

## Epiphytic mosses in the Humid Mountain Forests of the Sierra Madre Oriental, Mexico – species richness, rarity and composition

Patricia HERRERA-PANIAGUA<sup>a</sup>, Mahinda MARTÍNEZ<sup>a\*</sup>,  
Luis HERNÁNDEZ-SANDOVAL<sup>a</sup> & José GARCÍA-FRANCO<sup>b</sup>

<sup>a</sup>Laboratorio de Botánica, Escuela de Biología, Universidad Autónoma  
de Querétaro, Avenida de las Ciencias s/n, 76230, Juriquilla, Querétaro, Mexico

<sup>b</sup>Red de Ecología Funcional, Instituto de Ecología, A. C.,  
Km. 2.5 antigua carretera a Coatepec No. 351, Congregación,  
El Haya, CP 91070 Xalapa, Veracruz, Mexico

**Abstract** – The Humid Mountain Forests of Mexico (HMFs) harbor high species diversity and are subject to continuous fragmentation and disturbance. We inventoried the epiphytic mosses in forest fragments and on isolated trees located in the Eastern Sierra Madre (Sierra Madre Oriental). We determined the size and canopy openness of 60 trees and recorded the occurrence of epiphytic mosses on trunks. Ninety-three species and five varieties of mosses were detected, distributed among 61 genera and 26 families. Thirty-two moss taxa were strictly epiphytic and 61 were facultative. Eighteen percent (17 species) of all recorded species were rare and only 3% (3 species) were common. Nineteen genera of phorophytes were sampled. *Quercus* had the highest epiphytic richness. Species richness and epiphytic mosses assemblages differ between forest fragments and isolated trees. Canopy openness and mean host tree height determine the epiphytic moss richness and species assemblages. Our study further underlines the importance of the Mexican HMFs as a reservoir of epiphytic mosses.

**Biodiversity / bryophytes / checklist / conservation / phorophytes**

**Resumé** – Les Forêts Humides Montagneuses du Mexique (FHM) abritent une diversité d'espèces élevée et sont soumises à une fragmentation continue et à des perturbations. Nous avons inventorié les mousses épiphytes dans les fragments de forêts et sur les arbres isolés dans l'Est du Sierra Madre Oriental. Nous avons mesuré la taille et la couverture de la canopée de 60 arbres et le recouvrement des mousses sur les troncs. 93 espèces et 5 variétés de mousses appartenant à 61 genres et 26 familles ont été recensées. Trente-deux taxons sont exclusivement épiphytes et 61 facultatifs. Dix-huit pourcents des espèces (7 espèces) sont rares et seulement 3 % (3 espèces) sont communes. Dix-neuf genres de phorophytes furent échantillonnés, et *Quercus* supporte la plus grande diversité d'espèces épiphytes. La richesse et la composition d'espèces diffèrent entre les fragments forestiers et les arbres isolés. La couverture de la canopée et la taille moyenne des arbres déterminent la richesse et la composition des mousses épiphytes. Notre recherche souligne davantage l'importance des FHM comme réservoir de mousses épiphytes au Mexique.

**Biodiversité / bryophytes / liste floristique / conservation / phorophytes**

\* Corresponding author: mahindamartinez@gmail.com

**Resumen** – Los Bosques Húmedos de Montaña de México (BHM) son sitios diversos en especies que están sujetos a perturbación y fragmentación. Ante la falta de estudios sobre musgos epífitos en el país, se hizo un inventario en fragmentos de bosque y sitios con árboles aislados ubicados en el Este de la Sierra Madre Oriental. En este estudio medimos el tamaño y la cobertura de dosel de 60 árboles y colectamos todos sus musgos del tronco. Se encontraron 93 especies y cinco variedades de musgos pertenecientes a 61 géneros y 26 familias. De los taxones encontrados, 32 fueron epífitos estrictos y 61 facultativos. El 18% (7 especies) del total de especies fueron raras y el 3% (3 especies) fueron comunes. De los 19 géneros de forofitos, *Quercus* fue el más rico en epífitas. La riqueza y composición de especies de los fragmentos de bosque y de los árboles aislados es diferente. La cobertura de dosel y la altura promedio de los hospederos fueron parámetros relacionados con la riqueza y composición de los musgos epífitos. Nuestro estudio provee datos que apoyan la importancia de los BHM de México como reservorios de musgos epífitos.

**Biodiversidad / briofitas / forofitos / listado florístico /conservación**

## INTRODUCTION

Bryophytes are part of many ecosystems, but they are conspicuous elements in forests and particularly important components of tropical montane forests (Frahm, 1990; Gradstein, 1992). In cloud forests, also referred to as humid mountain forests (HMFs here on, *sensu* Villaseñor, 2010) or mesophytic mountain forests (*sensu* Rzedowski, 1996), epiphytic bryophytes play several important roles in ecosystem function such as maintenance of the hydrological cycle (cf. Köhler *et al.*, 2010; Gehrig-Downie *et al.*, 2011).

In Mexico, HMFs cover roughly seven percent of the country's area and constitute one of the most diverse vegetation types (6790 species of vascular plants; Rzedowski, 1996; Villaseñor, 2010; Cruz-Cárdenas *et al.*, 2012). Yet, they are subject to fragmentation in the main mountain systems (Sierra Madre Occidental and Sierra Madre Oriental; Challenger, 1998). Defined by their floristic and structural heterogeneity, they are difficult to delimit, although they contain restricted species that aid in their identification (Villaseñor, 2010).

It has been estimated that HMFs have lost 68.4% of their original area (Mulligan, 2010). These forests are threatened by urban development, farming, and agricultural activities, such as coffee plantations, and are regarded as one of the most threatened forests in Mexico (Challenger, 1998; CONABIO, 2010). In particular, the HMFs of the Sierra Madre Oriental are highly fragmented, and thus represent a "critical priority" for conservation (Arriaga *et al.*, 2000; CONABIO, 2010; Toledo-Aceves *et al.*, 2011).

Few studies have inventoried or analyzed the phytogeographic relationships of Mexican HMFs bryophytes. Delgadillo (1979) listed 194 species and varieties in *Liquidambar* forests within six states (Chiapas, Hidalgo, Puebla, San Luis Potosi, Tamaulipas and Veracruz). Juárez (1983) reported 146 species and varieties of mosses in HMFs fragments in Coatepec, Veracruz, 49 of which were epiphytic. Other moss species have been listed for the HMFs, but only as part of a regional flora (Herrera-Paniagua *et al.*, 2008). Only Thornburgh and Sharp (1975) make direct reference to Mexican epiphytic mosses listing 54 species growing on tree branches in HMFs and tropical forests.

Anthropogenic activities have immediate negative effects on epiphytic bryophytes. Logging and land use lead to loss of trees, reduced humidity and increased desiccation affecting species richness and epiphytic bryophytes composition, because many shade and old-growth-forest indicator species disappear, although desiccation-tolerant species may be favored (e.g. Hallingbäck & Hodgetts, 2000; Acebey *et al.*, 2003; Drehwald, 2003; Holz & Gradstein, 2005; Pereira & Cavalcanti, 2007; Löbel *et al.*, 2012). In contrast to canopy epiphytes, those growing on tree trunks are less tolerant to desiccation and are highly sensitive to prolonged periods of drought (Pardow & Lakatos, 2013). In the context of current environmental changes induced by global climate change, Benzig (1998) predicted that since the HMFs epiphytic communities follow patterns of saturation deficit along well defined physical gradients they will likely suffer modifications.

In addition to identifying the species found in the forests, it is relevant to determine their rarity and those species more likely to survive habitat disturbance (Hallingbäck & Hodgetts, 2000). To determine rarity in addition to taking into account the size of their distribution area, habitat specificity, and local abundance (Rabinowitz, 1981), it is important to consider the life history traits (e.g. sporophyte or diaspore production, Cleavitt, 2005; Söderström & Daring, 2005). However, given the lack of knowledge about bryophytes in many locations, presence and distribution data are essential to ultimately assessing their response to environmental change (Heinlen & Vitt, 2003; Benavides & Gutierrez, 2011).

Here, we present the first analysis of the HMFs epiphytic moss richness on tree trunks of the Eastern Sierra Madre Oriental, Mexico. The main aims were to: (1) provide insight into the richness patterns of epiphyte mosses of two disturbance stages, forest fragments and isolated trees in pastures, (2) characterize species rarity patterns at our study scale and (3) explore floristic epiphytic moss assemblages patterns.

## STUDY AREA

This research was conducted in the central portion of the Sierra Madre Oriental physiographic province, Mexico (Ferrusquía, 1998) (Fig. 1), within two conservation Priority Terrestrial Regions (Regiones Terrestres Prioritarias, CONABIO, 2010). The largest portion of the study area is part of the Sierra-Gorda-Rio Moctezuma priority region (RTP-101) in northern Queretaro and eastern San Luis Potosi, whereas the remaining portion, the Mesophilic Forest of the Sierra Madre Oriental (RTP-102) is located in the state of Hidalgo (Arriaga *et al.*, 2000).

Forests in the Sierra Madre Oriental have been extensively cut to develop farmland and pastures, provide lumber, and build roads. The majority of the HMFs in this area are fragmented and disturbed (Arriaga *et al.*, 2000; Cartujano *et al.*, 2002; CONABIO, 2010). The study area was therefore restricted to the natural floristic variation of the HMFs (21°51'–20°51' N and 99°27'–98°40' W). Five forest fragments with over 50 trees were selected, Copalillos and El Retén in San Luis Potosi, Los Xililites and Neblinas in Queretaro, and Lolotla in Hidalgo. In addition, two pasturelands in Queretaro that held 10 isolated trees were included: El Pemoche and San Onofre (Fig. 1, Table 1).

The elevation of the study sites varies from 989 to 1485 m. Mean annual temperature oscillates between 19.5 and 22.5°C and mean annual rainfall between

759 and 1340 mm (Hijmans *et al.*, 2005; Table 1). Floristic heterogeneity is typical of the HMFs, but the fragments and isolated trees were characterized by the occurrence of *Liquidambar styraciflua* L., a typical HMFs species, as well as several *Quercus* L. species (Villaseñor, 2010).

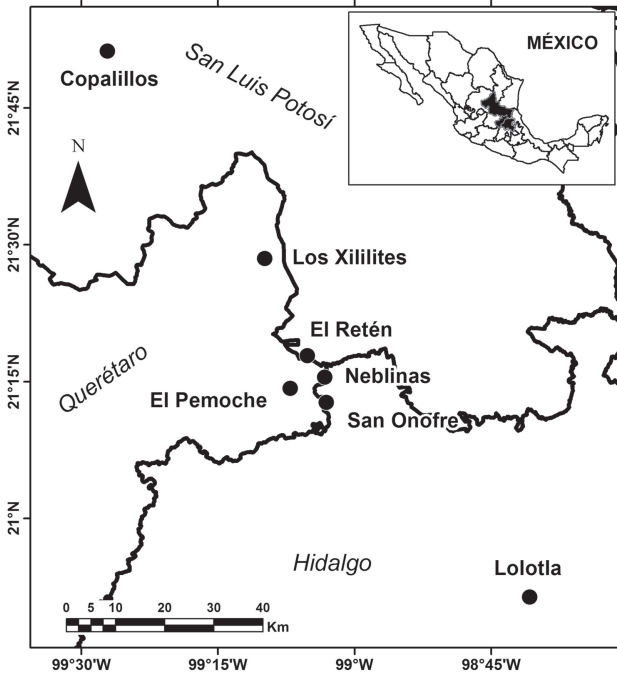


Fig 1. Forest fragments (Copalillos, Los Xililites, El Retén, Neblinas, Lolotla) and pasturelands (El Pemoche, San Onofre) study sites at the Sierra Madre Oriental in Hidalgo, Querétaro and San Luis Potosi States, Mexico.

Table 1. Biological and environmental variables in the study sites in Sierra Madre Oriental, Mexico. Environmental data extracted from WorldClim (Hijmans *et al.*, 2005). Biological data for the host tree (mean  $\pm$  SD). DBH, diameter at breast height at 1.3 m. CO, canopy openness. Forest fragments ( $\blacklozenge$ ). Pasturelands ( $*$ )

	Elevation (m)	Sampled area (m <sup>2</sup> )	Annual mean rainfall (mm)	Annual mean temperature (°C)	Tree height (m)	DBH (cm)	CO (%)
$\blacklozenge$ Copalillos	1252	1000	759	22.2	15.25 $\pm$ 6.67	38.61 $\pm$ 21.22	81.12
$\blacklozenge$ Los Xililites	1294	1000	1256	21.9	11.32 $\pm$ 5.24	29.60 $\pm$ 14.67	87.77
$\blacklozenge$ El Retén	1485	500	1203	21.6	11.98 $\pm$ 2.68	24.22 $\pm$ 14.75	75.32
$\blacklozenge$ Neblinas	989	1000	1324	22.5	15.4 $\pm$ 7.64	51.15 $\pm$ 18.67	93.88
$\blacklozenge$ Lolotla	1050	1000	1340	19.5	19.1 $\pm$ 4.50	23.93 $\pm$ 10.02	86.2
*San Onofre	1091	500	1103	21.9	23.4 $\pm$ 6.18	48.31 $\pm$ 16.68	24.96
*El Pemoche	1387	500	995	21.08	12.25 $\pm$ 4.49	44.88 $\pm$ 11.64	21.97

## MATERIALS AND METHODS

*Data collection.* Ten trees were randomly selected ( $n = 50$ ) within each of the five forest fragments, and five ( $n = 10$ ) in each pastureland site (Table 1). Only trees with a diameter at a breast height  $\geq 6$  cm and separated by  $\geq 10$  m were retained. The latter criterion was not used on isolated trees owing to the lack of arboreal continuity. Phorophyte specimens were collected for subsequent identification in the laboratory. The degree of canopy openness of each forest type was estimated with the measurements of each host taken at a determined time of the day using a concave spherical densiometer model C (Lemmon, 1956).

All clumps or individual mosses present on the phorophyte trunks, from the base of the trunk to the first branches ( $\leq 8$  m), were sampled with a knife or pole. Mosses were identified with the aid of the works of Allen (1994, 2002), Sharp *et al.* (1994), Buck (1998) and Pursell (2007). Nomenclature follows the electronic version of LATMOSS (Delgadillo, 2010). The species were categorized as strictly epiphytic (restricted to the bark) or facultative (growing not only on the bark but also on the ground or rock; Smith, 1982) based on species information of The Moss Flora of Mexico (Sharp *et al.*, 1994). Voucher specimens were deposited in the Herbarium of the Autonomous State University of Querétaro (QMEX) and the National Herbarium of Mexico (MEXU).

*Data analyses.* To ensure that sampling was complete, based on the observed richness of epiphytic mosses ( $S_{\text{obs}}$ ) on each tree, richness was estimated ( $S_{\text{est}}$ ) for each site. The non-parametric Jackknife 2 model was used (with 100 randomizations, without replacement), with EstimateS version 8.1 (Colwell, 2006). Jackknife 2 is considered one of the most precise estimators for uneven and highly uneven communities, and under low to intermediate sampling intensity is the least biased (Brose *et al.*, 2003). Rarefaction was used to get comparable estimates of species richness from the different sites (Gotelli & Colwell, 2011). Plot-based rarefaction curves were generated by permutation using EcoSim version 7 (Gotelli & Entsminger, 2004).

A one factor ANOVA was used to compare species richness among trees for all study sites. Post-hoc Tukey tests (HSD) were performed to compare averages. The number of species was square root transformed to account for lack of homoscedasticity (Quinn & Keough, 2002). The response of species richness to environmental variables (Table 1) was modeled using a generalized linear model (GLM) with a Poisson error distribution (Quinn & Keough, 2002). First performed a model with all explanatory variables and their interactions with the richness. The presence of not significant interactions would lead to remove from the model. Akaike Information Criterion (AIC) was also used to select an optimal model explaining epiphytic richness.

Species can be defined as common or rare in many ways (Magurran & Henderson, 2011). For mosses, categories based on occurrence have been used (Heinlen & Vitt, 2003; Benavides & Gutiérrez, 2011). In this study, species rarity was determined using their occurrence following Gaston (1994). We calculated a Rarity Index ( $RI = 1/n$ , where  $n$  is the number of phorophytes occupied by a given species). The values were square root transformed and normalized between 0 and 1 (Quinn & Keough, 2002). We identified three rarity classes using the RI. Rare species and common species were those present in the upper (4<sup>th</sup>) and lower (1<sup>st</sup>) quartiles respectively. Frequent species were those species present in the intermediary quartiles. Relationship between our study sites and the apportioning of species into

strictly epiphytic or facultative, and different rarity classes was analyzed by means of Chi-square test ( $\chi^2$ ).

Epiphytic moss assemblage structure was compared between study sites (forest fragments and isolated trees) using ordination by nonmetric multidimensional scaling (NMDS). This method has been shown to be robust for a range of data types and to be accurately representing underlying true dissimilarities (Legendre & Legendre, 1998). A two dimensional NMDS of the community data was calculated by means of the function “metaMDS (binary = TRUE)” that is incorporated in the “Vegan” library in R (Oksanen *et al.*, 2016). The environmental vectors with de maximum correlation were fitted on the NMDS ordination using the vegan function “envfit”. The significance of the fitted vectors was assessed using a permutation procedure (999 permutations) (Oksanen *et al.*, 2016). All statistical analyses and graphs were performed in R v.3.2.4 (R Development Core Team, 2011).

## RESULTS

**Richness.** A total of 1200 samples of epiphyte mosses were collected. They represented 93 species and five varieties of mosses in 61 genera and 26 families (Appendix). In the forest fragments, the number of species found was 86, and 35 for pasturelands. A total of 34 species (36.6%) of the recorded taxa had not been previously reported for the HMFs (see Delgadillo, 1979 and Juárez, 1983). This richness included mosses restricted to Mexico (*Cyclodictyon richardsii* Bowers & Magill, *Neckera angustifolia* Müll. Hal., and *Pylaisiadelphina sharpii* H.A. Crum), as well as those from HMFs (e.g., *Leucobryum crispum* Müll. Hal.; Sharp *et al.*, 1994), and disturbed forests (*Fabronia ciliaris* (Brid.) Brid. var. *polycarpa* (Hook.) W. R. Buck) (Herrera-Paniagua & Martínez, 2014).

The most speciose families contained 35.48% of the total species richness and were Meteororiaceae (10 species), Orthotrichaceae (9 species), Pottiaceae (7 species) and Sematophyllaceae (7 species). In the HMF fragments, the best represented families (i.e.  $\geq 5$  species) were Hypnaceae (El Retén), Meteororiaceae (Copalillos) and Orthotrichaceae (Los Xililites and Lolotla). In the fragment forest Neblinas, Anomodontaceae and Brachytheciaceae were the most common families, with only three species each. In the pasturelands (El Pemoche and San Onofre), the most diverse family was Meteororiaceae, with three and four species in each locality, respectively.

Patterns of epiphyte mosses richness varied among studied sites. According to the Jackknife 2 richness estimator, the predicted number of species for each site ranged from 31 to 68. Thus,  $S_{obs}$  represented 74% and 55% of  $S_{est}$ , respectively. The pasturelands localities sampling were the most complete in San Onofre, whereas the most incomplete in El Pemoche (Table 2). The rarefaction analysis showed that the gradients of species accumulation were dissimilar among forest fragments and pastureland sites (Fig. 2). In general, more species were found in the forest fragments than in pasturelands. Among the parameters analyzed, GLM showed only a weak but statistically significant response in total epiphyte species richness with the canopy openness ( $R^2 = 0.0026$ ,  $p < 0.001$ ).

In general, the number of epiphyte species of mosses per tree varied from null (one isolated phorophyte in El Pemoche) to 19 (one phorophyte of the Copalillos fragment), with an average richness of 8.3 ( $\pm 3.7$  S.D.) species per tree (Table 2).

Table 2. Study sites richness at the Sierra Madre Oriental, Mexico. Observed ( $S_{observed}$ ) and estimated ( $S_{estimated}$ ; Jackknife 2 estimator) epiphyte species richness. Number of strict and facultative epiphytes species. Unique percentage of species per site. Number of epiphyte mosses per host tree (mean  $\pm$  standard deviation). Percent of the completeness. Forest fragments ( $\blacklozenge$ ). Pasturelands (\*)

Locality	$S_{observed}$	Obligate epiphyte	Facultative epiphyte	Unique (%)	Richness per host tree	$S_{estimated}$	Percent of completeness
$\blacklozenge$ Copalillos	43	13	30	10.7	12.2 $\pm$ 3.9	64	67.1
$\blacklozenge$ Los Xililites	43	12	32	9.6	8.8 $\pm$ 2.9	68	65
$\blacklozenge$ El Retén	39	13	26	5.3	8.9 $\pm$ 2.2	58	67.24
$\blacklozenge$ Neblinas	27	7	20	3.2	5.5 $\pm$ 2.9	47	61.7
$\blacklozenge$ Lolotla	37	10	27	2.1	8.6 $\pm$ 3.8	58	63.8
*San Onofre	23	4	19	4.3	10.2 $\pm$ 2.7	31	74.2
*El Pemoche	21	8	13	3.2	6.6 $\pm$ 3.9	39	55.3
Total	93	32	61	38.3	8.3 $\pm$ 3.7	112	83.03

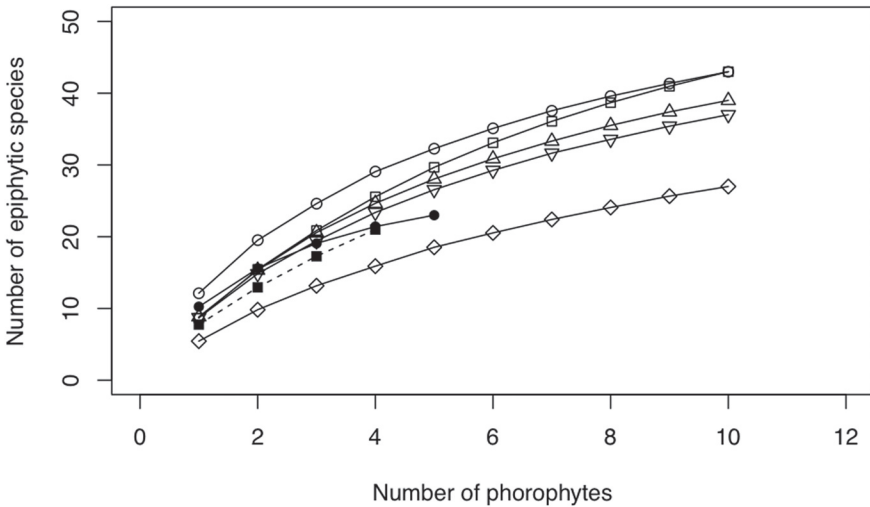


Fig. 2. Sample-based rarefaction curves of the number of epiphyte mosses species. Fragment forests: Copalillos ( $\circ$ ), Xililites ( $\square$ ), El Retén ( $\triangle$ ), Neblinas ( $\diamond$ ), Lolotla ( $\nabla$ ). Pasturelands: San Onofre ( $\bullet$ ), El Pemoche ( $\blacksquare$ ). One phorophyte of El Pemoche with 0 species of epiphytic mosses was not considered in the analysis.

Species richness was significantly different among study sites (ANOVA;  $F = 3.82$ ,  $df = 6, 53$ ,  $p < 0.003$ ) (Fig. 3). Specifically, epiphyte richness of trees from the forest fragment with the lowest average richness (Neblinas) was significantly poorer than the two richest sites, Copalillos (forest fragment) and San Onofre (pastureland). Besides, epiphytic richness of El Pemoche, (the second poorest locality and pastureland) was significantly lower to that found in Copalillos (the richest locality). The rest of the forest fragments did not show significant differences among them.

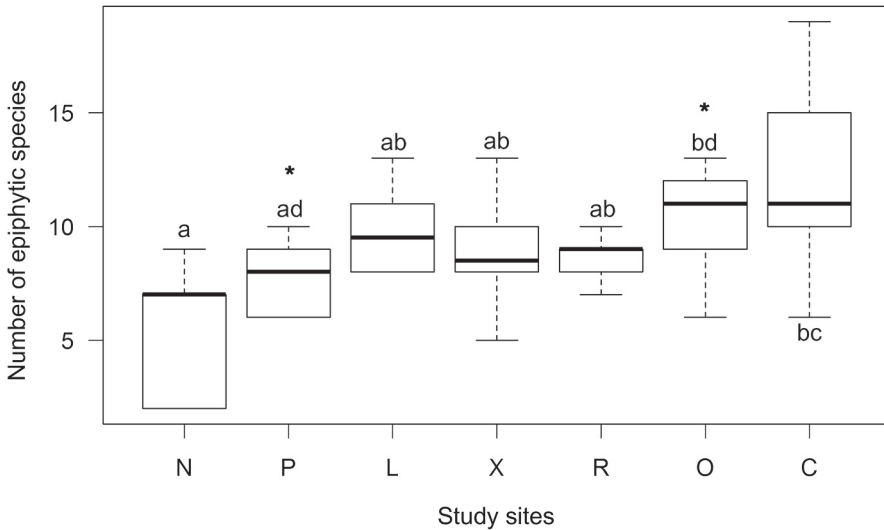


Fig. 3. Species richness of epiphyte mosses found on phorophytes by study site. Abbreviations: N, Neblinas; P, El Pemoche; L, Lolotla; X, Los Xililites; R, El Retén; O, San Onofre; C, Copalillos. Pasturelands (\*). Lines inside the box are means, boxes are standard error and dispersion lines are 95% confidence intervals. Significant differences among phorophytes (Tukey test,  $p < 0.05$ ) are marked by letters.

**Phorophytes.** In total, 19 phorophyte genera were sampled, with *Liquidambar* and *Quercus* being the most common (with 19 and 14 individuals, respectively). *Liquidambar* was absent in Lolotla and *Quercus* was absent in Neblinas and El Retén. The phorophyte genus with most moss species was *Quercus*, as it harbored 64 species of the total richness (Fig. 4). *Entodon jamesonii* (Taylor) Mitt. and *Prionodon densus* (Hedw.) Müll. Hal. were the only strictly epiphytic mosses exclusive to the above-mentioned tree genera (Appendix).

The *Clethra* L. phorophyte also harbored many moss species. For example, five trees held 33 epiphyte species. This host was only found in Copalillos, Los Xililites, Neblinas and Lolotla. The 15 remaining arboreal genera contained only one or two individuals and occurred in one or two sites. In these phorophytes epiphyte mosses richness was from 2 to 19 species. Two trees with the lowest epiphytes diversity: *Ligustrum* L. (*Rhynchosygium serrulatum* (Hedw.) A. Jaeger and *Sematophyllum subpinnatum* (Brid.) E. Britton) and *Ulmus* L. (*Brachythecium ruderale* and *Sematophyllum adnatum*) (Fig. 4).

**Epiphyte classification.** Thirty-two moss taxa were strictly epiphytic, such as *Cryphaea patens* Hornsch., *Fissidens serratus* Müll. Hal. var. *serratus* and *Orthostichidium quadrangulare* (Schwägr.) B.H. Allen & Magill. The remaining 61 taxa were facultative epiphytes such as *Anomodon attenuatus* (Hedw.) Huebener, *Herpetineuron toccocae* (Sull. & Lesq.) Cardot and *Pterobryon densum* Hornsch. (Table 2, Appendix). In general, strict epiphytes composed 26 to 38% of the species recorded for each site, whereas more than 62% were facultative. The study sites with most strictly epiphytic species were El Retén (with 30% of their recorded species) and El Pemoche (38%). In contrast, for Neblinas and San Onofre more than 73% of their recorded species were facultative. A Chi-square analysis indicates no significant differences among the proportion of strictly and facultative epiphytic species in the localities (forest fragment and isolated trees) ( $\chi^2 = 2.9634$ ,  $df = 6$ ,  $p < 0.8134$ ).



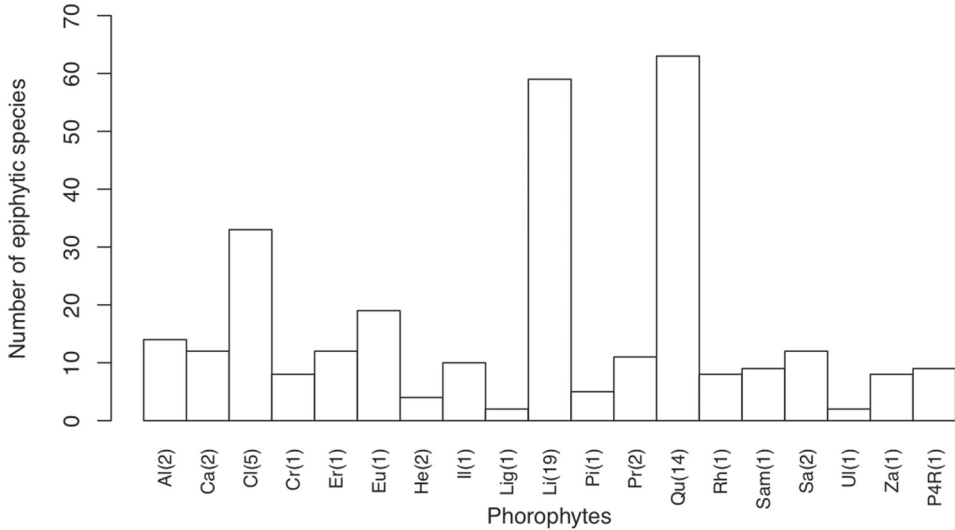


Fig. 4. Species richness of epiphyte mosses by phorophyte genus in forest fragments and pasturelands. Epiphyte hosts: Al, *Alnus*; Ca, *Carya*; Cl, *Clethra*; Cr, *Crataegus*; Er, *Erythrina*; Eu, *Eugenia*; He, *Heliocarpus*; Il, *Ilex*; Li, *Liquidambar*; Lig, *Ligustrum*; Pi, *Pinus*; Pr, *Prunus*; Qu, *Quercus*; Rh, *Rhus*; Sam, *Sambucus*; Sa, *Savia*; Ul, *Ulmus*; Za, *Zanthoxylum*; P4R, El Retén unknow host. The numbers indicate the total individuals that occur in each genus.

**Species rarity.** Rare species accounted for 18.3% of the recorded species (4<sup>th</sup> quartile; Fig. 5) and were found only on a single host, and included *Neckera chlorocaulis* Müll. Hal. (Copalillos) and *Syrrhopodon incompletus* Schwägr. var. *incompletus* (Neblinas). The rare class included seven strictly epiphytic mosses, such as the endemic *Cyclodictyon richardsii* and *Pylaisiadelphina sharpii*.

Seventy-three species (78.5%) had IR values ranging from 0.26 to 0.70 and were frequent species, and 28.8% of these were strictly epiphytic. In this rarity class were epiphytes that were found on two phorophytes, both in the same site (e.g. *Zelometeorium patulum* (Hedw.) Manuel in Copalillos) or at two different sites (*Orthostichidium quadrangulare* in Copalillos and Neblinas) (Appendix). The other frequent species were found on three (e.g. *Leucobryum crispum*) to 15 hosts (*Thuidium tomentosum* Schimp.).

Only three species (3.2%) were common (1<sup>st</sup> quartile; Fig. 5): *Meteorium deppei*, *Pilotrichella flexilis* and *Sematophyllum adnatum*. The first two common species are strictly epiphytic and were found on 24 or 25 hosts. In all study sites the rare and common classes included relatively few species and did not differ significantly from the species proportion in the three rarity classes ( $\chi^2 = 6.901$ ,  $df = 12$ ,  $p < 0.864$ ).

**Epiphytic mosses assemblages.** A total of 37 epiphyte moss species were recorded only in one study site (Table 2; Appendix). Forest fragments included 13 unique strictly epiphytic species such as *Macromitrium punctatum* (Hook. & Grev.) Brid. in Lolotla and *Syrrhopodon parasiticus* (Brid.) Besch. in Xililites. On isolated trees, seven epiphyte mosses were unique taxa, such as *Erythrodontium longisetum* (Hook.) Paris in San Onofre and *Orthotrichum pycnophyllum* Schimp. ex Müll. Hal. in El Pemoche. The NMDS ordination of the species assemblages showed that the

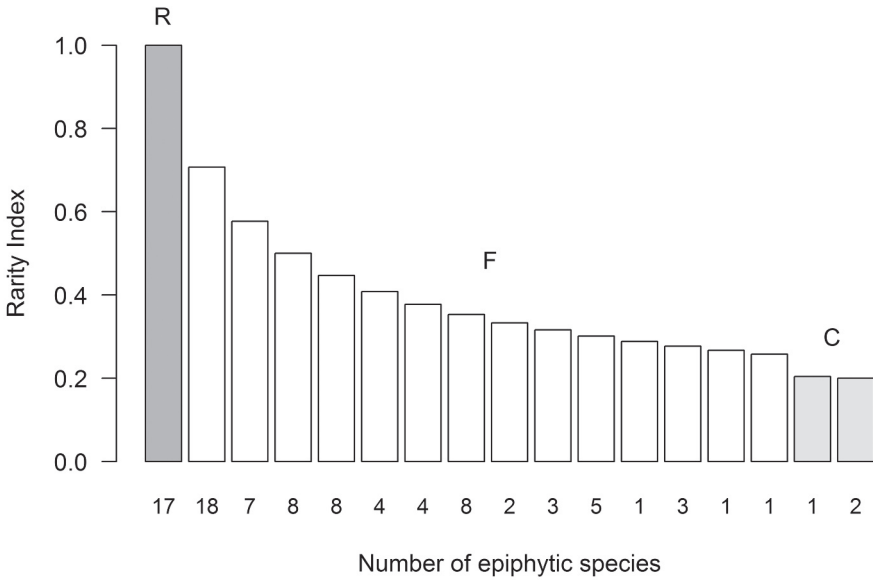


Fig. 5. Index of species rarity of epiphyte mosses. Rarity values are normalized. Rarity classes. R. Rare (0.75-1). F. Frequent (0.25-0.75). C. Common species (value 0-0.25).

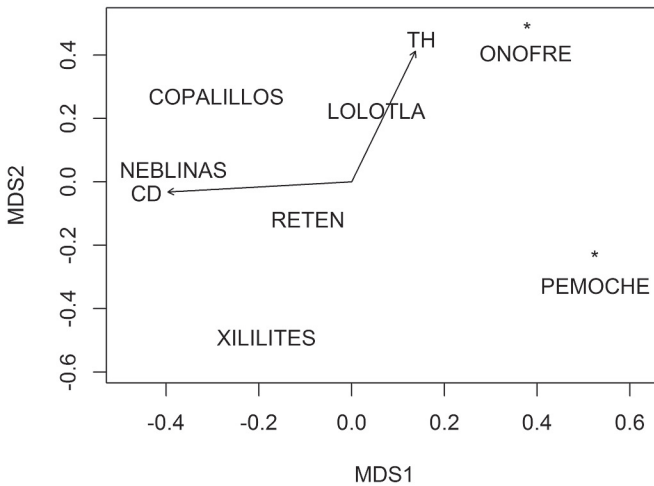


Fig. 6. NMDS ordination of the epiphyte mosses assemblages with fitted vector of significant environmental variables. Forest fragments: Copalillos, Xililites, El Retén, Neblinas, Lolotla. Pasturelands (\*): San Onofre, El Pemoche. CO. Canopy openness ( $r^2 = 0.856$ ,  $p < 0.05$ ). TH. Mean of the tree height ( $r^2 = 0.828$ ,  $p < 0.05$ ).

study sites aggregated in approximately three groups, mainly in accordance with forest type (Fig. 6; stress = 0.06). Forest fragments are to the left side of the plot and isolated trees at the top and on the bottom in the right. In the epiphyte mosses ordination, the canopy openness (CO;  $r^2 = 0.856$ ;  $p < 0.05$ ) and mean tree height (TH;  $r^2 = 0.828$ ;  $p < 0.05$ ) had a strong influence with the compositional differentiation. The fragment forest Copalillos, Neblinas and Lolotla were the sites with highest canopy coverage and tallest trees (Table 1; Fig. 6).

## DISCUSSION

One characteristic of the HMFs of America is the high richness of epiphytes (Gradstein *et al.*, 2010). Our study is the first inventory of epiphyte mosses in a Mexican HMF. Sampling completeness was ca. 60% (for forest fragments), which is similar to other bryophytes inventories (*sensu lato*) in tropical montane forests from other parts of the world (e.g. Ariyanti *et al.*, 2008; Gradstein & Culmsee, 2010), indicating that HMFs may harbor a higher moss diversity.

Since we found thirty-four species as new records for the HMFs compared to previous more general bryophytes inventories (Delgadillo, 1979; Juárez, 1983), this suggests that epiphytic trunk represents an important proportion of the total epiphyte richness in a cloud forest. The 5500 m<sup>2</sup> that constituted our study area contains 9.5% of the moss species of Mexico (Delgadillo, 2011).

Some studies report that epiphytic moss richness is higher in primary than in secondary forests (e.g. Acebey *et al.*, 2003; Drehwald, 2003). In general, our data followed this trend, in that the less disturbed forests fragments had more species than pasturelands, and their species assemblages was different. However, the number of species varied among fragments and pasturelands (Table 2), and richness appeared to be site-dependent (Fig. 2). For instance, the trees at Neblinas had the lowest species richness per tree, but its total richness within site was higher and harbored different species than those observed pasturelands (Fig. 5). The disturbance can also favor species that are better adapted to desiccation. There are no reports of species number differences for forests with different levels of disturbance, but certain studies show differences in composition (e.g. Holz & Gradstein, 2005; Pereira & Cavalcanti, 2007).

Presence or absence of epiphytic mosses among sites may reflect microhabitat variations. Host specificity of epiphytic bryophytes is unusual, and factors pertaining to altitude, solar exposure, mist regime may be more important (e.g. Wolf, 1994; Patiño & González-Mancebo, 2011). Despite clear differences in environmental variables among studied sites (Table 1), we only found significant interactions between species richness and assemblages with canopy openness and trees height.

Our data suggest a canopy openness-epiphytic richness relationship, but this was not strong ( $R^2 = 0.0026$ ). In epiphytes, the irradiance exposure influences in their trunk distribution and biomass (León-Vargas *et al.*, 2006). However, different factors predict species richness, e.g. bark pH, DBH, stand age, and forest continuity (e.g. Löbel *et al.*, 2006, Cleavitt *et al.*, 2009). Particularly, epiphyte richness and biomass can be positively correlated with DBH tree (e.g. Friedel *et al.*, 2006; Köhler *et al.*, 2010). We did not find such relationships, the lack of correlation was probably caused by non-balanced design. The phorophytes of Neblinas forest fragment were big trees with a low number of epiphytic species and the number of sampled host in pastureland sites was lower.

The interaction between canopy openness and tree size were far more successful to explain the differences in assemblages between forest fragments and pasturelands in our study. Other studies have established that habitats with closed canopy and tall trees are rich in species and have restricted species (e.g., Gradstein, 1992; Holz & Gradstein, 2005; Werner & Gradstein, 2009). Closed canopy favors a constant humidity and some species are characteristic of shady habitats, while others are of exposed habitats (e.g. Acebey *et al.*, 2003; Ariyanti *et al.*, 2008; Benavides & Gutiérrez, 2011). Open canopy had a negative effect in moss reproduction and relative growth rate in some old-growth-forest indicator species (Löbel *et al.*, 2012).

On isolated trees, the occurrence of species such as *Brachymenium systylium* and *Orthotrichum pycnophyllum* suggest a drier condition and higher light levels than in fragment forest (Sharp *et al.*, 1994). Certain species found in dense, shaded, and humid forests, such as *Orthostichidium quadrangulare*, *Prionodon densus*, *Squamidium leucotricum*, and *Toloxis imponderosa* (Sharp *et al.*, 1994; León-Vargas *et al.*, 2006) were found only in the forest fragments Copalillos and Los Xililites. It is worth noting that *Fabronia ciliaris* var. *polycarpa*, a strict epiphyte taxon associated with dry and disturbed habitats (Gradstein *et al.*, 2001; Cárdenas & Delgadillo, 2009), was frequent on the pasturelands.

No study for Mexico has quantified the rarity of bryophytes. Occurrences of epiphytic mosses were useful for early conclusions. For rarity species, the forest condition as well as species biology should be considered. *Meteorium deppei* and *Pilotrichella flexilis* were the only strictly epiphytic species common to virtually all studied sites (Appendix). These species appear to be tolerant to several environmental conditions, because they are recurrent in the HMFs (Delgadillo, 1979), in secondary vegetation and isolated trees (Drehwald, 2003; Herrera-Paniagua *et al.*, 2008). In particular, *P. flexilis* has a higher tolerance to desiccation and solar radiation when compared to other HMFs epiphytes (León-Vargas *et al.*, 2006), which would, at least partly, explain its wide distribution among our study sites.

The other common species, *Sematophyllum subpinnatum*, is a facultative epiphyte that can be found in other vegetation types and substrates and is a member of the one most common of Neotropical moss genera (Gradstein *et al.*, 2001). Facultative species composed most of the epiphytic moss richness on trunks (Smith, 1982). Genera such as *Atrichum* and *Tortella* usually grow on the ground (Cárdenas & Delgadillo, 2009), but in this study were also found on the tree base (Appendix). The lowest part of the tree is closest to the ground and epigeous taxa can survive because some humus and mineral soil occur on the trunk (Moe & Botnen, 2000).

Although rare species included facultative mosses, seven of the rare species were strictly epiphytic. Strict epiphytes such as the endemics *Cyclodictyon richardsii* and *Pylaisiadelphina sharpii*, were only found within the HMFs fragments. The first species is considered typical of HMFs (Sharp *et al.*, 1994) and has a distribution restricted to three sites: (1) the type locality in Xilitla, San Luis Potosí, (2) Neblinas (Querétaro) and (3) a tropical rainforest in Veracruz (Herrera-Paniagua & Martínez, 2014; C. Delgadillo, pers. com.).

The strict epiphytic species frequently occurred in other vegetation types and have a broad geographic distribution. For example, *Zelometeorium patulum*, a Caribbean species (Delgadillo, 2004), is considered a generalist epiphyte in South America (Pereira & Cavalanti, 2007) and has been reported from Florida (USA), but has not been collected since 1940 (Ignatov & Reese, 2009). Its presence is related to high and constant humidity (Buck, 1998) and those collected in Mexico occurred principally to the southern part of the country, mostly Chiapas (UNIBIO, 2013). We found this species on only two trees in the Copalillos forest fragment.

Loss of trees leads to microhabitat destruction for epiphytic mosses in our study area. Common hosts with high epiphytic species richness, *Clethra*, *Liquidambar* and *Quercus*, are representative HMFs trees (Villaseñor, 2010), but neither was common to all study sites. Host characteristics (e.g., bark texture) could have a positive effect on epiphytes (e.g. Friedel *et al.*, 2006; Gradstein & Culmsee, 2010). Oaks, with rough bark had generally high epiphytic bryophyte richness (e.g. Holz & Gradstein, 2005; Gil & Morales, 2014). However, *Quercus* is the second most commonly used timber species in Mexico, and 32 HMFs oak species are considered at extinction risk (González-Espinosa *et al.*, 2011; SEMARNAT, 2013). Current tree

extraction will seriously affected epiphyte diversity in the remaining HMFs fragments. Studies that evaluated the effect of different host tree species and their traits on epiphyte mosses are necessary.

It should be noted that mosses that span wide or global distributions, but are locally rare, represent a special form of rarity (Rabinowitz, 1981). Endemic epiphytes, as well as those with wider distributions are important species to be taken into account in conservation plans, particularly because the preservation of species at a local scale may ensure their existence at a regional or national scale (Heinlen & Vitt, 2003). Regrettably, the current trend in conservation is generally focused on preserving endemic species in specific habitats (Cleavitt, 2005). More studies are needed to understand the distribution and causes of rarity of moss species in Mexico.

In conclusion, this study points that trees in HMFs of the Sierra Madre Oriental of Mexico host a rich and diverse moss flora that include strictly epiphytic, as well as, facultative species. The interaction between the forest conditions (canopy openness) and the phorophytes (mean tree high) is important in explaining species richness and composition. Forest fragments and pasturelands had different richness and composition. The rarity pattern seemed associated with the absence of suitable habitat and the lack of moss ecological flexibility, but more studies are needed. Only two endemic species were found and both are strictly epiphytic and rare. Knowledge of the mosses of Mexico is far from complete, and it is also necessary to identify the factors that shape their richness, abundance and distribution. Additional studies of moss species composition and their relationships with different habitats would increase our knowledge of the ecology of Humid Mountain Forests, and further understanding how present conservation affects moss diversity in Mexico.

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## APPENDIX

Epiphyte moss taxa frequency in HMFs forest fragment and isolated tree at Sierra Madre Oriental, Mexico. Epiphyte: S, strict; F, facultative. Forest fragments: C, Copalillos; X, Los Xililites; R, El Retén; N, Neblinas; L, Lolotla. Pasturelands: O, San Onofre; P, El Pemoche. Rarity classes: Co, common; Fr, frequent; Ra, rare. Epiphyte hosts: Al, *Alnus*; Ca, *Carya*; Cl, *Clethra*; Cr, *Crataegus*; Er, *Erythrina*; Eu, *Eugenia*; He, *Heliocarpus*; Il, *Ilex*; Li, *Liquidambar*; Lig, *Ligustrum*; Pi, *Pinus*; Pr, *Prunus*; Qu, *Quercus*; Rh, *Rhus*; Sam, *Sambucus*; Sa, *Savia*; Ul, *Ulmus*; Za, *Zanthoxylum*; P4R, El Retén unknown host.

Taxon	Epiphyte	C	X	R	N	L	O	P	RC	Epiphyte host
<i>Anomodon attenuatus</i> (Hedw.) Huebener	F	2		1	3	3	2		Fr	Li, Qu, P4R, Ca
<i>Anomodon rostratus</i> (Hedw.) Schimp.	F			3	1			1	Fr	Li
<i>Anomodon tristis</i> (Ces.) Sull. & Lesq.	S	1						1	Fr	Eu, Li
<i>Atrichum oerstedianum</i> (Müll. Hal.) Mitt.	F			1					R	Al
<i>Brachymenium systylium</i> (Müll. Hal.) A. Jaeger	F						3		Fr	Er, Li, Qu
<i>Brachythecium occidentale</i> (Hampe) A. Jaeger	F	2	1	1	1	1			Fr	Cl, Li, Qu, Sam, Za
<i>Brachythecium ruderales</i> (Brid.) W. R. Buck	F		1	3	3	1	1		Fr	Li, Qu, Sam, Ul, Zan
<i>Bryum billarderi</i> Schwägr.	F		6						Fr	Li, Qu, Rh
<i>Calypothecium duplicatum</i> (Schwägr.) Broth.	F	4							Fr	Cl, Il, Qu
<i>Campylopus anderssonii</i> (Müll. Hal.) A. Jaeger	F	2							Fr	Pi, Rh
<i>Chryso-hypnum diminutivum</i> (Hampe) W. R. Buck	F	3				1			Fr	Li, Qu
<i>Cryphaea filiformis</i> (Hedw.) Brid.	S			2					Fr	Li, Za
<i>Cryphaea patens</i> Hornsch.	S			5		1		1	Fr	Qu, Sa, Za
<i>Ctenidium malacodes</i> Mitt.	F			4					Fr	Li, Sa
<i>Cyclodictyon richardsii</i> Bowers & Magill	S				1				Ra	Li
<i>Cyrtio-hypnum minutulum</i> (Hedw.) W. R. Buck & H. A. Crum	F					2	1		Fr	Ca, Er, Qu
<i>Donnellia commutata</i> (Müll. Hal.) W. R. Buck	S	1				1			Fr	Cl, Rh
<i>Entodon hampeanus</i> Müll. Hal.	S				1				Ra	Li
<i>Entodon jamesonii</i> (Taylor) Mitt.	S				1	1			Fr	Li, Qu
<i>Entodon macropodus</i> (Hedw.) Müll. Hal.	S	1					3		Fr	Ca, Qu, Pr
<i>Entodon serrulatus</i> Mitt.	S	3							Fr	Cl, Li, Qu
<i>Erythrodontium longisetum</i> (Hook.) Paris	F						2		Fr	Er, Qu
<i>Fabronia ciliaris</i> (Brid.) Brid. var. <i>polycarpa</i> (Hook.) W. R. Buck	S	1		2		3	2		Fr	Cl, Er, Li, Sam, Qu

<i>Taxon</i>	<i>Epiphyte</i>	<i>C</i>	<i>X</i>	<i>R</i>	<i>N</i>	<i>L</i>	<i>O</i>	<i>P</i>	<i>RC</i>	<i>Epiphyte host</i>
<i>Fissidens crispus</i> Mont.	F	1	1	2	2	2	3		Fr	Er, P4R, Li, Qu, Sam
<i>Fissidens dubius</i> P. Beauv.	F	1		2					Fr	Li, Qu
<i>Fissidens serratus</i> Müll. Hal. var. <i>serratus</i>	S	3	1	1	3				Fr	Cl, Eu, Li, Qu, Sam
<i>Fissidens steerei</i> Grout	F		2						Fr	Li, Qu
<i>Groutiella chimborazensis</i> (Spruce ex Mitt.) Florsch.	F		2	1		2			Fr	Li, Pr, Qu
<i>Groutiella tomentosa</i> (Hornsch.) Wijk & Margad.	F						1		Ra	Qu
<i>Haplocladium angustifolium</i> (Hampe & Müll. Hal.) Broth.	F		1	2		1		1	Fr	P4R, Li, Qu
<i>Helicodontium capillare</i> (Hedw.) A. Jaeger	F	2		2	3	2	2	1	Fr	Al, Cl, Er, Eu, F4R, He, Li, Pr, Qu, Sa
<i>Herpetineuron toccocae</i> (Sull. & Lesq.) Cardot	F	7	1		1	3	1		Fr	Cl, Il, Li, Pr, Qu
<i>Homalia glabella</i> (Hedw.) Schimp.	F	5							Fr	Eu, Li, Qu
<i>Hypopterygium tamarisci</i> (Sw.) Brid. ex Müll. Hal.	F	3		6	1	1			Fr	Al, Ca, Cl, Eu, P4R, Li, Qu, Sa
<i>Isopterygium tenerum</i> (Sw.) Mitt.	F	2	1	1	1				Fr	Al, Cl, Li, Pi
<i>Lepidopilum brevipes</i> Mitt.	F	2							Fr	Cl, Qu
<i>Leptodontium flexifolium</i> (Dicks. ex With.) Hampe	F		1						Ra	Pi
<i>Leskea</i> aff. <i>angustata</i> Taylor	S							1	Ra	Li
<i>Leucobryum crispum</i> Müll. Hal.	F	1	2						Fr	Li, Pi, Rh
<i>Leucodon cryptotheca</i> Hampe	S			3		3	1	1	Fr	P4R, Li, Qu, Sa
<i>Leucodon curvirostris</i> Hampe	F	2		2		4	2		Fr	Ca, Cl, Eu, Li, Qu, Sa
<i>Leucodon julaceus</i> (Hedw.) Sull.	S		1	1					Fr	Li, Qu
<i>Macrocoma tenuis</i> (Hook. & Grev.) subsp. <i>sullivantii</i> (Müll. Hal.) Vitt.	S		3			3			Fr	Al, Ca, Cr, Li, Qu
<i>Macromitrium fragilicuspis</i> Cardot	F		2	1		1		1	Fr	Li, Qu
<i>Macromitrium guatemaliense</i> Müll. Hal.	S		4	1				1	Fr	Qu, Li
<i>Macromitrium punctatum</i> (Hook. & Grev.) Brid.	S					1			Ra	Pr
<i>Meteorium deppei</i> (Hornsch. ex Müll. Hal.) Mitt.	S		1	5	1	8	5	4	Co	Al, Ca, Er, Li, Pr, Qu, Sa
<i>Meteorium illecebrum</i> Sull.	F	3				1	3	3	Fr	Il, Li, Pr, Qu
<i>Meteorium nigrescens</i> (Hedw.) Dozy & Molk.	F	1				1	5		Fr	Er, Il, Li, Qu
<i>Meteorium teres</i> Mitt.	F		2						Fr	Qu
<i>Mittenothamnium reptans</i> (Hedw.) Cardot	F	4	2	1					Fr	Al, Cl, Li, Qu

<i>Taxon</i>	<i>Epiphyte</i>	<i>C</i>	<i>X</i>	<i>R</i>	<i>N</i>	<i>L</i>	<i>O</i>	<i>P</i>	<i>RC</i>	<i>Epiphyte host</i>
<i>Neckera angustifolia</i> Müll. Hal.	S	1		4		4			Fr	Al, Ca, Eu, P4R, Qu
<i>Neckera chlorocaulis</i> Müll. Hal.	S	1							Ra	Eu
<i>Orthostichella pachygastrella</i> (Müll. Hal. ex Ångstr.) B. H. Allen & Magill	F	2							Fr	Cl, Il
<i>Orthostichella rigida</i> (Müll. Hal.) B. H. Allen & Magill	F	8							Fr	Cl, Eu, Li, Qu
<i>Orthostichidium quadrangulare</i> (Schwägr.) B.H. Allen & Magill	S	1	1						Fr	Eu, Qu
<i>Orthotrichum pycnophyllum</i> Schimp. ex Müll. Hal.	F							1	Ra	Li
<i>Palamocladium leskeoides</i> (Hook.) E. Britton	F	7	1	1		2	2	1	Fr	Ca, Cl, Eu, Li, Qu
<i>Pilotrichella flexilis</i> (Hedw.) Aongstr.	S	8	1	4		6	4	3	Co	Ca, Cl, Cr, Er, Eu, Li, Pr, Qu, Za
<i>Pireella pohlii</i> (Schwägr.) Cardot	F	7	1	2	2		1		Fr	Cl, Eu, Il, Li, Qu
<i>Pireella pycnothallodes</i> (Müll. Hal.) M. Fleisch.	F			2	1	1		1	Fr	P4R, Li, Qu
<i>Prionodon densus</i> (Hedw.) Müll. Hal.	S	3	1						Fr	Li, Qu
<i>Pterobryon densum</i> Hornsch.	F	3				2			Fr	Cl, Eu, Il, Qu, Pr
<i>Pterobryopsis mexicana</i> (Renauld & Cardot) M. Fleisch.	F	5	2			1			Fr	Cl, Eu, Qu
<i>Pylaisiadelpha sharpii</i> H.A. Crum	S		1						Ra	Pi
<i>Pylaisiadelpha tenuirostris</i> (Bruch & Schimp.) W. R. Buck	S		2	2	1				Fr	Al, Li, Qu, Rh
<i>Racopilum tomentosum</i> (Hedw.) Brid.	F	2	3		1			2	Fr	Cl, Li, Qu, Sam
<i>Rauiella praelonga</i> (Schimp. ex Besch.) Wijk & Margad.	F		1					1	Fr	Cr, Qu
<i>Rhynchostegium serrulatum</i> (Hedw.) A. Jaeger	F	2	2	2	4	1			Fr	Cl, Lig, Li, Sa, Sam
<i>Schlotheimia jamesonii</i> (Arnott) Brid.	F		5			3	2		Fr	Ca, Cr, Er Li, Qu, Rh
<i>Schlotheimia rugifolia</i> (Hook.) Schwägr.	F		2						Fr	Cl, Qu
<i>Sematophyllum adnatum</i> (Mx.) E. Britton	F		7	8	5	2	2	1	Co	Al, Cl, Cr, Er, He, Li, Qu, Rh, Sa, Ul, Za
<i>Sematophyllum cuspidiferum</i> Mitt.	F	1	1	3					Fr	Cl, Li, Sa, Za
<i>Sematophyllum subpinnatum</i> (Brid.) E. Britton	F	1	3	4	2	2	1	1	Fr	Al, Cr, He, Il, Lig, Li, Qu, Za
<i>Sematophyllum swartzii</i> (Schwägr.) Welch & H.A. Crum	F		1	1					Fr	Cl, Li
<i>Sphaerotheciella pachycarpa</i> (Schimp. ex Besch.) Manuel	S			1		7			Fr	Al, Ca, Pr, Qu, Za

<i>Taxon</i>	<i>Epiphyte</i>	<i>C</i>	<i>X</i>	<i>R</i>	<i>N</i>	<i>L</i>	<i>O</i>	<i>P</i>	<i>RC</i>	<i>Epiphyte host</i>
<i>Sphaerotheciella pinnata</i> (Schimp.) Manuel	S			1					Ra	P4R
<i>Squamidium leucotrichum</i> (Taylor) Broth.	S	1							Ra	Qu
<i>Stereophyllum radiculosum</i> (Hook.) Mitt.	F		1		1				Fr	Li
<i>Streptopogon matudianus</i> H.A. Crum	S			1					Ra	Sa
<i>Syntrichia amphidiacea</i> (Müll. Hal.) R. H. Zander	F						4	3	Fr	Al, Er, Li, Pr, Qu
<i>Syrrhopodon incompletus</i> Schwägr. var. <i>incompletus</i>	F				1				Ra	Cl
<i>Syrrhopodon parasiticus</i> (Brid.) Besch.	S		3						Fr	Cl, Cr, Rh
<i>Syrrhopodon prolifer</i> Schwägr. var. <i>prolifer</i>	F	1			2				Fr	Li, Sam
<i>Taxyphyllum taxirameum</i> (Mitt.) M. Fleisch.	F	3		2	4	3			Fr	Ca, Cl, Eu, Li, Qu, Sa
<i>Thuidium delicatulum</i> (Hedw.) Schimp.	F					1			Ra	Al
<i>Thuidium tomentosum</i> Schimp.	F	7	2		6				Fr	Cl, Eu, Il, Li, Qu, Sam
<i>Toloxis imponderosa</i> (Taylor) W.R. Buck	S	4							Fr	Cl, Qu
<i>Tortella humilis</i> (Hedw.) Jenn.	F						1		Fr	Li
<i>Tortella tortuosa</i> (Hedw.) Limpr.	F	1	4	1				2	Fr	Li, Qu
<i>Trichostomum brachydontium</i> Bruch	F							1	Ra	Qu
<i>Trichostomum crispulum</i> Bruch	F		2						Fr	Cr, Qu
<i>Zelometeorium patulum</i> (Hedw.) Manuel	S	2							Fr	Cl, Qu