



Lichen diversity on tree trunks in tropical dry forests is highly influenced by host tree traits

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Abstract

Tropical dry forests have been recognized as one of the most threatened ecosystems in the world due to deforestation. These ecosystems harbour a high endemicity of epiphytes, which play a major role in the functioning of the forests. Lichens constitute an important fraction of the epiphytes. These poikilohydric organisms respond drastically to disturbance, which is strongly linked to humidity and light availability. We hypothesized that richness and species composition of lichens would be related to differences in forest structure (e.g., canopy openness) promoted by deforestation, and by host tree characteristics, due to the fact that dry forests generally have poor microclimatic stratification and low diversity of tree species. In this study, we assessed the richness and composition of epiphytic lichens on the trunks of 513 trees in undisturbed and disturbed dry forests of southern Ecuador. Both lichen composition and richness were highly correlated with tree species and host tree traits such as bark structure and tree diameter. Additionally, epiphytic lichen diversity was related to canopy cover and tree richness at different disturbance levels. We conclude that epiphytic lichen communities in seasonal dry tropical forests of Ecuador are mainly limited by host tree traits and tree species. Loss of epiphytic lichen species in the studied forests is particularly due to loss of host trees such as *Cochlospermum vitifolium* and *Eriotheca ruizii*, that maintain high species richness.

Keywords Bark texture · Ecuador · Epiphytic communities · Forest disturbance · Lichens · Tree species

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Introduction

Tropical dry forests harbour high levels of endemism being one of the most threatened ecosystems in the world (Janzen 1988; Miles et al. 2006; Linares-Palomino et al. 2011; DRYFLOR 2016). These forests have been intensively deforested over time, and a large proportion of the original woodlands has been transformed into isolated fragments, pastures and croplands, due to timber or fuelwood extraction and cattle grazing (Fajardo et al. 2005; Kalacska et al. 2005; Leal-Pinedo and Linares-Palomino 2005). In Ecuador, dry forests are found in the dry interandean valleys located between about 800–2800 m (Quintana et al. 2016) and in the coastal, southwestern part of the country or Tumbesian region (Dinerstein et al. 1995), below 300 m. The latter area is recognized as a hotspot of plant diversity (Linares-Palomino et al. 2010), yet annual deforestation of the Tumbesian dry forests is about 2% with only 5% of the 55,000 km² of remaining dry forests being protected (Linares-Palomino et al. 2010; Sierra 2013).

Although tropical dry forests generally have a lower epiphytic diversity than tropical rain forests (Gentry and Dodson 1987; Werner and Gradstein 2009; Vergara-Torres et al. 2010; de la Rosa-Manzano et al. 2014), they can host relatively high levels of vascular epiphytic endemism (Werner 2008). Understanding how forest disturbance affects epiphytes is critical for the conservation of biodiversity in these threatened ecosystems. Several studies have shown that forest disturbance greatly affects the diversity of epiphytic communities in tropical rain forests (Barthlott et al. 2001; Acebey et al. 2003; Wolf 2005; Gradstein 2008; Gradstein and Sporn 2010; Benítez et al. 2015). However, dry forests have received little attention compared with other types of forest, and studies analyzing the effects of disturbance on the diversity of dry forests are scarce (Gillespie et al. 2000; Avila-Cabadilla et al. 2009; Espinosa et al. 2011; de la Rosa-Manzano et al. 2014). Additionally, very little is known about the effects of disturbance on the epiphytic diversity in these forests (Werner and Gradstein 2009). The latter authors found that in an interandean dry forest of Ecuador, subtle changes in humidity resulted in significant loss of epiphytic bryophyte diversity whereas epiphytic flowering plants were much less affected (Werner and Gradstein 2009). The impact of human disturbance on lichen diversity of tropical dry forests, however, remains unknown.

Lichens are poikilohydric organisms strongly linked to humidity, solar irradiance and temperature (Nash 1996; Green et al. 2008; Kranner et al. 2008). Therefore, changes in the microclimatic conditions produced by wood extraction or grazing (e.g., in air humidity and light availability) may affect the species composition of lichens and bryophytes (Nöske et al. 2008; Gradstein 2008; Gradstein and Sporn 2010; Benítez et al. 2015). Studies in humid tropical forests show that microclimatic changes associated with changes in forest structure (e.g., canopy cover and tree diameter) are principal drivers of epiphytic lichen diversity and distribution in these forests (Wolseley and Aguirre-Hudson 1997; Benítez et al. 2012). However, these insights may not be equally extrapolated to dry forests, due to its peculiar characteristics: (1) strong seasonality of abiotic conditions related with water availability (Mooney et al. 1995), (2) lower and more open forest canopies (Graham and Andrade 2004), and (3) low diversity of tree species (Murphy and Lugo 1986; Gentry 1995). In dry forests, epiphytes generally show little or no stratification in terms of their vertical distribution due to small humidity and light gradients (Benzing 1990; Graham and Andrade 2004). Because of this, epiphytes in dry forests may be more tolerant to microclimatic changes associated with changes in forest structure than in humid forests (Werner and Gradstein 2009).

Host tree traits such as substrate stability (Wolseley and Aguirre-Hudson 1997; Cáceres et al. 2007; Rivas-Plata et al., 2008), texture, pH and water holding capacity of bark (Wolseley and Aguirre-Hudson 1997; Soto-Medina et al. 2012; Rosabal et al. 2013), tree diameter (Aragón et al. 2010; Benítez et al. 2015) and tree age (Fritz et al. 2008; Nascimbene et al. 2009) may have important effects on the species diversity of epiphytic lichens. In addition, studies in temperate forests have revealed a relationship between host tree species and epiphytic lichen diversity (e.g., Barkman 1958; Löbel et al. 2006; Nascimbene et al. 2009; Király and Ódor 2010; Király et al. 2013). However, such relationship has not been found in humid tropical forests (Sipman and Harris 1989; Cornelissen and ter Steege 1989; Cáceres et al. 2007; Soto-Medina et al. 2012; Rosabal et al. 2013). Logging leads to loss of host tree diversity, available host tree traits and thus, potentially to loss of species diversity and changes in composition of epiphytic lichens (Wagner et al. 2015). However, this has not yet been studied in tropical dry forests.

Based on these premises, the goal of this study was to determine which factors influence the diversity of epiphytic lichen communities under contrasting levels of disturbance in tropical dry forests. For this purpose, we compared the species composition and richness of epiphytic lichen communities in undisturbed and disturbed dry forests of southern Ecuador. We hypothesized that lichen diversity and composition would be affected by differences in forest structure (e.g. canopy openness) and microclimate caused by forest logging. We also studied the possible effects of tree species and host tree traits, including bark texture and tree size, on the diversity of the epiphytic communities.

Methods

Study area

The study was conducted in the Ecological Reserve Arenillas (REA), located at 0–300 m in El Oro province, southwestern Ecuador (Fig. 1). The reserve comprises approximately 17 ha and is composed of dry deciduous lowland forest and scrub. The climate is characterized by a distinct rainy season (January–April) with an average precipitation of 515 mm and a dry season with 152 mm (weather station Huaquillas for a recorded period of 45 years, 1969–2014). The average temperature ranges between 21 and 25 °C with a maximum variation of 3.4 °C between the coldest and warmest months.

Fieldwork was carried out in four deciduous forests between January and December 2013, located at 40–70 m a.s.l. We selected two stands of well-preserved forests and two disturbed and managed forest stands within the protected area (Fig. 1). The establishment of military detachments, selective logging, timber extraction and livestock grazing were the main human activities in the disturbed forest areas although only grazing impacts were observed during fieldwork. The most conspicuous tree species in the well-preserved forests were *Bursera graveolens* (Burseraceae), *Cochlospermum vitifolium* (Bixaceae), *Cynophalla mollis* (Capparaceae), *Eriotheca ruizii* (Malvaceae), and *Tabebuia chrysantha* (Bignoniaceae), common shrubs were *Malpighia emarginata* (Malpighiaceae) and several *Croton* species. Disturbed forests are characterized by lower tree and shrub density and the presence of isolated trees. The dominant tree species in the disturbed forests were *C. mollis*, *T. chrysantha* and *Ziziphus thyrsoiflora* (Rhamnaceae). Canopy height was about 25 m in well-preserved forests and 20 m in disturbed forests.

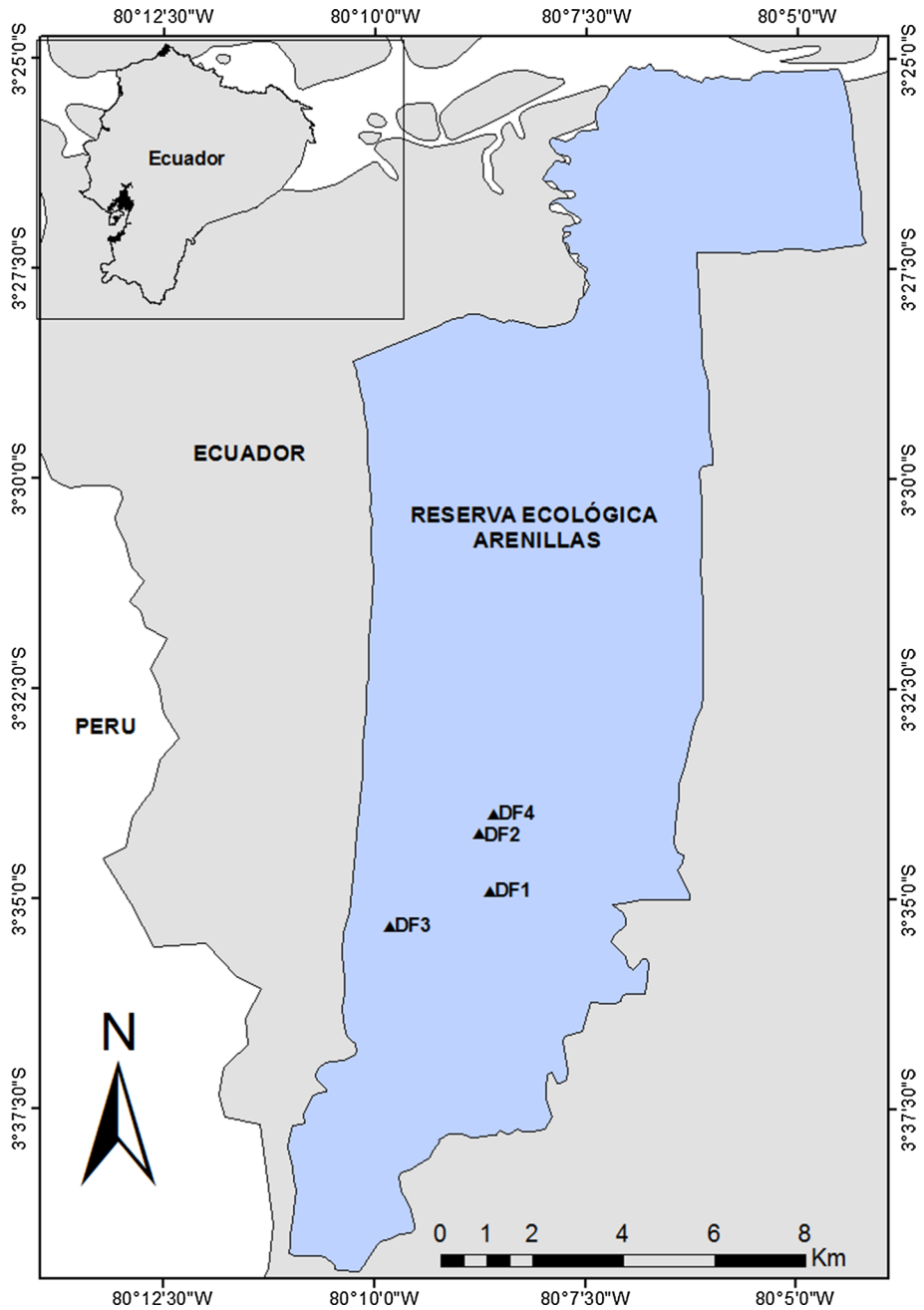


Fig. 1 Map of the study area in the Ecological Reserve Arenillas (REA) in southern Ecuador showing the location of the four tropical dry forest study sites. DF1 and DF2=undisturbed forests; DF3 and DF4=disturbed forests

Sampling design and data collection

Four plots of 20×20 m (400 m²) were randomly selected within each forest stand. The distance between plots within a forest stand was over 100 m. Within each plot, all trees and shrubs with a diameter greater than 5 cm were identified and the diameter at breast height (DBH) was measured. Lichen diversity was studied in a total of 513 trees and shrubs, ca. 11–60 per plot. The presence and cover of epiphytic lichens were estimated using 10×60 cm and 20×30 cm quadrats for shrubs and trees, respectively. The word “tree” in the rest of the paper is used in the broad sense and includes shrubs. Four sampling quadrats were established on each tree, at two different heights (0–100, and 101–200 cm) on the northern and southern sides. In addition, we measured elevation (m a.s.l.), slope (°), aspect (cosine transformed), canopy openness (%) and mean tree diameter (MTD, cm) for each plot as a proxy for forest stand structure (Table 1). For species identification, we used general keys (Brodo et al. 2001; Nash et al. 2002, 2004, 2007) and keys for specific groups (e.g. Egea and Torrente 1993; Tehler 1997; Rivas-Plata et al. 2006; Cáceres 2007; Aptroot et al. 2008, 2014; Lücking et al. 2008, 2009; Rivas-Plata et al. 2010; Aptroot 2012). Total species richness was defined as the total number of species found in the four quadrats per tree. For lichen composition, we calculated the mean estimated cover of each species in the four sampled quadrats.

Light conditions were recorded by measuring percent canopy openness using sixteen digital hemispherical photographs per plot. The distance between photographs within a plot was 5 m. Digital photographs were always taken on overcast days and at breast height (1.3 m), using a horizontally leveled digital camera (Nikon Coolpix 4500) aimed at the

Table 1 Means of the environmental variables in the studied undisturbed (DF1 and DF2) and disturbed (DF3 and DF4) dry forests (two stands with four plots of 20×20 m (400 m²) within of each forest type) in Ecuador

Plot	Forest	Canopy openness (%)	MTD (cm)	Elevation (m a.s.l.)	Slope (°)	Tree richness
1	DF1	19.26	12.89	41	6	10
2	DF1	19.87	16.23	36	2	10
3	DF1	23.68	11.66	43	5	11
4	DF1	23.22	13.33	42	10	14
5	DF2	30.08	11.79	47	4	14
6	DF2	28.10	12.13	46	2	12
7	DF2	28.26	12.31	45	5	12
8	DF2	29.66	13.04	42	8	13
9	DF3	39.80	18.99	68	2	8
10	DF3	42.42	11.61	66	2	8
11	DF3	50.97	26.65	67	6	7
12	DF3	38.09	17.74	69	10	9
13	DF4	41.25	20.89	54	2	8
14	DF4	46.12	24.03	64	4	8
15	DF4	35.05	23.22	60	2	8
16	DF4	39.54	23.77	51	4	6

MTD mean tree diameter

zenith and to the north, using the fish-eye lens (Nikon FCE8). Photographs were analyzed using the software Gap Light Analyzer 2.0 (Frazer et al. 1999).

Measured host tree parameters included diameter at breast height (DBH), tree slope ($^{\circ}$), tree aspect (cosine transformed), bark depth (mm) and bark texture. Bark texture was assessed using five categories: 1 = completely smooth, 2 = smooth without marked fissures, 3 = rough with fissures, 4 = fissured with deep crevices, and 5 = smooth peeling (Mistry 1998; Mistry and Berardi 2005; Vergara-Torres et al. 2010). In addition, host tree species were identified. Several woody species were selected as “potential host trees” (Table 2) based on their commonness in the studied forest stands and the apparent preference of the majority of lichen species for these tree species.

Data analyses

Alpha diversity was calculated using species richness and the Simpson and Shannon diversity indices. The Simpson index is considered as a measure of species dominance whereas the Shannon index is based on the assumption that individuals are randomly selected and that all species are represented in the sample (Magurran 2004). The two diversity indices were calculated per tree and per plot with PRIMER 6.1.11 (Primer-E Ltd., Plymouth, UK).

The effects of host tree species and host tree traits (tree slope, tree aspect, bark depth, bark type and diameter at breast height) on alpha diversity were analyzed separately using Generalized Mixed Linear Models (GLMMs; McCullagh and Nelder 1989) at tree level. In these models, tree species and host tree traits were used as predictors (fixed factors) whereas forest and plot were included as random sources of variation. We assumed Poisson errors for the response variables with the log link function. Effects of random factors were tested using the Wald Z-statistic test and GLMMs were fit using package ‘lme4’ with the function `glmer` (Bates et al. 2013). Following Bolker et al. (2009), we used the Laplace approximation for the likelihood estimates. For GLMMs, the minimal adequate model was selected based on Akaike’s Information Criterion (AIC).

To determine differences between lichen species richness per plot in each forest stand, we used one-way analysis of variance (ANOVA). We tested the normality of distributions of richness with the Shapiro–Wilk test (p value > 0.05). We tested the effect of canopy openness, mean tree diameter (MTD) and tree richness over alpha diversity using GLMMs with a Laplace approximation (Bolker et al. 2009) and with a Poisson error. Data were analysed based on a multi-level approach, considering forest as random factor and introducing the explanatory variables as fixed factors (Bolker et al. 2009). All analyses were performed using R statistical software version 3.1.13 (R Core Team 2015). To test whether the disturbance level was related with composition of epiphytic species and to detect the possible effects of forest, plot and host variability, we performed a three-factor permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008). In this analysis, the experimental design included three factors: forest (four levels, fixed factor), plot (four levels, random factor nested within forest) and host tree (21 levels, random factor nested within plot and forest); the sampled trees constituted the replicates ($n=513$). The cover data (cover percentage of each lichen per tree) were $\log_{10}(x+1)$ transformed to account for contributions by both rare and abundant taxa.

Non-metric multidimensional scaling (NMDS) was performed separately to detect the patterns of species composition in relation to forest structure (forest, canopy openness, mean tree diameter and tree richness), host tree traits (tree slope, tree aspect, bark depth, bark type and diameter at breast height) and host tree species. We used the Bray–Curtis

Table 2 Characteristics of woody tree species and shrubs

Host tree species	Species code	Bark texture	Tree number	MTD (cm, ± SE)	OS (Chao 2; ± SE)
<i>Albizia multiflora</i>	Alb_mult	Fissured with deep crevices	20	8.33 (± 4.03)	28 (32; ± 4.12)
<i>Armatocereus cartwrightianus</i>	Arm_cart	Completely smooth	5	10.96 (± 0.78)	17 (17; ± 0.87)
<i>Bursera graveolens</i>	Bur_grav	Completely smooth	18	21.26 (± 6.52)	33 (61; ± 19.83)
<i>Caesalpinia glabrata</i>	Cas_gla	Smooth peeling	60	15.26 (± 6.97)	16 (35; ± 14.85)
<i>Chloroleucon mangense</i>	Chl_man	Smooth peeling	16	13.55 (± 8.58)	4 (4; ± 1.23)
<i>Cochlospermum vitifolium</i>	Coch_vit	Smooth without marked fissures	29	24.81 (± 11.99)	53 (102; ± 34.04)
<i>Collicodendron scabridum</i>	Coli_sca	Fissured with deep crevices	7	14.84 (± 6.36)	11 (15; ± 4.81)
<i>Croton</i> sp.	Crot_sp	Completely smooth	21	7.78 (± 1.98)	26 (28; ± 3.03)
<i>Cynophalla mollis</i>	Cyn_moll	Rough with fissures	73	9.71 (± 4.21)	38 (42; ± 4.26)
<i>Eriotheca ruizii</i>	Eri_ruiz	Completely smooth	58	18.84 (± 11.05)	58 (87; ± 17.6)
<i>Erythrina velutina</i>	Ery_velu	Smooth without marked fissures	4	30.02 (± 13.77)	11 (14; ± 4.27)
<i>Erythroxylum glaucum</i>	Eryth_gla	Rough with fissures	15	8.88 (± 3.41)	29 (36; ± 5.97)
<i>Geoffroea spinosa</i>	Geof_spi	Fissured with deep crevices	41	12.75 (± 7.11)	42 (75; ± 21.43)
<i>Jacquinia sprucei</i>	Jac_spru	Rough with fissures	2	26.9 (± 5.55)	2 (2; ± 0.13)
<i>Malpighia emarginata</i>	Mal_emar	Rough with fissures	15	10.27 (± 4.78)	17 (18; ± 1.74)
<i>Mimosa acantholoba</i>	Mim_acan	Rough with fissures	12	9.80 (± 5.56)	18 (43; ± 19.6)
<i>Pithecellobium excelsum</i>	Pith_exc	Rough with fissures	11	7.48 (± 1.84)	25 (33; ± 6.77)
<i>Randia aurantiaca</i>	Ran_aura	Rough with fissures	4	6.7 (± 1.17)	10 (11; ± 2.25)
<i>Tubebuia billbergii</i>	Tab_bill	Fissured with deep crevices	63	19.53 (± 9.96)	45 (57; ± 10.07)
<i>Tubebuia chrysantha</i>	Tab_chry	Fissured with deep crevices	20	22.78 (± 10.39)	40 (52; ± 8.6)
<i>Ziziphora thyrsoiflora</i>	Ziz_thyr	Rough with fissures	20	8.49 (± 4.56)	28 (36; ± 6.87)

Trees selected as potential host trees are in bold

Species richness of lichens on the host trees is indicated as observed species (OS)

Chao 2 estimated total richness, MTD mean tree diameter, SE standard error, Tree number number of sampled trees per species

dissimilarity distance to compute the resemblance matrix between trees. The results were plotted in a NMDS ordination diagram. Values of the relative species cover and tree species, host tree traits and forest structure were then fitted into the first two axes of the NMDS ordination. Squared correlation coefficients (r^2) and empirical p -values (p) were calculated for these linear fittings. The analyses were performed with package ‘vegan’ (Oksanen et al. 2013) using R software.

Results

A total of 122 epiphytic lichen species were recorded and collected from 513 trees (“Appendix 1”). One hundred and eight species were registered in undisturbed forests, whereas 90 species were found in disturbed forests. The highest epiphytic lichen richness was found in non-disturbed forests (90% of total richness, versus 74% in disturbed forests; Fig. 2c), with 28 exclusive species (“Appendix 1”), 18 of which were found on only one or two trees. In contrast, eleven species occur exclusively in the disturbed forests. Lichen communities were dominated by crustose lichens, with 110 species (90% of all species), followed by foliose and fruticose species with eleven and one species respectively. The most frequent lichen species were *Coniocarpon cinnabarinum*, *Dirinaria picta*, *Lecanora helva*, *Leucodecton occultum*, *Opegrapha trilocularis*, *Pseudopyrenula subnudata* and *Syncesia leproloba*, which were found in more than 100 sampled trees. The highest lichen richness, including the highest values for estimated richness (Chao 2), were found on tree

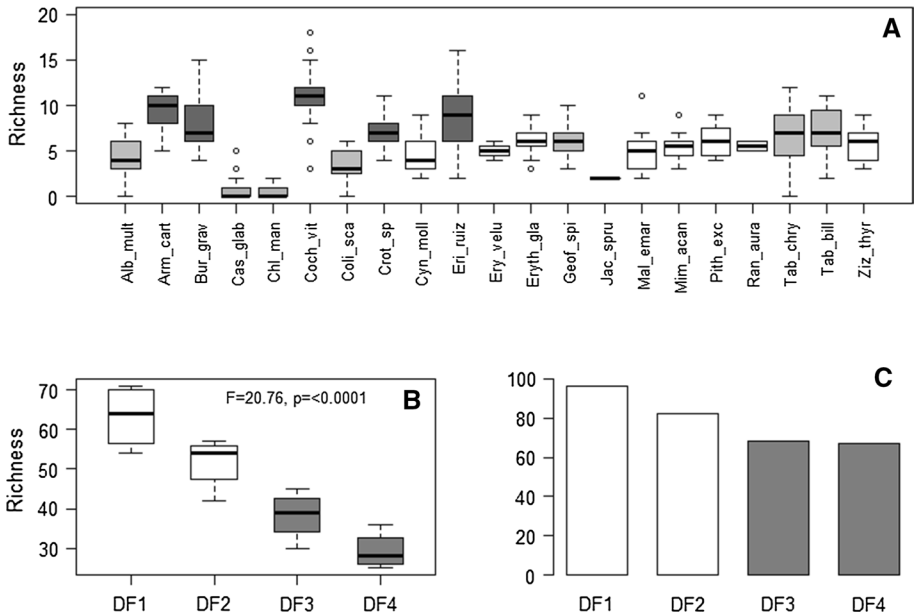


Fig. 2 Species richness of epiphytic lichens in the two studied dry forest types **a** host tree species and codes (Table 2), tree with smooth bark (black), rugose bark (white) and fissured bark (grey); **b** maximum, minimum and median richness values and lower and upper quartiles at plot level, F f value and P p value of ANOVA analysis, and **c** richness at forest level. DF1 and DF2=undisturbed forests, DF3 and DF4=disturbed forests. Axis X, forest type; Axis Y, lichen species richness

species with smooth bark, like *B. graveolens*, *C. vitifolium* and *E. ruizii*, while trees with fissured and peeling bark such as *Caesalpinia glabrata*, *Chloroleucon mangense*, *C. mollis* and *Z. thyrsoflora* were much poorer in lichen species (Table 2, Fig. 2a).

Host tree species had a significant effect on species richness and diversity (Table 3). Thus, *B. graveolens*, *C. vitifolium* and *E. ruizii* showed the highest and positive coefficients for lichen species richness and Shannon and Simpson indices, while the coefficients for *C. glabrata*, *C. mangense*, *C. mollis*, *Geoffroea spinosa*, *Tabebuia billbergii*, *T. chrysantha* and *Z. thyrsoflora* had the lowest values (Table 3). Correlations between lichen diversity and the random variables “forest” and “plot” were not significant.

Host tree traits including bark texture, bark depth and DBH showed significant effects on lichen richness and diversity indices (Table 4). Additionally, canopy openness and DBH had negative effects on lichen species richness and diversity indices at tree level. At plot level, lichen richness was different in each forest type (Fig. 2b); both canopy openness and tree richness were the main factors affecting lichen species richness (Table 4).

Multivariate statistical analyses showed that epiphytic lichen composition was structured according to the different spatial scales (forests, plot and tree), but a large component of variation (i.e. 40%) was associated with the tree level, followed by forest and plot with 17% and 10%, respectively (Table 5).

Tree species and host tree traits showed a significant relationship with the NMDS ordination axes (Table 6). These correlations were strong with tree species, bark texture and depth, and diameter at breast height (DBH) on the two axes of the species ordination (Table 6). Host tree species, bark structure and DBH were the most relevant predictors of epiphytic lichen communities in the studied forests (Fig. 3). Host trees with smooth bark and a large diameter (e.g., *B. graveolens*, *C. vitifolium* and *E. ruizii*) showed the greatest occurrence of crustose lichens of the family Graphidaceae (*Fibrillithecia*, *Glyphis*, *Graphis*, *Leucodecton*, *Phaeographis*, *Schismatomma*). In contrast, the lichen genera *Bathelium*, *Caloplaca*, *Cresponea*, *Opegrapha* and *Trypethelium* were more abundant on trees with fissured bark including *C. mollis*, *G. spinosa*, *T. billbergii*, *T. chrysantha* and *Ziziphus thyrsoflora*.

Discussion

Our results indicate that host traits (i.e. bark texture and tree diameter) and tree species are important determinants for epiphytic lichen diversity in tropical dry forests. The majority of the lichen species preferred a small group of host trees with specific traits. Additionally, forest disturbance seemed to have a negative impact on epiphytic lichen diversity, promoting the loss of richness, diversity and changes in the species composition. This loss was related to changes in forest structure (i.e. canopy openness) and, particularly, with the removal of potential host trees.

Deforestation causes loss of tree species diversity. In the disturbed forests studied, shrub vegetation was absent and diversity and abundance of potential host trees for epiphytic lichens (e.g. *C. vitifolium* and *E. ruizii*) was lower than in undisturbed forest. Our results suggest that the higher diversity of the forest tree community helps to maintain lichen richness and diversity in tropical lowland dry forests. Several studies in temperate and boreal forests have also shown that tree diversity is a key factor for epiphyte richness and composition (Nascimbene et al. 2009; Király et al. 2013; Sales et al. 2016). Correlations between epiphytic diversity and host tree species have been found in forests with low tree diversity,

Table 3 Results of the Generalized Linear Mixed Models showing the effects of host tree species on the richness and diversity of epiphytic lichens

Tree species	Richness			Shannon index			Simpson inverse index		
	Coef.	Z	P	Coef.	Z	P	Coef.	Z	P
	<i>Albizia multiflora</i>	0.4662	11.373	<0.0001	0.2232	15.106	<0.0001	0.3427	10.542
<i>Armatocereus cartwrightianus</i>	0.6032	3.152	0.0016	0.4693	2.592	0.0098	0.5115	0.722	0.4709
<i>Bursera graveolens</i>	0.5198	3.692	0.0002	0.4591	3.903	0.0001	1.2740	2.765	0.0058
<i>Caesalpinia glabrata</i>	-2.0573	-10.153	<0.0001	-1.1086	-11.856	<0.0001	-2.8530	-7.792	<0.0001
<i>Chloroleucon mangense</i>	-2.3255	-5.901	<0.0001	-1.1950	-9.839	<0.0001	-2.9436	-6.189	<0.0001
<i>Cochlospermum vitifolium</i>	0.9056	7.330	<0.0001	0.7951	7.554	<0.0001	2.9788	7.227	<0.0001
<i>Colicodendron scabridum</i>	-0.2376	-1.022	0.3068	-0.3026	-1.903	0.0576	-1.0269	-1.649	0.0997
<i>Croton</i> sp.	0.3266	2.288	0.0221	0.4907	4.337	<0.0001	1.6478	3.719	0.0002
<i>Cynophalla mollis</i>	-0.0084	-0.069	0.9451	0.0005	0.006	0.9948	-0.1359	-0.380	0.7043
<i>Eriotheca ruizii</i>	0.6373	5.351	<0.0001	0.4928	5.248	<0.0001	1.1974	3.256	0.0012
<i>Erythrina velutina</i>	0.0818	0.327	0.7438	0.1400	0.706	0.4806	0.1404	0.181	0.8566
<i>Erythroxylum glaucum</i>	0.2243	1.453	0.1462	0.2810	2.272	0.0234	0.5840	1.206	0.2285
<i>Geoffroea spinosa</i>	0.2874	2.269	0.0232	0.3133	3.173	0.0016	0.7504	1.940	0.0529
<i>Jacquinia sprucei</i>	-0.896	-1.745	0.0809	-1.1133	-4.145	<0.0001	-2.2948	-2.182	0.0295
<i>Malpighia emarginata</i>	0.0023	0.015	0.9883	0.0992	0.802	0.4229	0.1856	0.383	0.7017
<i>Mimosa acantholoba</i>	0.2437	1.471	0.1412	0.2543	1.923	0.0550	0.6903	1.333	0.1830
<i>Pithecellobium excelsum</i>	0.3511	2.109	0.0349	0.2856	2.101	0.0361	0.4392	0.825	0.4096
<i>Randia aurantiaca</i>	0.0333	0.134	0.8933	0.2627	1.325	0.1858	0.4414	0.568	0.5700
<i>Tabebuia billbergii</i>	0.4825	4.023	<0.0001	0.4941	5.317	<0.0001	1.7165	4.717	<0.0001
<i>Tabebuia chrysantha</i>	0.3719	2.590	0.0095	0.3326	2.905	0.0038	1.2544	2.797	0.0053
<i>Ziziphus thyrsoiflora</i>	0.3609	2.443	0.0145	-0.007	-0.062	0.9506	-0.4078	-0.910	0.3635

Coef. coefficient, Z z value, P p value

Table 4 Results of the Generalized Linear Mixed Models of community traits in relation with host tree traits and plot characteristics

Host tree traits	Richness			Shannon index			Simpson inverse index		
	Coef.	Z	P	Coef.	Z	P	Coef.	Z	P
	Tree aspect	0.0161	0.5420	0.5877	0.0034	0.205	0.8378	-0.0059	-0.236
Diameter at breast height	-0.0030	-1.1260	0.2600	-0.0042	-2.632	0.0084	-0.0056	-2.451	0.0142
Tree slope	-0.0041	-2.2380	0.0252	-0.0026	-2.526	0.0115	-0.0034	-2.228	0.0259
Bark depth	0.2628	1.7890	0.0736	0.2393	2.985	0.0028	0.2409	2.053	0.0401
Bark texture									
Completely smooth	2.8097	14.2830	<0.0001	0.9892	6.028	<0.0001	2.0720	9.872	<0.0001
Fissured with depth crevices	-0.4104	-3.8830	0.0001	-0.2064	-3.483	0.0004	-0.1539	-1.773	0.0763
Rugose with fissures	-0.6485	-7.8890	<0.0001	-0.4220	-8.706	<0.0001	-0.4568	-6.104	<0.0001
Smooth with fissures	0.3091	4.1920	<0.0001	0.2171	5.172	<0.0001	0.36384	6.368	<0.0001
Smooth peeling	-2.8443	14.0380	<0.0001	-0.0639	-1.540	<0.0001	-0.1452	1.880	<0.0001
Canopy openness	-0.0097	-2.6370	0.0083	-0.0056	-1.409	0.1588	-0.0060	-1.183	0.2368
Plot characteristics									
Canopy openness	-0.0139	-2.3820	0.0172	0.0014	0.5430	0.5874	0.0141	2.1580	0.0609
Tree richness	0.0861	3.8500	0.0001	0.0187	2.9310	0.0033	0.0446	3.9070	<0.0001
MTD	-0.0037	-0.2970	0.7667	-0.0047	-1.4950	0.1349	-0.0368	-4.1350	0.0856

DBH diameter at breast height, *MTD* mean tree diameter, *Coef.* coefficient, *Z* z value, *P* p value

Table 5 Results of three-factor PERMANOVA analysis of species composition by forest, plot and host tree

Source	df	MS	Pseudo-F	<i>P</i>	CV (%)
Forest	3	33307.0	7.7048	0.001	17.048
Plot (Forest)	12	4247.6	2.8899	0.001	10.574
Host tree	21	32153.0	11.1470	0.001	40.199
Error	299	1469.8			38.338

Significant values ($p < 0.05$) are shown in bold

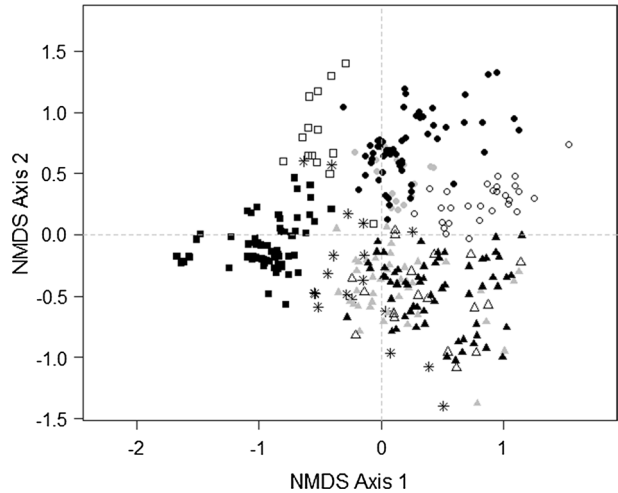
df degrees of freedom, *MS* mean sum of squares, *Pseudo-F* F value obtained by permutation, *P* p-value, *CV* coefficient of variation

Table 6 Squared correlation coefficients (r^2) fitted on the first two axes of the NMDS ordination for host tree species, host tree traits and environmental factors

	NMDS1	NMDS2	r^2	<i>P</i>
Host tree species			0.7176	0.0009
<i>Albizia multiflora</i>	−0.2752	−0.2355		
<i>Bursera graveolens</i>	0.2240	0.4810		
<i>Cochlospermum vitifolium</i>	0.8249	0.2226		
<i>Cynophalla mollis</i>	−0.9703	−0.0340		
<i>Eriotheca ruizii</i>	0.3118	0.7362		
<i>Geoffroea spinosa</i>	0.1234	−0.4201		
<i>Tabebuia billbergii</i>	0.4070	−0.4862		
<i>Tabebuia chrysantha</i>	0.3310	−0.5231		
<i>Ziziphus thyrsoiflora</i>	−0.4341	0.4035		
Host tree traits				
Diameter at breast height	0.9956	0.0927	0.3421	0.0010
Bark depth	0.0675	−0.9977	0.5044	0.0010
Bark type			0.6534	0.0010
Completely smooth	0.2919	0.6784		
Fissured with depth crevices	0.2229	−0.4379		
Rugose with fissures	−0.8679	0.0496		
Smooth with fissures	0.8249	0.2226		
Tree aspect	0.8815	0.4721	0.0013	0.8101
Tree slope	−0.9912	0.1316	0.0090	0.2168
Environmental factors				
Canopy openness	0.9337	−0.3578	0.0279	0.0110
Forests			0.0320	0.0030
DF1	−0.0973	0.0681		
DF2	−0.0412	−0.0450		
DF3	0.2821	−0.1174		
DF4	0.0707	0.0001		
MTD	0.8866	−0.4624	0.0613	0.0010
Tree richness	−0.6971	0.7169	0.0510	0.0020

Significant values ($p < 0.05$) with strong correlations are shown in bold
DBH diameter at breast height, *MTD* mean tree diameter, *P* p value.
DF1 and *DF2* undisturbed forests; *DF3* and *DF4* disturbed forests

Fig. 3 Non-metric multidimensional scaling analysis of species composition for the samples (host trees) in the four studied dry forests. *Albizia multiflora* (asterisk); *B. graveolens* (gray colour filled circle); *C. vitifolium* (open circle); *C. mollis* (filled square); *E. ruizii* (filled circle); *G. spinosa* (open triangle); *T. billbergii* (filled triangle); *T. chrysantha* (gray colour filled triangle); *Z. thyrsoiflora* (open square)



such as temperate forests and dry forests (Löbel et al. 2006; Nascimbene et al. 2009; Vergara-Torres et al. 2010; Király and Ódor 2010; Király et al. 2013; Sales et al. 2016). In contrast, in humid tropical forests tree diversity is high and relationships with host trees are absent because usually there are more than one tree species with shared traits (Sipman and Harris 1989; Cáceres et al. 2007; Gradstein and Culmsee 2010; Soto-Medina et al. 2012; Rosabal et al. 2013). Seasonal dry tropical forests, in contrast, such as the forests studied here, are characterized by low tree species diversity (Murphy and Lugo 1986; Gentry 1995). Therefore, much of the variability of the lichen species richness, diversity and composition could be explained by trunk traits of the host tree species, emphasising their importance for epiphytic lichens.

Host tree traits affecting the richness, diversity and composition of epiphytic lichens are related with substrate quality (i.e. bark texture and bark depth), which depends on the host tree species. Thus, host trees with a smooth bark (*C. vitifolium* and *E. ruizii*) had higher lichen species richness and diversity than trees with fissured (e.g., *C. mollis*) or peeling bark (*C. glabrata*), which were much poorer in lichen species. Similarly, Löbel et al. (2006), Cáceres et al. (2007) and Rosabal et al. (2013) found a negative correlation between bark roughness and species richness of lichens (although only for those with a crustose growth form). Host trees such as *B. graveolens*, *C. vitifolium* and *E. ruizii* with a smooth bark hosted a different epiphytic lichen community than trees with a fissured bark like *C. mollis* and *T. billbergii*. In accordance, Fritz and Brunet (2010) showed that several crustose lichens were associated with smooth-barked mature trees, and distributionally limited primarily by the availability of smooth bark.

We observed that crustose lichens were dominant in the dry forest and preferred smooth-barked hosts. This could be related to the closely attached growth of the thin thalli on the bark surface, being tightly anchored to the substrate by means of the medullary hyphae (Büdel and Scheidegger 2008). The observed changes in epiphytic lichen composition may thus be explained by the substrate requirements of the lichen species. The preference we found of Graphidaceae and several other genera of crustose lichens (e.g., *Stirtonia* and *Syncesia*) for smooth bark and of other genera (*Bathelium*, *Caloplaca*, *Cresponea*, *Opegrapha*, *Physcia* and *Trypethelium*) for fissured bark is in accordance with the literature (e.g., Wolseley and Aguirre-Hudson 1997; Aptroot and Sparrius 2008; Rivas-Plata et al. 2008;

Bungartz et al. 2010; Cáceres et al. 2007). In addition, bark characteristics such as bark stability, water-holding capacity and pH, which were not analyzed in this study and are considered important factors determining the distribution and establishment of epiphytic lichen communities (Löbel et al. 2006; Cáceres et al. 2007; Gradstein and Culmsee 2010; Soto-Medina et al. 2012; Rosabal et al. 2013), may have affected the local lichen diversity.

We also found that epiphytic lichen composition was significantly influenced by diameter at breast height. This idea is supported by other studies that have also found a relationship between the epiphytic composition and the tree diameter or tree age (Nascimbene et al. 2009; Marmor et al. 2011; Aragón et al. 2010; Soto-Medina et al. 2012; Rosabal et al. 2013; Benítez et al. 2015). However, lichen species richness at plot level declined with increased DBH. This result is in contrast with previous studies (e.g., Fritz et al. 2008; Lie et al. 2009; Benítez et al. 2015), which demonstrate that epiphytic lichen diversity was highest on old and big trees. Our finding might be explained in part by the presence of a relatively high number of large trees (ca. 75 trees) of *C. glabrata* and *C. mangense* in the undisturbed forests with low lichen richness (one or two species per tree) due to bark shedding.

The negative relationship found in this study between canopy openness and epiphyte richness and diversity is a general phenomenon in tropical forests (Gradstein 2008; Li et al. 2013; Benítez et al. 2012, 2015). Werner and Gradstein (2009) found that disturbance in tropical dry forests related with canopy disruption caused severe loss of epiphytic bryophyte diversity whereas vascular epiphytes were much less affected, although these results were restricted to monospecific forests of *Acacia macracantha*. Studies in montane rainforests showed that forest disturbance creates a drier microclimate due to canopy disruption that affects negatively the richness and diversity of non-vascular epiphytes (Nöske et al. 2008; Li et al. 2013; Benítez et al. 2015). For example, studies in southern Ecuador showed that the number of non-vascular epiphytic species decreased severely from primary forests towards secondary vegetation, with a most severe decline in species number in secondary monospecific stands of *Alnus acuminata* (Werner and Gradstein 2009; Benítez et al. 2012, 2015, 2018). In the present study, species richness was lower in disturbed dry forests with ca 45% canopy openness in comparison with undisturbed forests (ca 25% openness). However, our results show that lichen richness in these tropical dry forests is less influenced by disruption of the canopy than by changes in host tree traits.

Conclusions and implications for conservation

We conclude that tree species composition and diversity play an important role in shaping epiphytic lichen communities in the seasonally tropical dry forests, with the main drivers being host traits (e.g. bark texture and tree diameter) and tree species. In addition, our study shows that disturbance of dry tropical forests reduces lichen epiphytic diversity by the removal of host trees especially through the loss of species such as *C. vitifolium* and *E. ruizii*, that have harbour high lichen species richness. Protection of the undisturbed forests remnants, with a high host tree diversity and potential host trees, is necessary to preserve the richness and diversity of epiphytic lichen communities of these Ecuadorian dry forests.

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Appendix 1

See Table 7.

Table 7 Lichen species and number of trees on which each species appears in the four forests

Taxa	DF1	DF2	DF3	DF4
<i>Arthonia</i> aff. <i>antillarum</i>	5*			
<i>Arthonia antillarum</i>	22	15	14	5
<i>Arthonia</i> aff. <i>conferta</i>		1*		
<i>Arthonia elegans</i>	4		1	
<i>Arthonia pruinata</i>	6	3	2	
<i>Arthonia</i> sp.	1	1		
<i>Bacidia</i> sp. 1	5	4		1
<i>Bacidia</i> sp. 2		1*		
<i>Bacidia</i> sp. 3	2	8		
<i>Bactrospora denticulata</i>				8*
<i>Bactrospora myriadea</i>			2*	
<i>Bathelium degenerans</i>	14	3	3	7
<i>Buellia</i> sp.	8	4	5	
<i>Caloplaca</i> sp.	5	12	14	1
<i>Caloplaca wrightii</i>	4	1	5	2
<i>Coccocarpia pellita</i>		1*		
<i>Coenogonium pineti</i>	4	4		
<i>Coniocarpon cinnabarinum</i>	139	97	26	26
<i>Chapsa dilatata</i>	2*			
<i>Chapsa diploschistoides</i>	2	16		
<i>Chapsa</i> sp.	1*			
<i>Cresponea flava</i>	6	17	7	4
<i>Cryptothecia striata</i>		1	1	
<i>Chrysothrix</i> sp.	1		2	4
<i>Chrysothrix xanthina</i>	1	9	20	5
<i>Dirinaria aegialita</i>			4*	
<i>Dirinaria</i> aff. <i>aegialita</i>	4	2		
<i>Dirinaria</i> aff. <i>confluens</i>			2	8
<i>Dirinaria applanata</i>	1	2		
<i>Dirinaria confluens</i>			1	1
<i>Dirinaria papillulifera</i>	8	13	6	7
<i>Dirinaria picta</i>	35	39	23	20
<i>Dirinaria</i> sp.				1*
<i>Diplolabia afzelii</i>	2*			
<i>Enterographa compunctula</i>	18	1		

Table 7 (continued)

Taxa	DF1	DF2	DF3	DF4
<i>Enterographa quassiaecola</i>	1	2		
<i>Fibrillithecis halei</i>	5	4	1	1
<i>Fissurina incrustans</i>		1*		
<i>Fissurina</i> aff. <i>nitidescens</i>	5	1		1
<i>Fissurina egena</i>		3	1	
<i>Fissurina</i> sp.	1	4		
<i>Glyphis scyphulifera</i>	6	8	6	4
<i>Glyphis cicatricosa</i>	3	2		2
<i>Graphis</i> aff. <i>dendrogramma</i>	5*			
<i>Graphis</i> aff. <i>subcontorta</i>	1		1	
<i>Graphis anfractuosa</i>	23	4	2	3
<i>Graphis argentata</i>	4	10	1	4
<i>Graphis dendrogramma</i>	31	13	4	6
<i>Graphis leptoclada</i>	12*			
<i>Graphis subcontorta</i>	45	37	10	1
<i>Graphis caesiella</i>	2*			
<i>Graphis</i> sp.	8	6	3	1
<i>Gyalidea</i> sp.	4	6		
<i>Haematomma</i> aff. <i>nicoyense</i>			1*	
<i>Helminthocarpon leprevostii</i>	3*			
<i>Herpothallon</i> sp.	31	12	19	2
<i>Hyperphyscia adglutinata</i>		1	2	
<i>Lecanographa laingiana</i>	13	8	13	
<i>Lecanographa illecebrosula</i>			1*	
<i>Lecanographa lyncea</i>	7	13	2	2
<i>Lecanora chlarotera</i>	1	3		
<i>Lecanora helva</i>	50	39	15	12
<i>Lecanora</i> sp. 1	6	1	4	1
<i>Lecanora</i> sp. 2	4*			
<i>Lecanora</i> sp. 3			1*	
<i>Leptogium cyanescens</i>		1*		
<i>Leucodecton occultum</i>	52	53	13	6
<i>Lithothelium illotum</i>	10	2	1	1
<i>Mazosia carnea</i>	8	1		
<i>Megalospora sulphurata</i> var. <i>sulphurata</i>		1*		
<i>Melaspilea</i> sp.			1*	
<i>Mycoporum eschweileri</i>	1		1	
<i>Ocellularia</i> sp.	1	4		
<i>Oppegapha</i> aff. <i>vulgata</i>	6*			
<i>Oppegapha difficilior</i>	40	22	6	3
<i>Oppegapha trilocularis</i>	55	53	34	12
<i>Oppegapha</i> sp.	6*			
<i>Parmotrema exquisitum</i>	2	1		3
<i>Pertusaria texana</i>	3*			
<i>Pertusaria</i> sp. 1	1*			

Table 7 (continued)

Taxa	DF1	DF2	DF3	DF4
<i>Pertusaria</i> sp. 2	14	4	11	1
<i>Phaeographis punctiformis</i>				1*
<i>Phaeographis decipiens</i>	1*			
<i>Phaeographis inusta</i>	7	2		
<i>Phaeographis subtrigina</i>	4	2		
<i>Phaeographis intricans</i>	18	4	4	2
<i>Phaeographis lobata</i>				1*
<i>Phaeographis brasiliensis</i>	20	15	2	1
<i>Phaeographis</i> sp. 1		1*		
<i>Phaeographis</i> sp. 2	1*			
<i>Porina nucula</i>			1*	
<i>Porina tetracerae</i>	1	4	1	
<i>Physcia crispa</i>		5	3	1
<i>Physcia endochrysea</i>	3	28	5	6
<i>Physcia solediosa</i>	15	21	14	7
<i>Phyllopsora</i> sp.	40	55	7	4
<i>Polymeridium subcinereum</i>	25	1		
<i>Pyrenula erumpens</i>	40	26	4	3
<i>Pyrenula immissa</i>	9	25		
<i>Pyrenula ochraceoflava</i>	34	12	3	
<i>Pyrenula psoriformis</i>	2*			
<i>Pyrenula subcongruens</i>	34	18		
<i>Pseudopyrenula diluta</i>	12	5		1
<i>Pseudopyrenula subnudata</i>	68	49	24	16
<i>Pyxine cocoës</i>	2	1	10	8
<i>Ramalina darwiniana</i> var. <i>darwiniana</i>			1	3
<i>Ramonia valenzueliana</i>	1*			
<i>Rinodina</i> sp.	2	6	3	1
<i>Sarcographa tricola</i>	22	24	4	6
<i>Schismatomma spierii</i>	5	10	7	3
<i>Stigmatochroma gerontoides</i>		1*		
<i>Stirtonia dubia</i>	5*			
<i>Stirtonia ramosa</i>	36	8	4	
<i>Stirtonia</i> sp.	15		2	
<i>Syncesia effusa</i>	2	7	1	
<i>Syncesia glyphysoides</i>	2*			
<i>Syncesia leprobola</i>	107	20	8	1
<i>Syncesia farinacea</i>	3		1	1
<i>Syncesia graphica</i>	5	4	3	2
<i>Tephromela atra</i>	15	8	3	1
<i>Thelotrema</i> sp.	1*			
<i>Trypethelium eluteriae</i>	9	10	4	15

Asterisks denote exclusive species per forest

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