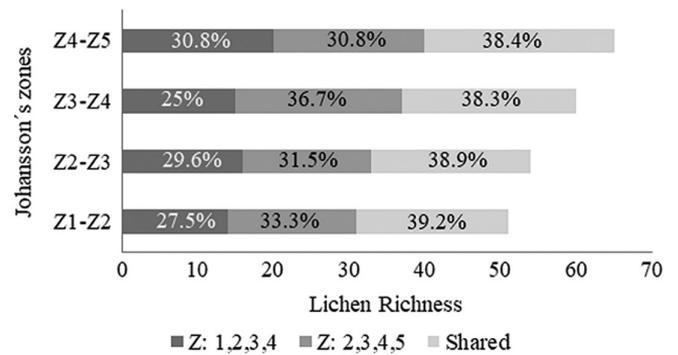


Figure 5. Species richness between pairs of Johansson's zones (Z), the percentage of species that corresponds to each zone is indicated, as well as the percentage of shared species.

One of the distinctive features of the mountain cloud forests is the temperate climate, with a high moisture content as mist (Rzedowski 1978), which undoubtedly favors the presence of lichens (Normann et al. 2010, Obregon et al. 2011). In the case of *Q. laurina*, the older parts of the trunk are from the ground level to 5 m in height, which correspond to zones 1 and 2. These areas present the largest diameters and have been available for colonization and development of the lichen community for a longer time. However, our results showed that the highest species richness and cover were found in zones 4 and 5. This may be due to the heterogeneity of the micro-habitats along tree trunks, given by the different height of phorophyte zones, as pointed out by various authors (Kuusinen 1994, Freiberg 1997, Fanning et al. 2007, Li et al. 2015) and, due to the intrinsic species restriction.

Armstrong and Welch (2007) consider that an additional factor that defines the community structure of lichens is the distribution of each individual species in relation to their

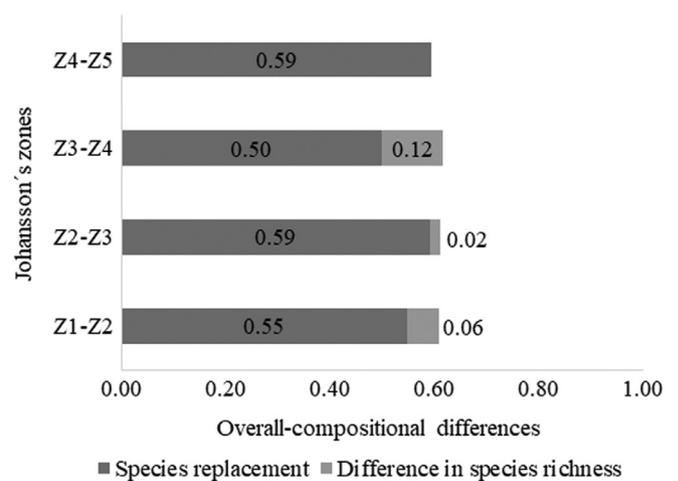


Figure 6. Total dissimilarity between pairs of Johansson's zones, the proportion resulting from species replacement, and the difference in species richness in the comparison of species composition among five Johansson's zones.

growth forms. In our study, although foliose lichens (especially those in the family Parmeliaceae) had higher overall cover than the crustose lichens (dominated by the family Graphidaceae), the latter exhibited the highest species richness. Johansson et al. (2010) considered that the abundance of macrolichens decreases with tree age; hence, it is not uncommon that the highest abundance is observed in the higher zones, as non-scaly and fissured bark is more suitable for colonization (Normann et al. 2010). On the other hand, Fanning et al. (2007) indicated that fruticose lichens are less diverse than crustose and foliose lichens along the vertical gradient of trees, dominating in the highest zone because of their higher light requirement (Giordani et al. 2012). This is the case of the genera *Ramalina* and *Usnea*, although the latter was found in all Johansson zones. McCune et al. (1997) indicated that foliose lichens which have cyanobacteria as photobionts (e.g. Lobariaceae) are more sensitive to light, while those with green-algae photobionts grow well all along the vertical gradient (e.g. Parmeliaceae).

Other authors consider that the presence or absence of lichens in phorophytes sharing homogeneous conditions within a forest (environmental and/or characteristics) is related to the distance between them and the dispersal ability of lichens; therefore, phorophytes separated by greater distances may display differences in species richness (Gradstein et al. 1996, Pérez-Pérez et al. 2011). In this study, the average number of lichen species per phorophyte was 18 of 92 total species, indicating that phorophytes shared only a few species; by contrast, the average number of species between Johansson zones was 5, that is because at this scale the high species turnover is strongly evident along the gradient of the trunk of *Q. laurina* phorophytes.

The pattern of vertical distribution of the lichen community observed in this study is consistent with the proposal by Li et al. (2015), who suggested that a common pattern in the tropics is that lichen species richness and cover tend to increase from the base of the tree to zones higher up in the trunk. It is important to mention that the family Parmeliaceae is the largest of lichen-forming fungi, with a cosmopolitan distribution (Blanco et al. 2006), followed by Graphidaceae, one of the largest families of tropical crustose lichens (Rivas Plata et al. 2012); consequently, it is not unusual to find both families in the cloud forest in La Cortadura, Veracruz, Mexico.

Several studies illustrate the importance of the diversity of phorophytes of different ages, along with canopy height and architecture, for the vertical diversity of lichens (Freiberg 1997, Fanning et al. 2007, Johansson et al. 2010, Hauck 2011). Other authors, however, suggest that differences in vertical distribution pattern are related to the time of exposure and the space available for the establishment of lichen communities, which vary according to the particular conditions of each ecosystem (geographical location, altitude, topography) where phorophytes thrive, the history of the forests and the particular ecological demands of each species (Hinds 1970, Pirintsos et al. 1995, McCune et al.

1997, Freiberg 1999, Freiberg and Freiberg 2000, Liu et al. 2000, Sillet and Rambo 2000, Holz et al. 2002, Holz and Gradstein 2005, Hauck 2011, Pérez-Pérez et al. 2011, Cazzolla Gatti et al. 2017). The results obtained in this study suggest that a set of variables including DBH, height, zone of the tree trunk, and lichen growth forms, do contribute to define the vertical distribution of the lichen community on *Quercus laurina*.

Conclusions

This study shows the existence of a highly diverse lichen community associated with *Quercus laurina* phorophytes, as well as the vertical distribution and cover of lichen species along *Q. laurina* trunks, and our results are consistent with a number of studies conducted at various latitudes throughout the world. In particular, some lichen species displayed a wide tolerance range, being very frequent and abundant in phorophytes, while others showed a relatively restricted distribution. However, long-term studies that record microclimatic conditions in specific zones of the trees will be needed to provide more conclusive information about the characteristics that either foster or restrain the establishment and growth of lichen species. On the other hand, the present study is a relevant contribution to the knowledge of lichens associated with woody vegetation, as it addresses lichen richness and distribution beyond the lower portions of phorophytes trunks (ca 2 m height). The lichen community inhabiting the mountain cloud forest at La Cortadura, Veracruz, Mexico, is a well-preserved relict. Thus, detailed studies of species and processes in this region can provide relevant information about Neotropical lichens in general.

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.jm63xsj6f>> (Castillo-Campos et al. 2019).

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References

- Aptroot, A. 2012. A world key to the species of *Anthracotheicum* and *Pyrenula*. – *Lichenologist* 44: 5–53.
- Aptroot, A. and Cáceres, M. E. S. 2013. Pyrenocarpous lichens (except Trypetheliaceae) in Rondônia. – *Lichenologist* 45: 763–785.
- Aptroot, A. and Cáceres, M. E. S. 2014. A refined species concept in the tropical lichen genus *Polymeridium* (Trypetheliaceae) doubles the number of known species, with a worldwide key to the species. – *Nova Hedwigia* 98: 1–29.
- Aptroot, A. and Lücking, R. 2016. A revisionary synopsis of the Trypetheliaceae (Ascomycota: Trypetheliales). – *Lichenologist* 48: 763–982.
- Aptroot, A. et al. 2008. Pyrenocarpous lichens with bitunicate asci. A first assessment of the lichen biodiversity inventory in Costa Rica. – *Bibliotheca Lichenologica*, J. Cramer in Borntraeger Science Publishers.
- Armstrong, R. A. and Welch, R. A. 2007. Competition in lichen communities. – *Symbiosis* 43: 1–12.
- Asplund, J. et al. 2015. Removal of secondary compounds increases invertebrate abundance in lichens. – *Fungal Ecol.* 18: 18–25.
- Barker, M. G. and Sutton, S. L. 1997. Low-tech methods for forest canopy access. – *Biotropica* 29: 243–247.
- Barker, M. G. and Pinard, M. A. 2001. Forest canopy research: sampling problems, and some solutions. – *Plant Ecol.* 153: 23–38.
- Blanco, O. et al. 2006. Major clades of parmelioid lichen (Parmeliaceae, Ascomycota) and the evolution of their morphological and chemical diversity. – *Mol. Phylogenet. Evol.* 39: 52–69.
- Boch, S. et al. 2013. Up in the tree – the overlooked richness of bryophytes and lichens in tree crowns. – *PLoS One* 8: e84913.
- Breuss, O. and Lücking, R. 2015. Three new lichen species from Nicaragua, with keys to the known species of *Eugeniella* and *Malmidea*. – *Lichenologist* 47: 9–20.
- Cáceres, M. E. S. 2007. Corticolous crustose and microfoliose lichens of northeastern Brazil. – IHW-Verlag, Libri Botanici, Eching, Alemania.
- Campbell, J. and Coxson, D. S. 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce–fir forest. – *Can. J. Bot.* 79: 537–555.
- Carvalho, J. C. et al. 2012. Determining the relative roles of species replacement and species richness differences in generating beta diversity patterns. – *Global Ecol. Biogeogr.* 21: 760–771.
- CastilloCampos, G. et al. 2019. Data from: Vertical distribution of epiphytic lichens on *Quercus laurina* Humb. & Bonpl. in a remnant of cloud forest in the state of Veracruz, México. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.jm63xsj6f>>.
- Cazzolla Gatti, R. et al. 2017. Exploring the relationship between canopy height and terrestrial plant diversity. – *Plant Ecol.* 218: 899–908.
- Cleavitt, N. L. et al. 2009. Influence of tree composition upon epiphytic macrolichens and bryophytes in old forests of Acadia National Park, Maine. – *Bryologist* 112: 467–487.
- Cobanoglu, G. and Sevgi, O. 2009. Analysis of the distribution of epiphytic lichens on *Cedrus libani* in Elmali Research Forest (Antalya, Turkey). – *J. Environ. Biol.* 30: 205–212.
- Córdova-Chávez, O. 2015. Diversidad vertical de hongos liquenizados en forofitos del género *Quercus* en el bosque de niebla de La Cortadura, Coatepec, Veracruz. – MS thesis, Instituto de Ecología, A. C. Xalapa, Veracruz, México.
- De La Rosa, I. N. and Negrete-Yankelevich, S. 2012. Distribución espacial de la macrofauna edáfica en bosque mesófilo, bosque secundario y pastizal en la reserva La Cortadura, Coatepec, Veracruz, México. – *Rev. Mex. Biodivers.* 83: 201–215.
- Ertz, D. 2009. Revision of the corticolous *Opegrapha* species from the Paleotropics. – *Bibliotheca Lichenologica*, J. Cramer in Borntraeger Science Publishers.
- Fanning, E. et al. 2007. Vertical distribution of lichen growth forms in tree canopies of Great Smoky Mountains National Park. – *Southeast. Nat. Special Issue 1*: 83–88.
- Flores-Palacios, A. and García-Franco, J. G. 2008. Habitat isolation changes the beta diversity of the vascular epiphyte community in lower montane forest, Veracruz, Mexico. – *Biodivers. Conserv.* 17: 191–207.
- Freiberg, M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. – *Biotropica* 28: 345–355.
- Freiberg, M. 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. – *Selbyana* 18: 77–84.
- Freiberg, M. 1999. The vascular epiphytes on a *Virola michelii* tree (Myristicaceae) in French Guiana. – *Ecotropica* 5: 75–81.
- Freiberg, M. and Freiberg, E. 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. – *J. Trop. Ecol.* 16: 673–688.
- Galloway, D. J. and Thomas, M. A. 2004. *Stictia*. – In: Nash III, T. H. et al. (eds), *Lichen flora of the Greater Sonoran Desert Region*. Thomson–Shore, Inc., Dexter, MI, pp. 513–524.
- García-Franco, J. G. et al. 2008. Composición florística de un bosque mesófilo del centro de Veracruz, México. – *Bol. Soc. Bot. Mex.* 83: 37–52.
- Giordani, P. et al. 2012. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. – *Ecol. Indic.* 18: 413–420.
- Gradstein, S. R. et al. 1996. How to sample the epiphytic diversity of tropical rain forest. – *Ecotropica* 2: 59–72.
- Gradstein, S. R. et al. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forest. – *Selbyana* 24: 105–111.
- Harris, R. C. 1984. The family Trypetheliaceae (Loculoascomycetes: lichenized Melanommatales) in Amazonian Brazil. – *Acta Amazon.* 14: 55–80.
- Harris, R. C. 1995. More Florida Lichens, including the 10 cent tour of the Pyrenolichens. – *N. Y. Bot. Gard.*
- Hauck, M. 2011. Site factors controlling epiphytic lichen abundance in northern coniferous forests. – *Flora* 206: 81–90.
- Hauck, M. et al. 2001. Relevance of element content of bark for the distribution of epiphytic lichens in a montane spruce forest affected by forest dieback. – *Environ. Pollut.* 112: 221–227.
- Herrera-Campos, M. A. et al. 2016. Lichens of Mexico. The Parmeliaceae – keys, distribution and specimen descriptions. – *Bibliotheca Lichenologica*, J. Cramer in Borntraeger Science Publishers.
- Hinds, R. H. 1970. Vertical distribution of lichens on aspens in Michigan. – *Bryologist* 73: 626–628.
- Hölscher, D. et al. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. – *J. Hydrol.* 292: 308–322.
- Holz, I. and Gradstein, S. R. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. – *Plant Ecol.* 178: 89–109.

- Holz, I. et al. 2002. Bryophyte diversity, microhabitat differentiation and distribution of life forms in Costa Rican upper montane *Quercus* forest. – *Bryologist* 105: 334–348.
- Johansson, V. et al. 2010. Detection probability and abundance estimation of epiphytic lichens based on height-limited surveys. – *J. Veg. Sci.* 21: 332–341.
- Juárez Ramírez, M. C. et al. 2015. Protected natural areas and the conservation of amphibians in a highly transformed mountainous region in Mexico. – *Herpetol. Conserv. Biol.* 11: 19–28.
- Kashiwadani, H. and Nash III, T. H. 2004. Ramalina. – In: Nash III, T. H. et al. (eds), *Lichen flora of the Greater Sonoran Desert Region*. Thomson–Shore, Inc., Dexter, MI, pp. 440–455.
- Kiebacher, T. et al. 2016. Hidden crown jewels: the role of tree crowns for bryophyte and lichen species richness in sycamore maple wooded pastures. – *Biodivers. Conserv.* 25: 1605–1624.
- Kivistö, L. and Kuusinen, M. 2000. Edge effects on the epiphytic lichen flora of *Picea abies* in middle boreal Finland. – *Lichenologist* 32: 387–398.
- Komposh, H. and Hafellner, J. 2000. Diversity and vertical distribution of lichens in a Venezuelan tropical lowland rain forest. – *Selbyana* 21: 11–24.
- Kuusinen, M. 1994. Epiphytic lichen diversity on *Salix caprea* in old-growth southern and middle boreal forests of Finland. – *Ann. Bot. Fenn.* 31: 77–92.
- Li, S. et al. 2015. Species richness and vertical stratification of epiphytic lichens in subtropical primary and secondary forests in southwest China. – *Fungal Ecol.* 17: 30–40.
- Liu, Ch. et al. 2000. Biomass of arboreal lichens and its vertical distribution in a boreal coniferous forest in central Finland. – *Lichenologist* 32: 495–504.
- Lücking, R. 2014. A key to species of the *Ocellularia papillata*, *perforata* and *terebrata* morphodemes (Ascomycota: Graphidaceae). – *GLALIA* 6: 1–35.
- Lücking, R. et al. 2009. A world-wide key to the genus *Graphis* (Ostropales: Graphidaceae). – *Lichenologist* 41: 1–90.
- Lücking, R. et al. 2011. The lichens of Fakahatchee Strand Preserve State Park, Florida: proceedings from the 18th Tuckerman Workshop. – *Bull. Florida Museum Nat. Hist.* 49: 127–186.
- Maceda-Veiga, A. and Gómez-Bolea, A. 2017. Small, fragmented native oak forests have better preserved epiphytic lichen communities than tree plantations in a temperate sub-oceanic Mediterranean climate region. – *Bryologist* 120: 191–201.
- Marbach, B. 2000. Corticole and lignicole Arten der Flechtengattung *Buellia* sensu lato in den Subtropen und Tropen. – *Bibliotheca Lichenologica*, J. Cramer in Borntreger Science Publishers.
- Marmor, L. et al. 2012. Species richness of epiphytic lichens in coniferous forests: the effect of canopy openness. – *Ann. Bot. Fenn.* 49: 352–358.
- McCune, B. and Grace, J. B. 2002. Analysis of ecological communities. – MjM Software Design, Gleneden Beach, Oregon.
- McCune, B. and Mefford, M. J. 2018. PC-ORD. multivariate analysis of ecological data. – Ver. 7.07 MjM Software, Wild Blueberry Media, Corvallis, Oregon, USA.
- McCune, B. et al. 1997. Vertical profile of epiphytes in a Pacific northwest old-growth forest. – *Northwest Sci.* 71: 145–152.
- Merinero, S. et al. 2014. Environmental factors that drive the distribution and abundance of a threatened cyanolichen in southern Europe: a multi-scale approach. – *Am. J. Bot.* 101: 1876–1885.
- Meyer, H. A. et al. 2014. Tardigrada of the West Gulf Coastal Plain, with descriptions of two new species from Louisiana. – *Southeast Nat.* 13: 117–130.
- Moncada, B. et al. 2013. Phylogeny of the Lobariaceae (lichenized Ascomycota: Peltigerales), with a reappraisal of the genus *Lobariella*. – *Lichenologist* 45: 203–263.
- Mongkolsuk, P. et al. 2015. The lichen family Physciaceae in Thailand – II. Contributions to the genus *Heterodermia* sensu lato. – *Phytotaxa* 235: 001–066.
- Mukherjee, A. et al. 2010. Association of spiders and lichen on Robben Island, South Africa: a case report. – *J. Threat. Taxa* 2: 815–819.
- Nelsen, M. P. et al. 2014. Elucidating phylogenetic relationships and genus-level classification within the fungal family Trypetheliaceae (Dothideomycetes: Ascomycota). – *Taxon* 63: 974–992.
- Normann, F. et al. 2010. Diversity and vertical distribution of epiphytic macrolichens in forest and lowland cloud forest of French Guiana. – *Ecol. Indic.* 10: 1111–1118.
- Oregon, A. et al. 2011. Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity. – *Agric. For. Meteorol.* 151: 290–300.
- Peck, J. et al. 2002. The lichen communities of the southeastern Missouri Ozarks: lessons in species associations, habitat partitioning and distribution from the MOFEP study. – A report to the Missouri Department of Conservation–Missouri Ozark Forest Ecosystem Project, Jefferson City Missouri.
- Pérez-Pérez, R. E. et al. 2011. Scale-dependent effects of managements on richness and composition or corticolous macrolichens in pine-oak forests of Sierra de Juárez, Oaxaca, Mexico. – In: Bates, S. T. et al. (eds), *Recognizing the lichenological legacy of Thomas H. Nash III. On his 65th birthday*. Bibliotheca Lichenologica, J. Cramer. Borntreger Science Publishers, pp. 243–258.
- Pérez-Pérez, R. E. et al. 2015. Diversity of corticolous lichens in cloud forest remnants in La Cortadura, Coatepec, Veracruz, México in relation to phorophytes and habitat fragmentation. – *Cryptogamie Mycol.* 36: 79–92.
- Pike, L. H. 1978. The importance of epiphytic lichens in mineral cycling. – *Bryologist* 81: 247–257.
- Pirintzos, S. A. et al. 1993. Analysis of the vertical distribution of epiphytic lichens on *Pinus nigra* (Mount Olympos, Greece) along an altitudinal gradient. – *Vegetatio* 109: 63–70.
- Pirintzos, S. A. et al. 1995. Analysis of the distribution of epiphytic lichens within homogeneous *Fagus sylvatica* stands along an altitudinal gradient (Mount Olympos, Greece). – *Vegetatio* 116: 33–40.
- Pos, E. T. and Slegers, A. D. M. 2010. Vertical distribution and ecology of vascular epiphytes in a lowland tropical rain forest of Brazil. – *Bol. Mus. Para. Emílio Goeldi. Ciênc. Nat.* 5: 335–344.
- Rivas Plata, E. and Lücking, R. 2008. Clave y guía ilustrada para géneros de Graphidaceae. – *GLALIA* 1: 1–41.
- Rivas Plata, E. et al. 2012. A new classification for the family Graphidaceae (Ascomycota: Lecanoromycetes: Ostropales). – *Fungal Divers.* 52: 107–121.
- Rosabal, D. et al. 2010. Diversity and distribution of epiphytic macrolichens on tree trunks in two slopes of the montane rain-forest of Gran Piedra, Santiago de Cuba. – *Bryologist* 111: 313–321.
- Rzedowski, J. 1978. La vegetación de México. – Limusa, México.
- Sales, K. et al. 2016. Factors influencing epiphytic moss and lichen distribution within Killarney National Park. – *Biosci. Horizons Int. J. Student Res.* 9. <<http://dx.doi: 10.1093/biohorizons/hzw008>>

- Sillet, S. C. and Rambo, T. R. 2000. Vertical distribution of dominant epiphytes in Douglas-fir forests of the central Oregon Cascades. – *Northwest Sci.* 74: 44–49.
- Sporn, S. G. et al. 2010. Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. – *Biodivers. Conserv.* 19: 745–760.
- Staiger, B. 2002. Die Flechtenfamilie Graphidaceae. – *Bibliotheca Lichenologica*, J. Cramer in Borntraeger Science Publishers.
- StatSoft Inc. 2004. STATISTICA. – Data analysis software system, ver. 7. – <www.statsoft.com>.
- Uliczka, H. and Angelstam, P. 2000. Assessing conservation values of forest stands based on specialised lichens and birds. – *Biol. Conserv.* 95: 343–351.
- Yarranton, G. A. 1972. Distribution and succession of epiphytic lichens on black spruce near Cochrane, Ontario. – *Bryologist* 75: 462–480.