Taxonomy and Floristics / Taxonomía y Florística

Shedding light on the diversity of epiphytic mosses in some Mexican forests

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Abstract
Background: Epiphytic mosses are one of the most common groups in forest environments but among the most neglected by researchers in Mexico.
Questions: What is the epiphytic mosses diversity, measured in richness, turnover, and community composition in Mexican forests?
Species of study: Epiphytic mosses.
Study site and years: Humid mountain forest, pine-oak and tropical evergreen forests. Study period: 2015 to 2021.
Methods: Through a literature review and field work we compiled data on epiphytic mosses in three forest types in Mexico. We assessed the data using alpha and beta diversity analysis, indicator species, and community composition. Additionally, we explored the influence of elevation and forest type on the observed diversity patterns.
Results: We report a richness of 147 species of epiphytic mosses across three types of Mexican forests. The humid mountain forest was the best sampled forest with the highest moss species richness. Although species richness is different for the forests studied, species turnover is similar among them. We demonstrated that elevation and forest type are highly correlated with species richness of epiphytic mosses.
Conclusions: The epiphytic mosses studied here collectively represent over 15 % of the moss richness of Mexico. Forest type and elevation seem to be the drivers of this widely distributed richness. Finally, we call for more in-depth studies of the forests presented here, as well as those in other latitudes including variables such as humidity and host traits, to provide a more complete picture of an overlooked Mexican flora.
Key words: Bryophytes, cryptogams, habitat loss, indicator species, Mexican flora.

Resumen
Antecedentes: Los musgos epífitos son uno de los grupos más comunes en ambientes forestales, pero de los más desatendidos de México.
Preguntas: ¿Cuál es la riqueza, recambio y composición de la comunidad de musgos epífitos en los bosques de México?
Especies de estudio: Musgos epífitos.
Sitios y años de estudio: Bosque húmedo de montaña, de pino-encino y tropical perennifolio. Periodo de estudio: 2015-2021.
Métodos: Mediante una revisión bibliográfica y trabajo de campo recopilamos datos de musgos epífitos en tres tipos de bosques de México. Evaluamos los datos mediante análisis de diversidad alfa y beta, especies indicadoras y composición de la comunidad. Además, exploramos la influencia de la altitud y el tipo de bosque en los patrones de diversidad observados.
Resultados: Reportamos una riqueza de 147 especies de musgos epífitos para tres tipos de bosques de México. El bosque húmedo de montaña es el mejor muestreado y con la mayor riqueza de musgos. El recambio de especies es similar entre los bosques estudiados. Constatamos que la elevación y el tipo de bosque están relacionados con la riqueza de musgos epífitos.
Conclusiones: Los musgos epífitos estudiados aquí representan más del 15 % de la riqueza de musgos de México. El tipo de bosque y la elevación parecen ser los impulsores de esta riqueza ampliamente distribuida. Finalmente, continuar la exploración de los bosques estudiados aquí, así como de aquellos en otras latitudes incluyendo variables como la humedad y rasgos de los árboles hospederos, es urgente para mejorar el conocimiento de esta flora mexicana.
Palabras clave: Briofitas, criptógamas, especies indicadoras, flora de México, pérdida de hábitat.

Forests offer a variety of microhabitats for bryophytes all over the world. Consequently, these ecosystems foster a remarkable diversity of mosses, liverworts, and hornworts (Pócs 1982, Holz & Gradstein 2005). Epiphytic bryophytes are one of the richest and most conspicuous plant groups in forest ecosystems and their diversity has reportedly been influenced by the forest microclimates and their host tree species (Bates 2000, Gradstein & Sporn 2010).

Epiphytic bryophytes play important ecological roles such as water capture, storage, and release (Gradstein 2008, Ah-Peng *et al.* 2017). In addition, they contribute to the establishment and survival of epiphyte vascular plants, such as bromeliads and orchids, by accumulating moisture and promoting the formation of mycorrhizae (Tremblay *et al.* 1998, Zotz & Vollrath 2003, Osorio-Gil *et al.* 2008, Wyse & Burns 2011). Studies have demonstrated their potential use as indicator organisms of successional stages in forests, environmental disturbances (Holz & Gradstein 2005, Gradstein & Sporn 2010, Déleg *et al.* 2021) and air quality (Sim-Siam *et al.* 2000, Sérgio *et al.* 2016). Despite their ecological services in forests, epiphytic bryophytes have not received the same attention in Mexico as their vascular counterparts, leading to a knowledge gap in diversity assessments (Cornwell *et al.* 2019). This is concerning, considering that factors such as habitat loss and fragmentation put these communities at risk of local population extinction (Hallingbäck & Tan 1996, Gradstein & Sporn 2010). For example, at the end of the last century, Mexican temperate and humid mountain forest had lost over 40 and 50 % of their surface area due to land use change respectively (Challenger 1998). This loss of vegetative cover has been hypothesized to negatively impact the diversity of bryophytes in these areas. Until these populations are more fully cataloged, however, the extent of this impact cannot fully be assessed (Delgadillo-Moya 2014).

In examinations of Mexican epiphytic bryophytes, mosses have emerged as the most extensively studied group, offering valuable insights into the overall community structure and richness of these organisms (Herrera-Paniagua *et al.* 2017, Hernández-Rodríguez & Aguirre-Hidalgo 2020). Earlier studies have explored various factors related to epiphytic mosses in humid and temperate forests, including richness, rarity, community composition (Thornburgh & Sharp 1975, Herrera-Paniagua *et al.* 2017, Hernández-Rodríguez & Aguirre Hidalgo 2020, Hernández-Rodríguez *et al.* 2021a), the effects of forestry practices on their richness and community composition (Hernández-Rodríguez *et al.* 2021b), as well as the use and management of some species by human populations (Hernández-Rodríguez & Delgadillo-Moya 2021, Hernández-Rodríguez & López-Santiago 2021). Despite significant progress in this field there are no estimates available for the diversity and distribution of epiphytic mosses in Mexico.

The present study aims to explore species richness of epiphytic mosses in Mexico, with a particular focus on three forest ecosystems (*sensu* Rzedowski 2006, Villaseñor 2010) in three physiographic provinces (INEGI 2008): the humid mountain forest of the Sierra Madre Oriental, the humid mountain forest and pine-oak forest in the Sierra Madre del Sur and the tropical evergreen forest in the Southern Gulf Coastal Plain. The objectives of this study are 1) to generate a list of epiphytic moss species found in these Mexican forests, 2) to assess the diversity (taxonomic diversity and species turnover) and community composition of their epiphytic mosses in relation to elevation and forest type, and 3) to evaluate if there are associated species for each forest type. This knowledge will serve as a basis for future ecological and conservation studies of the non-vascular flora of Mexico.

Materials and methods

Study design and data collection. In establishing a baseline of expected moss species for our study ecosystems, we first drew upon existing datasets from ecological studies (Herrera-Paniagua *et al.* 2017, Hernández-Rodríguez & Aguirre Hidalgo 2020, Hernández-Rodríguez *et al.* 2021a). The data from these datasets have been obtained from four sites across three physiographic provinces in Mexico (Figure 1). The initial dataset corresponds to the work of Herrera-Paniagua *et al.* (2017) conducted in the humid mountain forest (HM1) of the eastern Sierra Madre Oriental (elevation 989-1,485 m asl). This study encompassed five forest fragments within the Sierra Gorda-Rio Montezuma and Sierra Madre Oriental regions (Arriaga *et al.* 2000), which span the states of San Luis Potosí, Querétaro, and
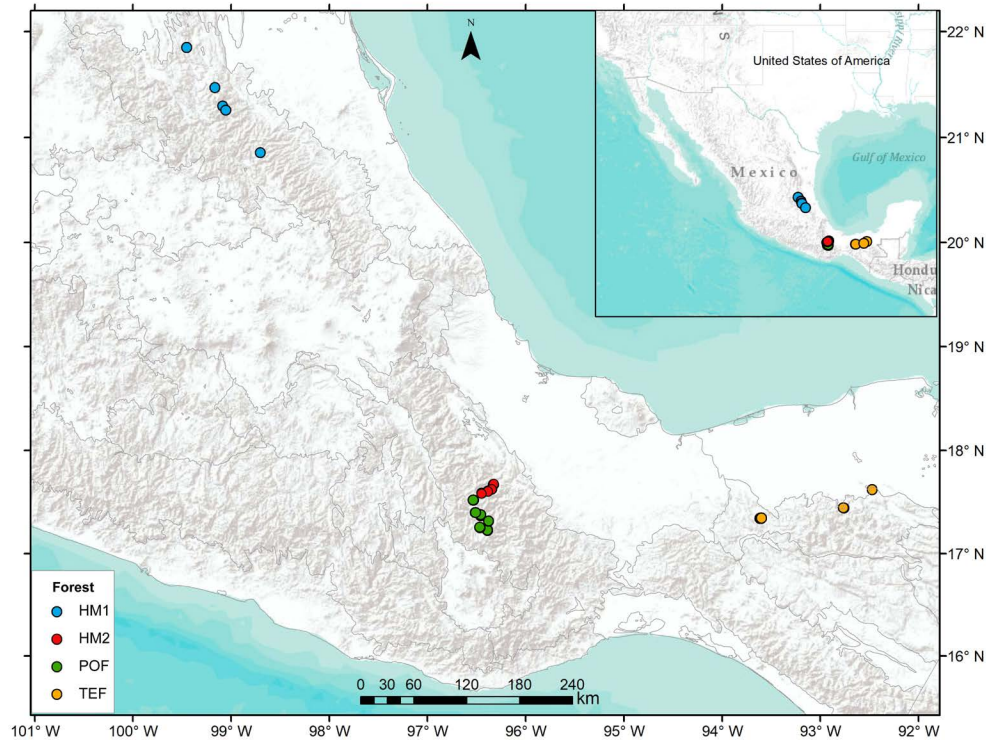
Figure 1. Vegetation types and sampling sites (color points) included in this work: HM1 (humid mountain forest in the Sierra Madre Oriental), HM2 (humid mountain in the Sierra Madre del Sur), POF (pine-oak forest in the Sierra Madre del Sur) and TEF (tropical evergreen forest in the Southern Gulf Coastal Plain).

Hidalgo. Notably, these regions hold high conservation priority in Mexico. The study focused on recording epiphytic mosses on 50 host trees (with a diameter at breast height, DBH, of ≥ 6 cm), predominantly belonging to the genera *Quercus* L. and *Liquidambar* L.

The second dataset corresponds to Hernández-Rodríguez & Aguirre Hidalgo (2020) in the humid mountain forest (HM2) of the Sierra Norte de Oaxaca (elevation 1,140-2,138 m asl) in the physiographic province of the Sierra Madre del Sur. This forest represents a protected area and has the highest level of conservation and represents the largest humid mountain forest rest in Mexico (Rzedowski 1996, CONABIO 2010, Ponce-Reyes *et al.* 2012). The moss sampling involved a comprehensive floristic survey of the habitat, where samples were collected from all microhabitats across eight sites. This study included documentation on the richness of epiphytic mosses specifically on host trees and shrubs.

The third dataset, sourced from Hernández-Rodríguez *et al.* (2021a), pertains to the pine-oak forest (POF) within the Sierra Norte of Oaxaca (elevation 2,274-2,840 m asl). This research spanned three conservation areas and three areas designated for reduced impact logging. A crucial component of this study involved the assessment of moss richness on 60 *Quercus* L. trees (with a diameter at breast height, DBH, of ≥ 6 cm). As reported by the authors, the richness and community composition of epiphytic mosses were found to be similar in both conservation and reduced impact logging areas. This similarity allows for the utilization of the data to characterize the diversity of epiphytic mosses in this forest.

Finally, the fourth dataset pertains to fieldwork conducted in three conserved fragments of the tropical evergreen forest (TEF) in the state of Tabasco during November 2012, May and July 2013 and September 2015. The study areas included Las Flores Ecotourism Zone, Huimanguillo, and Agua Blanca State Park, Macuspana, within the Southern Gulf Coastal Plain physiographic province (elevation 59-445 m asl). Mosses were collected from 13 different host tree species.

In all the aforementioned datasets, the host trees sampled were separated by a distance of at least 10 m from each other and mosses were collected from the base of the trunk up to a maximum of 8 m. With the information collected, a list of registered taxa was compiled, and the nomenclature was updated based on the electronic version of LATMOSS (Delgadillo-Moya 2010) and Goffinet & Buck (2008). Using the list of taxa, we constructed a presence/absence database of species by host tree in each forest, which we used for our subsequent analyses.

Data analysis. To assess diversity and completeness of inventories between forests we performed sample coverage curves using the methodology proposed by Hsieh *et al.* (2016) and Chao *et al.* (2014). Sample coverage is the proportion of individuals (or incidences) that belong to observed species in a sample (Chao & Jost 2012). Thus, instead of using sample size, the sample coverage approach compares species assemblages with a more accurate representation of the relationship between species assemblage richness (Chiu 2023). To compare the taxonomic diversity of epiphytic mosses among the three forest types we performed species diversity curves based on sample size using Hill numbers (q0 = richness; q1 = frequent species, and q2 = dominant species) using incidence data (Hill 1973, Jost 2006). We used host trees sampled in each forest (total of 123) as the sampling unit. Data from HM2 were only used for species checklist and were excluded from the statistical analyses because the available information is at the site scale and not at the host tree scale like the other datasets. Consequently, the forests analyzed included HM1, POF, and TEF. An advantage of curves by sample coverage is that they incorporate rarefaction/extrapolation analysis which allows comparisons between different forests with different sampling efforts (Chao & Jost 2012, Chiu 2023). In our case, we were able to make comparisons between sites with different numbers of host trees sampled. This method is currently considered the best tool for measuring taxonomic diversity between sites (Jost 2010, Moreno & Rodríguez 2011). In all cases, extrapolations were performed at twice the reference sample, with 84 % confidence intervals (MacGregor-Fors & Payton 2013) with 999 permutations.

To evaluate the effect of elevation and forest type on the epiphytic mosses richness, a generalized linear model (GLM) with no interaction was performed, using a Poisson error distribution and the logarithmic link function (McCullagh & Nelder 1989). Elevation was selected because of the influence it has been found to have on alpha diversity patterns in bryophytes and to be the main factor measured in the analyzed forests (*e.g.,* Wolf 1993). Where significant differences were obtained between forest type within richness, a pairwise comparison was made using Tukey's multiple comparison procedure (α = 0.05).

Beta diversity for each forest was assessed using the methodology proposed by Carvalho *et al.* (2012). The beta diversity of a forest was calculated as the average turnover among all pairwise comparisons of its sampled trees (Legendre 2014). The values obtained follow the beta diversity partitioning approach where total beta diversity is explained by species replacement and by differences in richness between sites (Podani & Schmera 2011, Carvalho *et al.* 2012). Species composition among different forests was assessed by nonmetric multidimensional scaling (NMDS) analysis using the Bray-Curtis distance. To analyze the effect of environmental variables (elevation and forest type), a permutation-based multivariate analysis (PERMANOVA) was performed with 999 Monte Carlo permutations.

To determine whether epiphytic moss species are associated with a given forest type, we performed an indicator species analysis (Dufrêne & Legendre 1997). This analysis allows us to obtain an indicator value between 0 and 1 that indicates the level of association of a species, or groups of species, to a given environment. Subsequently, to identify the best indicator species for each forest type, we analyzed the specificity (A) and fidelity (B) components of the indicator values (Dufrêne & Legendre 1997, De Cáceres & Legendre 2009). Specificity (A) refers to the probability that a given species belongs to a given forest type, while fidelity (B) indicates the probability that a given species is found in a given forest type. Those species that possess indicator values with high specificity and fidelity will therefore be better indicator species. The analysis was performed with a statistical significance of 0.05 and evaluated with 999 permutations.

All analyses were performed in the statistical software R v. 3.2.2 (R Core Team 2021). The iNEXT package (Chao *et al.* 2014) were used for sample coverage, diversity, and species rarefaction curves with Hill numbers. We also used the packages lsmeans (Lenth 2016) for the Tukey test, BAT (Cardoso *et al.* 2017) to assess beta diversity within each

forest, and vegan (Oksanen *et al.* 2022) for NMDS and PERMANOVA analyses. Finally, we used the indicspecies package (De Caceres & Legendre 2009) for indicator species analysis.

Results

Species diversity and sampling completeness. We recorded a total of 147 species of epiphytic mosses for three forest types in Mexico (Table 1). According to the results of the sample coverage analysis the site with the highest species completeness was HM1, followed by POF and TEF (Figures 2, 3, Table 2). The sample coverage values indicated that the 82 species recorded at HM1 corresponded to 97 % of its total richness, while the 34 species at POF and the 15 at TEF to 83 and 82 % respectively (Figure 3). Thus, the likelihood of finding new species is higher in the POF and TEF than in the HM1. The trends of the curves also supported the previous results, showing significant differences between species richness assemblages for each forest. For HM1 the asymptotic trend of the curve suggested a much more complete and accurate sampling than in the POF and TEF (Figure 3).

Table 1. Epiphyte moss taxa recently report in Mexico. Vegetation types: HM = humid mountain forests, POF = pine-oak forest, TEF = tropical evergreen forest.

Taxon	HM	POF	TEF
Acroporium longirostre (Brid.) W.R. Buck	X		
Adelothecium bogotense (Hampe) Mitt.	X	X	
Anomodon attenuatus (Hedw.) Huebener	X		
Anomodon rostratus (Hedw.) Schimp.	X		
Anomodon tristis (Ces.) Sull. & Lesq.	X		
Aerolindigia capillacea (Hornsch.) M. Menzel		X	
Anacamptodon compactus (Thér.) W.R. Buck		X	
Atrichum oerstedianum (Müll. Hal.) Mitt.	X		
Atractylocarpus longisetus (Hook.) E.B. Bartram	X		
Brachymenium systylium (Müll. Hal.) A. Jaeger		X	
Brachythecium occidentale (Hampe) A. Jaeger	X		
Brachythecium ruderale (Brid.) W.R. Buck	X	X	
Braunia squarrulosa (Hampe) Müll. Hal.		X	
Bryum billarderi Schwägr.	X	X	
Callicostella pallida (Hornsch.) Ångstr.	X		
Calymperes afzelii Sw.			X
Calyptothecium duplicatum (Schwägr.) Broth.	X		
Campylopus anderssonii (Müll. Hal.) A. Jeger	X		
Campylopus arctocarpus (Hornsch.) Mitt.	X		
Campylopus flexuosus (Hedw.) Brid.	X		
Campylopus tallulensis Sull. & Lesq.	X		
Chryso-hypnum diminutivum (Hampe) W.R. Buck	X		
Cryphaea filiformis (Hedw.) Brid.	X		

Taxon	HM	POF	TEF
Cryphaea patens Hornsch.	X		
Chryso-hypnum diminutivum (Hampe) W.R. Buck	X		
Ctenidium malacodes Mitt.	X		
Cyclodictyon richardsii Bowers & Magill	X		
Cyrto-hypnum minutulum (Hedw.) W.R. Buck & H.A. Crum	X		
Daltonia longifolia Taylor	X		
Donnellia commutata (Müll. Hal.) W.R. Buck	X		
Entodon hampeanus Müll. Hal.	X		
Entodon jamesonii (Taylor) Mitt.	X		
Entodon macropodus (Hedw.) Müll. Hal.	X		
Entodon serrulatus Mitt.	X		
Erythrodontium longisetum (Hook.) Paris		X	
Fabronia ciliaris (Brid.) Brid. var. *polycarpa* (Hook.) W.R. Buck	X		
Fissidens crispus Mont.	X		
Fissidens dubius P. Beauv.	X		
Fissidens serratus Müll. Hal. var. *serratus*	X		
Fissidens steerei Grout	X		
Groutiella apiculata (Hook.) H.A. Crum & Steere	X		
Groutiella chimborazensis (Spruce ex. Mitt.) Florsch.	X		
Groutiella tomentosa (Hornsch.) Wijk & Margad.			X
Haplocladium angustifolium (Hampe & Müll. Hal.) Broth.	X		
Helicodontium capillare (Hedw.) A. Jaeger	X		
Helicophyllum torquatum (Hook.) Brid.			X
Herpetineuron toccoae (Sull. & Lesq.) Cardot	X		
Herzogiella cylindricarpa (Cardot) Z. Iwats.		X	
Heterophyllium nemorosum (W.D.J. Koch ex Brid.) Kindb.	X		
Holomitrium arboreum Mitt.	X		
Holomitrium pulchellum Mitt.	X	X	
Homalia glabella (Hedw.) Schimp.	X		X
Homaliodendron flabellatum (Sm.) M. Fleisch.	X		
Hypopterygium tamarisci (Sw.) Brid. ex Müll. Hal.	X		
Isodrepanium lentulum (Wilson) E. Britton	X		
Isopterygium tenerum (Sw.) Mitt.	X		
Leiomela bartramioides (Hook.) Paris	X		
Lepidopilidium portoricense (Müll. Hal.) H.A. Crum & Steere	X		

Taxon	HM	POF	TEF
Lepidopilum amplirete (Sull.) Mitt.	X		
Lepidopilum brevipes Mitt.	X		
Lepidopilum muelleri (Hampe) Hampe	X		
Leptodontium flexifolium (Dicks. ex With.) Hampe	X		
Leptodontium viticulosoides (P. Beauv.) Wijk & Margad.	X	X	
Leucobryum antillarum Schimp. ex Besch.	X		
Leucobryum crispum Müll. Hal.	X		
Leucobryum martianum (Hornsch.) Hampe ex Müll. Hal.	X		
Leucodon cryptotheca Hampe	X		
Leucodon curvirostris Hampe	X	X	
Leucodon julaceus (Hedw.) Sull.	X		
Leucoloma cruegerianum (Müll. Hal.) A. Jaeger	X		
Leucoloma serrulatum Brid.	X		
Leucoloma subimmarginatum (Müll. Hal.) A. Jaeger	X		
Macrocoma tenuis (Hook. & Grev.) var. *sullivantii* (Müll. Hal.) Vitt.	X		
Macromitrium cirrosum (Hedw.) Brid.	X		
Macromitrium fragilicuspis Cardot	X		
Macromitrium guatemaliense Müll. Hal.	X	X	
Macromitrium longifolium (Hook.) Brid.	X		
Macromitrium punctatum (Hook. & Grev.) Brid.	X		
Macromitrium sharpii H.A. Crum ex Vitt	X	X	
Meteoridium remotifolium (Müll. Hal.) Manuel	X		
Meteorium deppei (Hornsch. ex Müll. Hal.) Mitt.	X	X	
Meteorium nigrescens (Hedw.) Dozy & Molk.	X		
Meteorium teres Mitt.	X		
Mittenothamnium reduncum (Schimp. ex Mitt.) Ochyra		X	
Mittenothamnium reptans (Hedw.) Cardot	X	X	
Neckera angustifolia Müll. Hal.	X		
Neckera chlorocaulis Müll. Hal.	X	X	
Neckera ehrenbergii Müll. Hal.		X	
Neckera urnigera Müll. Hal.	X		
Neckeropsis undulata (Hedw.) Reichardt	X		X
Octoblepharum albidum Hedw.	X		X
Octoblepharum erectifolium Mitt. ex R.S. Williams	X		
Orthostichella pachygastrella (Müll. Hal. ex Ångstr.) B.H. Allen & Magill	X		

Taxon	HM	POF	TEF
Orthostichella rigida (Müll. Hal.) B.H. Allen & Magill	X		
Orthostichidium quadrangulare (Schwägr.) B.H. Allen & Magill	X		
Palamocladium leskeoides (Hook.) E. Britton	X		
Pelekium schistocalyx (Müll. Hal.) Touw		X	X
Pilotrichella flexilis (Hedw.) Aongstr.	X		
Pilotrichella mauiensis (Sull.) A.Jaeger	X	X	
Pireella guatemalensis E.B. Bartram	X		
Pireella pohlii (Schwägr.) Cardot	X		X
Pireella pycnothallodes (Müll. Hal.) M. Fleisch.	X		X
Porotrichum longirostre (Hook.) Mitt.	X	X	
Porotrichum tenuinerve B.H. Allen	X		
Prionodon densus (Hedw.) Müll. Hal.	X	X	
Pterobryon densum Hornsch.	X		
Pterobryopsis mexicana (Renauld & Cardot) M. Fleisch.	X		
Pylaisia falcata Schimp.		X	
Pylaisiadelpha sharpii H.A. Crum	X		
Pylaisiadelpha tenuirostris (Bruch & Schimp.) W.R. Buck	X		
Pyrrhobryum spiniforme (Hedw.) Mitt.	X		
Racopilum tomentosum (Hedw.) Brid.	X		
Rauiella praelonga (Schimp. ex Besch.) Wijk & Margad.	X		
Rhynchostegiopsis flexuosa (Sull.) Müll. Hal.	X		
Rhynchostegium serrulatum (Hedw.) A. Jaeger	X		
Rigodium toxarion (Schwägr.) A. Jaeger		X	
Schlotheimia jamesonii (Arnott) Brid.	X		
Schlotheimia rugifolia (Hook.) Schwägr.	X		
Schlotheimia tecta Hook. & Wilson	X		
Sematophyllum adnatum (Mx.) E. Britton	X	X	
Sematophyllum cuspidiferum Mitt.	X		
Sematophyllum subpinnatum (Brid.) E. Britton	X		
Sematophyllum swartzii (Schwägr.) Welch & H.A. Crum	X		
Sphaerotheciella pachycarpa (Schimp. ex Besch.) Manuel	X		
Sphaerotheciella pinnata (Schimp.) Manuel	X		
Stereophyllum radiculosum (Hook.) Mitt.	X		
Streptopogon matudianus H.A. Crum	X		
Syntrichia amphidiacea (Müll. Hal.) R.H. Zander	X		
Syntrichia fragilis (Taylor) Ochyra		X	

| Taxon	HM	POF	TEF
Syrrhopodon gaudichaudii Mont.	X		
Syrrhopodon incompletus Schwägr. var. *incompletus*	X		X
Syrrhopodon lycopodioides (Sw. ex Brid.) Müll. Hal.	X		
Syrrhopodon parasiticus (Brid.) Besch.	X		
Syrrhopodon prolifer Schwägr. var. *prolifer*	X		X
Taxithelium planum (Brid.) Mitt.	X		X
Taxyphyllum taxirameum (Mitt.) M. Fleisch.	X		
Thuidium delicatulum (Hedw.) Schimp.	X	X	
Thuidium tomentosum Schimp.	X		
Toloxis imponderosa (Taylor) W.R. Buck	X		
Tortella tortuosa (Hedw.) Limpr.	X		
Trichostomum crispulum Bruch	X		
Trichostomum tenuirostre (Hook. & Taylor) Lindb.		X	
Zygodon ehrenbergii Müll. Hal.		X	
Zygodon liebmannii Schimp.		X	
Zygodon obtusifolius Hook.		X	
Zygodon reinwardtii (Hornsch.) A. Braun	X	X	
Zygodon viridissimus (Dicks.) Brid.		X	
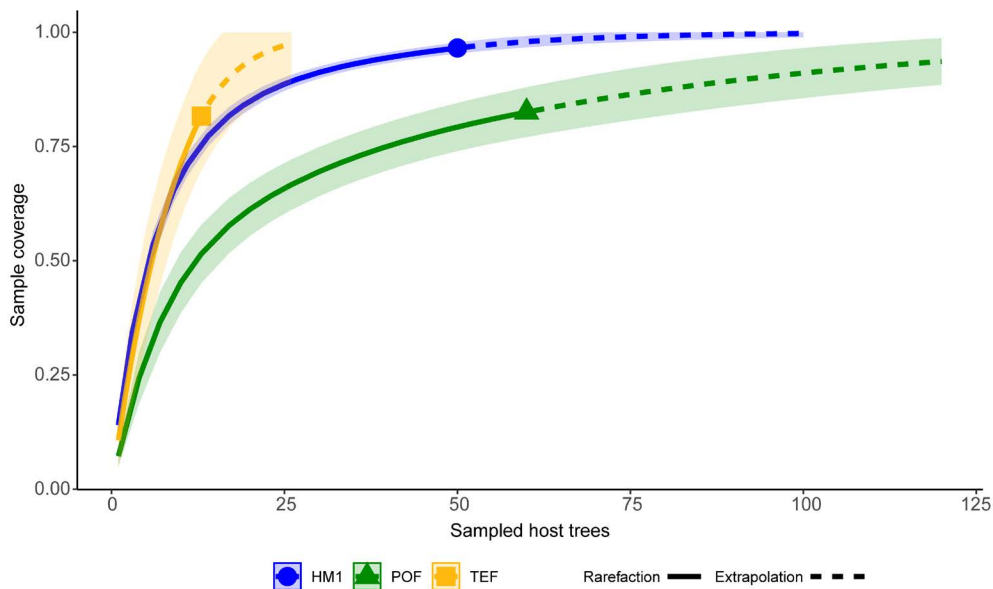
Figure 2. Rarefaction/extrapolation curve of sample coverage for epiphytic mosses in three forests in Mexico (HM1= humid mountain forest 1, POF = pine-oak forest, TEF = tropical evergreen forest). The graph shows how sample coverage behaves as a function of sample size (number of trees sampled). The extrapolation was performed at twice the number of trees sampled in each forest. The overlap of the 84 % confidence intervals of the HM1 and the TEF indicates that there are no significant differences between the coverage of their samples. The narrower the confidence intervals, the more precise the sample coverage.
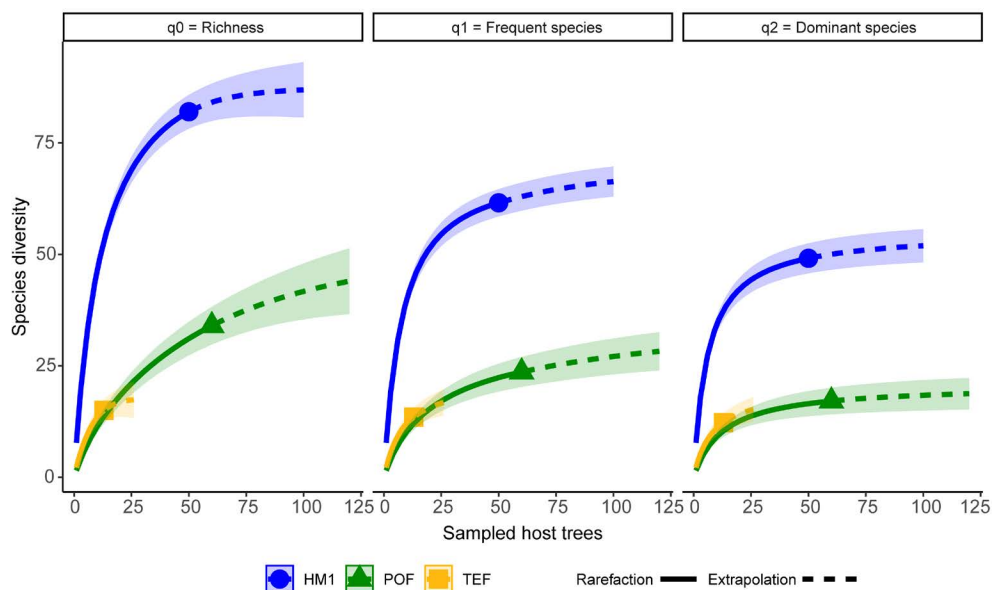
Figure 3. Epiphytic moss diversity curves using Hill numbers in three different forests in Mexico (HM1 = Humid mountain forest 1, POF = pine-oak forest, TEF = tropical evergreen forest). The separation of the 84 % confidence intervals indicates that there are significant differences between the diversity of mosses using the three Hill numbers.

Table 2. Species richness values, number of host trees sampled and sample coverage for each forest studied.

Forest	Richness	Sampled host trees	Sample coverage %
Humid mountain forest	82	50	97
Pine oak forest	34	60	83
Tropical evergreen forest	15	13	82

According to the richness curves (q0) based on the number of host trees sampled, we recorded a significantly higher richness of epiphytic mosses in HM1 (82 species) than in POF (34 species) and TEF (15 species) ([Figure 3](#)). Furthermore, we estimate that there may be as many as 87 species in HM1, 50 in POF and 18 in TEF extrapolating to twice the number of trees in each forest. In the case of POF and TEF, the curves showed similar richness at 13 host trees. This pattern was repeated when considering frequent species (q1) as well as dominant species (q2). For HM1 there were 62 frequent species, while for POF 24, and for TEF 13. Following this pattern, we recorded 49 dominant species for HM1, 17 for POF and 12 for TEF.

Regarding the GLM results, species richness in HM1 is positively affected by forest type and elevation. Conversely, forest type has a negative influence on EP and TEF ([Table 3](#)). The Tukey's multiple comparison procedure showed that association between species richness and forests confirms that HM1 is significantly different from EP and TEF, thus is the forest with the highest species diversity

Table 3. GLM results between species richness and forest and elevation variables. *P* values: $*P < 0.05$, $**P < 0.001$. Different letters indicate significant differences among forest type for richness ($P < 0.05$, Tukey HSD).

Variable	Estimate	SE	*Z* value	*P*
Humid mountain forest	1.3879	0.3229	4.298	< 0.0001**[a]
Pine-oak forest	-2.2333	0.3634	-6.146	< 0.0001**[b]
Tropical evergreen forest	-0.7375	0.3271	-2.254	0.0242*[b]
Elevation	0.0005	0.0003	2.08	0.0376*

Community composition. The beta diversity analysis revealed that, on average, 93 % of species changed across the three forest types ([Figure 4](#)). Within this percentage, 55-65 % was attributed to species replacement, whereas 28-33 % was associated with variations in richness. High beta diversity values across all three forest types suggest a substantial turnover of species among trees ([Figure 4](#)).

The Non-metric Multidimensional Scaling (NMDS) analysis revealed that the composition of epiphytic mosses varied across the three types of forests. However, the dissimilarity was more pronounced when comparing POF with HM1 and TEF ([Figure 5](#)). PERMANOVA results reveal that forest type and elevation influenced moss composition ([Table 3](#)). Forest type explained the greatest variability in species composition per tree (8 %), while elevation explained only 1 % ([Table 4](#)).
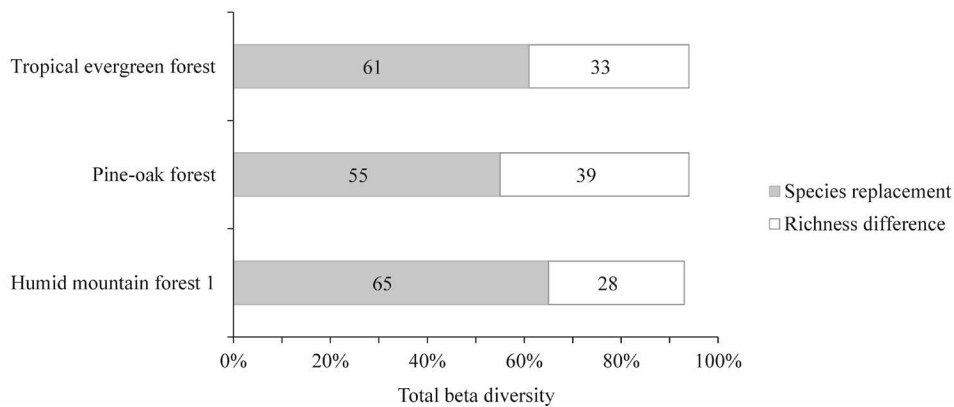

Figure 4. Total beta diversity of epiphytic mosses in each studied forest explained by the species replacement and richness difference.
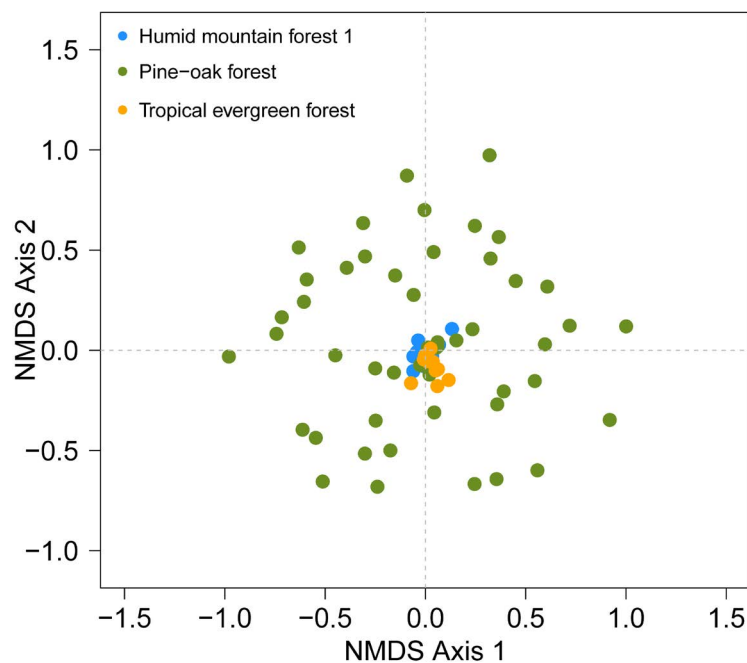

Figure 5. Non-metric multidimensional scaling analysis of epiphytic moss species composition in three forest types in Mexico. Stress = 0.2031

Table 4. PERMANOVA results of the diversity of epiphytic mosses in three humid forests of Mexico. The analysis includes variation by forest type and elevation. *P* values: *P < 0.05, **P < 0.001

	df	SS	SM	*F*	*R*	*P*
Forest	2	39.76	19.8797	5.183	0.08363	0.001**
Elevation	1	6.1	6.0955	1.589	0.01282	0.013*
Residuals	112	429.57	3.8354		0.90355	
Total	115	475.42			1	

Habitat indicator species. The results of the indicator species analysis revealed the association of 23 epiphytic moss species to HM1, 4 to POF and 8 to TEF. In general, the species had an indicator value between 0.3 and 0.6. When analyzing the specificity (A) and fidelity (B) components, we observed that most species have a high probability of being specific to a forest type. However, they have a low probability of being localized in each of them (Table 5). The species that can be considered as the best indicators due to their indicator values, and the highest levels of A and B, are *Sematophyllum adnatum* (Mx.) E. Britton (Indval = 0.6, A = 0.9, B = 0.4) and *Meteorium deppei* (Hornsch. ex Müll. Hal.) Mitt. (Indval = 0.6, A = 0.9, B = 0.4) for HM1 and *Syrrhopodon prolifer* Schwägr. (Indval = 0.5, A = 0.9, B = 0.3) for TEF.

Table 5. Indicator species for each forest type. A = species specificity, B = species fidelity. *P* values: *P < 0.05, **P < 0.001.

Forest type	A	B	Indicator value	*P*
Cloud forest				
Sematophyllum adnatum	0.9	0.4	0.6	0.003**
Meteorium deppei	0.9	0.4	0.6	0.003**
Herpetineuron toccoae	1	0.2	0.5	0.003**
Hypopterygium tamarisci	1	0.2	0.5	0.008**
Palamocladium leskeoides	1	0.2	0.5	0.004**
Pilotrichella flexilis	1	0.2	0.5	0.006**
Anomodon attenuates	1	0.2	0.4	0.007**
Helicodontium capillare	1	0.2	0.4	0.007**
Neckera angustifolia	1	0.2	0.4	0.011*
Rhynchostegium serrulatum	1	0.2	0.4	0.009**
Sematophyllum subpinnatum	0.7	0.2	0.4	0.026*
Fissidens crispus	1	0.2	0.4	0.05*
Fissidens serratus var. *serratus*	1	0.2	0.4	0.042*
Orthostichella rigida	1	0.2	0.4	0.039*
Schlotheimia jamesonii	1	0.2	0.4	0.036*
Sphaerotheciella pachycarpa	1	0.2	0.4	0.04*
Taxyphyllum taxirameum	1	0.2	0.4	0.047*
Thuidium tomentosum	1	0.2	0.4	0.034*
Brachythecium occidentale	1	0.1	0.3	0.018*
Cryphaea patens	1	0.1	0.3	0.019*
Leucodon cryptotheca	1	0.1	0.3	0.022*
Macrocoma tenuis	1	0.1	0.3	0.018*
Bryum billarderi	0.9	0.1	0.3	0.035*

Forest type	A	B	Indicator value	*P*
Pine-oak forest				
Zygodon viridissimus	1	0.2	0.4	0.017*
Braunia squarrulosa	1	0.2	0.4	0.037*
Neckera chlorocaulis	0.9	0.2	0.4	0.028*
Pylaisia falcata	1	0.1	0.3	0.033*
Tropical evergreen forest				
Syrrhopodon prolifer	0.9	0.3	0.5	0.002**
Calymperes afzelii	1	0.2	0.5	0.001***
Meteorium nigrescens	0.9	0.2	0.4	0.012*
Helicophyllum torquatum	1	0.2	0.4	0.012*
Neckeropsis undulata	1	0.2	0.4	0.011*
Octoblepharum albidum	1	0.2	0.4	0.016*
Taxithelium planum	1	0.2	0.4	0.01**
Syrrhopodon incompletes	0.9	0.2	0.4	0.028*

Discussion

The richness of epiphytic mosses in the three Mexican forest types analyzed comprises 147 species representing 15 % of that reported for the country (Delgadillo-Moya 2014). This percentage is comparable to the diversity of vascular epiphytes in Mexico (1,813 spp. = 10 % of vascular plants, Villaseñor 2016, Espejo-Serna *et al.* 2021). However, the number of epiphytic moss species is expected to increase with future sampling, particularly in the POF and TEF, where a higher number of species is predicted, and sampling effort has been lower (Figures 2, 3). In contrast, HM1 is the best inventoried forest with the highest richness of epiphytic species likely due to its higher humidity conditions (Tng *et al.* 2009, Marline *et al.* 2020). Thus, these results agree with the diversity reported for humid mountain forests in other countries (Gradstein *et al.* 2001, Acebey *et al.* 2003, León-Vargas *et al.* 2006). Humid mountain forest represents some of the most diverse vegetation types, thus offering a variety of host tree genera such as *Clethra* L., *Liquidambar* L. and *Quercus* L. (Villaseñor 2010) with numerous microhabitats for epiphytic mosses. Furthermore, characteristics of phorophytes (host tree), like bark texture and height, and environmental factors, such as precipitation and humidity, have been identified as key factors contributing to the high richness and biomass of epiphytic mosses in humid mountain forests (Bates 2000, Gradstein & Sporn 2010).

Analyzing the community patterns of the epiphytic mosses, we found that their richness and composition are influenced by large-scale variables such as forest type and elevation (Wolf 1993, Tusiime *et al.* 2007, Song *et al.* 2015, Gil-Novoa *et al.* 2017). In turn, these variables have a notable impact on local and microclimatic conditions, contributing significantly to the observed patterns of community structure and richness in epiphytic mosses (Acebey *et al.* 2003, Holz & Gradstein 2005, Tusiime *et al.* 2007, Song *et al.* 2015). An interesting finding from our study is the consistent turnover of epiphytic moss species across different forest types. This suggests a significant variation in moss species from one tree to another within each studied forest. The observed species turnover could be attributed to the low host specificity among tropical bryophytes (Patiño & González-Mancebo 2011). For example, microhabitat preference observations of the mosses *Calymperes afzelii* Sw. and *Shyrrhopodon incompletus* Schwägr. in the TEF appears to be more closely associated with trees featuring bark with high water retention rather than trees belonging to a specific phylogenetic group (i.e., same taxonomical group) (Escolástico-Ortiz & Delgadillo-Moya 2023). Therefore, host tree traits such as diameter, bark type, and pH are factors that will help to understand better the richness and composition of epiphytic moss communities in future studies (Holz & Gradstein

2005, Benítez *et al.* 2015, Déleg *et al.* 2021). Additionally, habitat characteristics such as the conservation status or disturbance regimes will also contribute to understanding the diversity drivers of this bryophyte group (Acebey *et al.* 2003, Holz & Gradstein 2005).

With respect to habitat indicator species, we did not find species strongly associated with any forest type (*e.g.,* Indval = > 0.9, A= > 0.9, B= > 0.9). Although three species were shown to be related to the studied forests, they have a wide distribution, inhabiting different vegetation types (Cárdenas Soriano & Delgadillo-Moya 2009). For the HM, *S. adnatum* was identified as indicator*,* but it is also frequent in *Pinus* L., oak and *Abies* L. forests (Cárdenas Soriano & Delgadillo-Moya 2009) and can inhabit a wide altitudinal range (25-2,134 m asl) (Mateo Jiménez *et al.* 2018). *M. deppei* was shown to be associated with HM but is also found in pine-oak forests (Cárdenas Soriano & Delgadillo-Moya 2009). Likewise, *S. prolifer* was identified as a TEF indicator species. However, this species can be found from sea level to 2,000 m, being frequent in mesophytic forests (Reese 1993, Allen 1994, Delgadillo-Moya *et al.* 2017, Herrera-Paniagua *et al.* 2017). The lack of a strong association between species and forest type is primarily explained by a preference for microclimatic conditions rather than a vegetation type. The report of these species is supported by studies in temperate and tropical ecosystems (Sharp *et al.* 1950, Delgadillo-Moya *et al.* 2017). Moreover, bryophytes possess a high dispersal capacity and occupy different environments (Vanderpoorten *et al.* 2019). Incorporating traits such as species biomass in future studies can significantly enhance our understanding of the specificity of Mexican epiphytic mosses to specific vegetation types.

Given the accelerated deterioration of Mexican forests, urgent attention must be given to developing research on epiphytic bryophytes. Particularly, the state of Tabasco has experienced a change in land use, leaving 38.7 % of remnant vegetation (Castillo-Acosta & Zavala-Cruz 2009) and is one of the entities with little information on bryophyte diversity (Delgadillo-Moya & Zamudio 1988, Rivas-Acuña & Escolástico-Ortiz 2019, Delgadillo-Moya 2021). Furthermore, certain species of epiphytic mosses are harvested illegally (*e.g., Pilotrichella flexilis* (Hedw.) Ångstr*., Dendropogonella rufescens* (Schimp.) E. Britton), posing a threat to the diversity of epiphytic bryophytes and the species reliant on them, while also worsening the degradation of ecosystem functioning (Hernández-Rodríguez & Delgadillo-Moya 2022, Hernández-Rodríguez & López-Santiago 2021).

Finally, an exhaustive bibliographic and herbarium review is needed to have a more complete listing of the Mexican epiphytic moss flora. To reach the last purpose, the exploration of forests in other areas of the country is also necessary. For future studies of epiphytic bryophytes, we recommend paying specific attention to the primary humid mountain forests in the Serranías de Nayarit and the Southern Coastal Range, along with the mixed pine-oak forests in the Sierra Madre Oriental and Occidental, owing to their humid conditions. In addition, mangrove ecosystems are other humid environments that harbor a particular richness of epiphytic mosses (Salazar-Allen *et al.* 2022) that have gone unnoticed in Mexico. To enhance our knowledge of the mosses of the aforementioned forests, as well as those examined in this review, we recommended including sampling in the canopy of the host trees. Some bryophytes are only distributed at the canopy level (Sporn *et al.* 2010), and studies of canopy moss flora in Mexico would be novel, as the species reported here were sampled up to eight meters in height. Thus, research on different forest types and expanding the record of the Mexican epiphytic flora can significantly enhance our understanding of the biodiversity at risk due to the constant and increasing loss of its habitats. It should be emphasized that the study of Mexican epiphytic mosses could improve our knowledge of bryophyte ecology. For example, moss evaluation in latitudinal gradients would explain part of their biogeography (Patiño *et al.* 2022), and the study of host tree species and their traits (*e.g.,* size, bark type, diameter) would explain in more detail the structure and composition of their communities (Gradstein *et al.* 2003, Király *et al.* 2013).

In summary, our work presents the first preliminary species checklist of epiphytic mosses in Mexico. Additionally, we provide insights into a wide moss richness influenced by elevation and forest type, as well as high species turnover within some humid forests. Finally, we offer suggestions on how to enrich our knowledge of Mexican epiphytic mosses and contribute to their ecological understanding.

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