# Functional traits of epiphytic lichens in response to forest disturbance and as predictors of total richness and diversity

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## ABSTRACT

Epiphytic lichens are good ecological indicators of climatic and environmental changes. The physiology of lichens is related with their morphology and anatomy (traits) and thus the response to changes in the environment could be related with these traits. In this study we evaluate lichen functional traits to understand the mechanisms of community assembly in response to deforestation of tropical montane forests in Ecuador. Based on this, we propose and indicator value as a complement to evaluate the disturbance level of forests. Finally, we evaluate the use of selected functional traits to infer total species richness and diversity of tropical montane forests. We assessed nine different traits related with photobiont type, growth form, reproductive strategy and chemistry of epiphytic lichens on the trunk bases of 240 trees in three types of forests according to a disturbance gradient (primary forests and secondary vegetation). Most functional traits of the lichen communities were related to structural changes (i.e canopy cover and tree diameter) along the forest disturbance gradient. Several functional groups of lichens as cyanolichens, and those with a gelatinose, filamentose and squamulose growth forms and species without secondary compounds were more abundant in primary forests. On the other hand, fruticose, foliose species with narrow lobes, and with lirellae were most abundant in disturbed forest. Growth forms are useful to infer total lichen richness and diversity in montane tropical forests. Based on these results we recommend the use of lichen functional traits as a tool and a complement for conservation studies and forest management.

## 1. Introduction

Despite tropical montane rain forests are among the richest biologically and ecologically ecosystems in the world, they are disappearing at alarming rates due to anthropogenic threats (Myers et al., 2000; Gardner et al., 2009; Laurance et al., 2011; Gibson et al., 2011). A large proportion of the original landscapes of montane rain forests have been transformed into secondary vegetation, croplands or grasslands in order to satisfy human needs related with food, fiber, timber, and other goods (Dirzo and Raven, 2003; Foley et al., 2005; Chazdon, 2008; Gibbs et al., 2010). Consequently, this scenario of rapid deforestation and forest conversion has caused the decline and disappearance of numerous organisms (Lawton et al., 1998; Sillett and Antoine, 2004; Kessler et al., 2005; Gray et al., 2007; Nöske et al., 2008). Among these, lichens are a significant part in terms of diversity, biomass and nutrient cycling (Holz and Gradstein, 2005), and are also affected by forest logging and deforestation (Gradstein, 2008; Nöske et al., 2008; Aragón et al., 2010; Benítez et al., 2015).

Numerous studies have used the species richness and diversity to understand the impact of forest disturbance on communities, but sometimes these data are not sufficient to fully understand the ecological processes shaping these communities (Lawton et al., 1998; Schulze et al., 2004; Gradstein and Sporn, 2010). An alternative approximation to understand the mechanisms of community assembly and thus, how communities will respond to rapid environmental changes (*e.g.* forest disturbance) is to consider functional traits, as they are directly related to biotic and abiotic factors (Díaz et al., 2007; Laliberté et al., 2010; Webb et al., 2010; Pinho et al., 2012; Carreño-Rocabado et al., 2016).

Lichens are sensitive indicators of climatic conditions, because their poikilohydric physiology depends directly on water availability, surrounding temperature and light received (Nash, 1996; Green et al., 2008; Kranner et al., 2008). Thus, they are related to environmental changes as land use (Pinho et al., 2012), forest disturbance (Nöske et al., 2008), forest management (Aragón et al., 2010; Nascimbene et al., 2013; Pinho et al., 2016); fragmentation (Belinchón et al., 2007; Cardós et al.,2016), forests sucession (Koch et al., 2013), air pollution

(Käffer et al., 2011; Pinho et al., 2011; Llop et al., 2012; Munzi et al., 2014; Paoli et al., 2015), nitrogen deposition (Giordani et al., 2014; McMurray et al., 2015) or climate change (Matos et al., 2015; Nascimbene et al., 2016).

Forests conversion and logging alter microclimatic conditions related with moisture and light. Lichens present functional strategies related with their photobionts, growth form, reproduction strategy, presence of cortical pigments and secondary metabolites which depend on the environmental conditions and provide (dis)-advantages to them (Kranner et al., 2008; Marini et al., 2011; Giordani et al., 2012; Hauck et al., 2013). Previous studies have shown that several functional traits as photobiont type, growth form, reproductive structure and chemistry are directly related to microclimatic factors associated with forest structure (*e.g.* canopy cover, and tree age) and abiotic factors as humidity, temperature and light availability (Ellis and Coppins, 2006; Pinho et al., 2012; Li et al., 2013; Prieto et al., 2017).

In order to study the diversity of lichens it would be very useful to use indicator species instead of using species, genera or families due to the effort required for identification and sampling (Bergamini et al., 2005, 2007; Aragón et al., 2013). Several studies related with non-vascular epiphytes (bryophytes and lichens) suggest that the richness of growth forms is a robust estimator for detection of species richness of bryophytes and lichens in biodiversity hotspots as tropical forests and Mediterranean forests (Oishi, 2009; Pardow et al., 2012; Aragón et al., 2016). Therefore, from a conservation perspective, the use of easily recognizable growth forms in lichens could be used to detect areas of high lichen biodiversity.

Our main goal was to evaluate changes in lichen functional traits in relation with the disturbance level of tropical montane rainforests. We hypothesized that forest structure, in particular, canopy cover and tree diameter, would affect the individual species traits and the community weighted mean (CWM). Second, we suspect that the richness of growth forms would be an indicator of total species richness and diversity of lichens. Specifically, we addressed the following questions: 1) how do the richness of each functional trait and the CWM respond to forest disturbance? 2) can lichen functional traits be used as indicators of forest disturbance?, and 3) can the total lichen species richness and diversity be predicted by the richness of growth forms alone?

## 2. Materials and methods

### 2.1. Study area

Experimental design and details of the geographical location of the study is detailed in Benítez et al. (2012; 2015), and only a brief summary is included here. The survey was conducted in six remnants of tropical montane forests in southern Ecuador. The climate is humid tropical with a mean annual temperature of 20 °C, annual rainfall of ca. 1900 mm and relative humidity of ca. 80% (data from the National Institute of Meteorology and Hydrology, INAMI). The altitude of the studied remnants ranged from 2200 to 2800 m a.s.l. These forests were chosen to cover a disturbance gradient, with the following three categories: (1) remnant primary forest fragments (PF) of evergreen montane tropical vegetation characterized by a dense canopy layer and large trees, (2) secondary forest fragments (SF) that have regrown after selective logging events which took place some 40 years ago and (3) secondary monospecific vegetation (MF) dominated by *Alnus acuminata* Kunth which have regrown after a total logging of the original forests, and are characterized by a more open canopy cover and young trees.

### 2.2. Sampling design and data collection

Two forests per disturbance category were studied. Within each forest, we established 10 plots, of 5 m x 5 m each. In each plot, four trees were selected to estimate the occurrence of epiphytic lichens. For these trees, lichen frequency and coverage were visually estimated on

**Table 1**
Functional trait categories and codes.

| Functional trait | Categories |
|---|---|
| Photobiont type | C = Chlorococcoid; CY = Cyanobacteria; T = Trentepohlia |
| Growth form | C = Crustose; CP = Crustose with prothallus; FB = Foliose with broad lobes; FN = Foliose with narrow lobes; FP = Foliose placodiod; FL = Filamentose; F = Fruticose, G = Gelatinose; S = Squamulose |
| Size | M = Macrolichens; MC = Microlichens |
| Reproduction type | A = Asexual; S = Sexual; AS = Asexual and sexual; N = None |
| Reproductive structure | A = Apothecia; I = Isidia; L = Lirellae; P = Perithecia; S = Soredia |
| Ascospores septation | S = Simple; S = Septate; M = Muriform |
| Ascospores size[a] | S = Small ($< 100\,\mu m^2$); M = Medium ($> 100\,\mu m^2$); L = Large ($> 500\,\mu m^2$) |
| Thallus colour | D = Dark; L = Light |
| Chemistry[b] | A = Acids; O = Other compounds; N = No compounds |

[a] Ascospore size was calculated as the product of the length and width ($\mu m^2$).
[b] Acids correspond to atranorin, parietin, furmarprotocetraric, stictic, norstictic and usnic. Other compounds refer to those that are exclusive in several species with an unknown function.

six $20 \times 30$ cm grids located at three heights (0–50 cm, 51–150 cm, 151–200 cm), and at the north and south aspects. In addition, the following variables were measured at plot level: canopy cover (%), elevation (m a.s.l.), slope (°), aspect (cosine transformed) and mean tree DBH (diameter at breast height in cm) of the 4 trees analyzed per plot.

For species identification, we used general and specific taxonomic and floristic papers (*e.g.* Brako, 1991; Egea and Torrente, 1993; Brodo et al., 2001; Nash III et al., 2002, 2004; Rivas-Plata et al., 2006; Nash III et al., 2007; Brodo et al., 2008; Lücking et al., 2008, 2009; Timdal, 2008; Aptroot et al., 2008, 2009; Aptroot, 2012; Moncada et al., 2013).

### 2.3. Functional traits

For each lichen species found in the study area, nine traits were assessed to perform the functional analysis: (1) Photobiont type; (2) Growth form; (3) Size; (4) Reproduction type; (5) Type of reproductive structure; (6) Ascospores septation; (7) Ascospores size; (8) Thallus colour; and (9) Chemistry (Table 1). The information related to these traits was obtained from specific taxonomic literature (cited above), observed directly from the specimen collected and using the Database for the Rapid Identification of Lichens (www.lias.net).

The functional traits were selected based on previous studies, due to its relation with ecosystems functioning (Ellis and Coppins, 2006; Stofer et al., 2006; Johansson et al., 2006, 2007; Marini et al., 2011; Giordani et al., 2012; Pinho et al., 2012; Li et al., 2013; Prieto et al., 2017). Specifically, photobiont type is related with light, temperature and water requirements for the photosynthesis and respiration processes (Lange et al., 1986; Lakatos et al., 2006; Marini et al., 2011). Growth form (thallus morphology) is related with water uptake and loss (Lakatos et al., 2006; Büdel and Scheidegger, 2008). Secondary metabolites (*e.g.* usnic acid) contribute to protect lichens from solar irradiation and herbivory (Cocchietto et al., 2002; Hauck and Huneck, 2007; Hauck et al., 2009). Finally, the reproductive strategy is related with dispersal ability and establishment (Stofer et al., 2006; Koch et al., 2013).

It is important to mention that growth forms of lichens are easy to recognize by non-specialists and without knowing the taxonomical identity of the species.

### 2.4. Data analysis

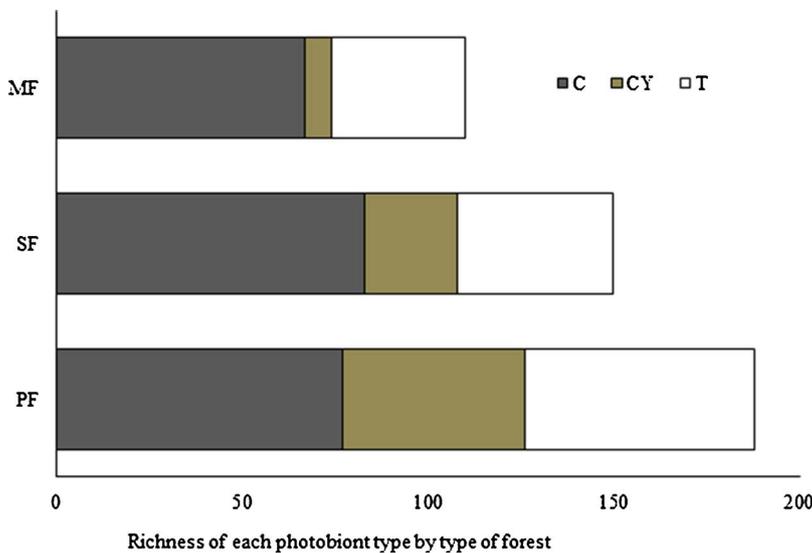We calculated species richness as the total number of different

**Fig. 1.** Richness of each photobiont type by type of forest (PF = primary forests; SF = secondary forests; MF = monoespecific forests of *Alnus acuminata*). C = Chlorococcoid; CY = Cyanobacteria; T = *Trentepohlia*.
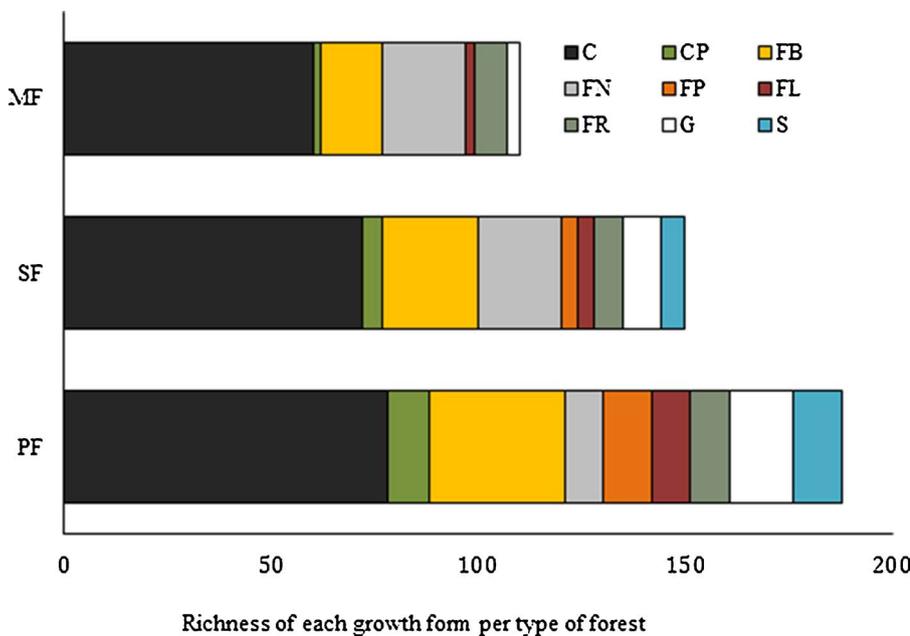
Richness of each photobiont type by type of forest



**Fig. 2.** Richness of each growth form per type of forest (PF = primary forests; SF = secondary forests; MF = monoespecific forests of *Alnus acuminata*). C = Crustose; CP = Crustose with prothallus; FB = Foliose with broad lobes; FN = Foliose with narrow lobes; FP = Foliose placodiod; FL = Filamentose; F = Fruticose, G = Gelatinose; S = Squamulose.

Richness of each growth form per type of forest

lichen species occurring in a plot. To analyze species diversity we calculated the Simpson's and Shannon's indices (Magurran, 2004) per plot with PRIMER v 6.1.11 (Anderson et al., 2008). In addition, we calculated floristic similarities using Sørensen's and Bray-Curtis similarity indices (Chao et al., 2005), using EstimateS 9.1.0 (Colwell, 2013).

To characterize the community structure from a functional perspective (Ricotta and Moretti, 2011) we used the community weighted mean (CWM), which describes the trait averages over a community (de Bello et al., 2007) and reflects the dominant trait in a given community (Garnier et al., 2004; Lepš et al., 2006; Violle et al., 2007; Lavorel et al., 2008).

The total species richness of each functional trait category was calculated as the total number of species with each trait category found in the four trees per plot. Community weighted means, considering a continuous trait, represents the sum of each species trait value weighted by its relative abundance in the community (Lavorel et al., 2008). For multinomial traits, we have calculated it as the sum of the cover of all species sharing a trait divided by the total species cover, representing the proportion of each individual trait-category per community (*i.e.* mean trait values weighted with the abundance). The effect of

environmental variables (canopy cover, elevation, slope, aspect and mean tree diameter per plot) on richness and CWM of the different lichen functional trait categories was modelled by fitting Generalized Linear Mixed Models (GLMMs) (McCullagh and Nelder, 1989). The richness and CWM models of each functional trait category were fitted with Poisson errors. Significance was estimated by means of deviance analysis (Guisan et al., 2002). All GLMMs computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT).

To determine which lichen functional trait category was associated with the forest type, in order to identify it as indicator trait, we used the indicator species analysis developed by Dufrêne and Legendre (1997) and used by Koch et al. (2013). This analysis calculates an indicator value for each trait category based on the mean cover of each functional trait category per forest, which results from multiplying the relative abundance for each trait category by the frequency for each trait category in each forest. The indval function with the labdsv package was used for this purpose (Roberts, 2012), using R 3.2.2 (R Development Core and Team, 2015). The indicator value ranges from 0 (when one species trait was absent from one forest type) to 100 (when one species
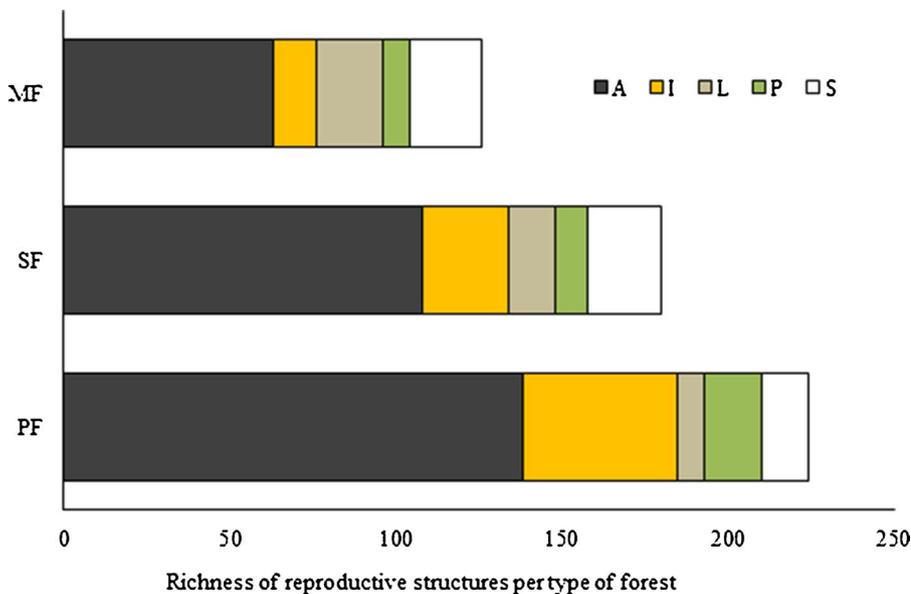
**Fig. 3.** Richness of reproductive structures per type of forest (PF = primary forests; SF = secondary forests; MF = monoespecific forests of *Alnus acuminata*). A = Apothecia; I = Isidia; L = Lirellae; P = Perithecia; S = Soredia.
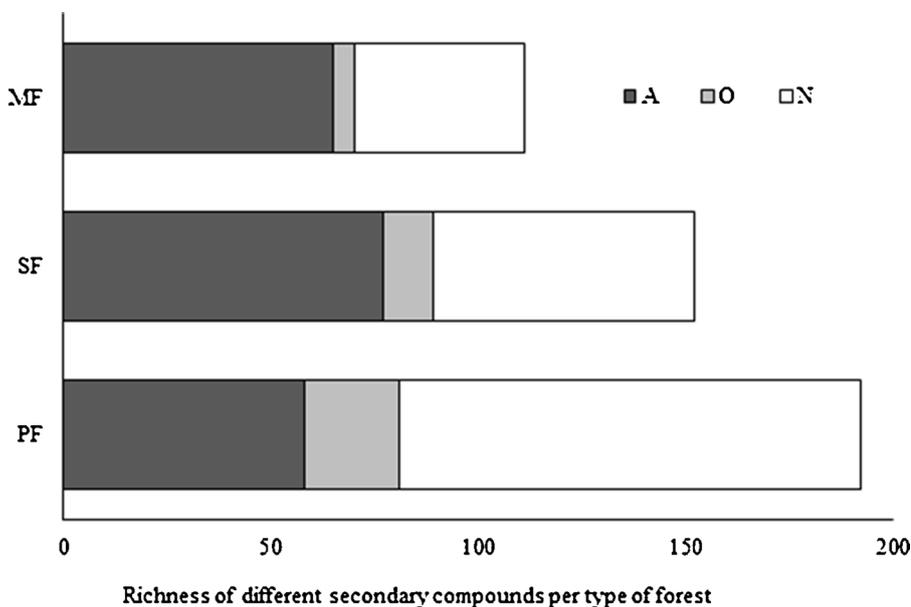


**Fig. 4.** Richness of different secondary compounds per type of forest (PF = primary forests; SF = secondary forests; MF = monoespecific forests of *Alnus acuminata*). A = Acids; O = Other compounds; N = No compounds.

trait occurred in all plots of one forest type and was absent from other plots). The significance was tested using a Monte Carlo permutation with 1000 replicates.

To determine whether a single functional category could be used as predictor for the total species richness of lichens, we used Pearson's linear correlation coefficients to explore the relationships between the species richness per growth forms (pairwise tests) and the total species richness and diversity indices. When testing correlation, the number of species of each growth form was subtracted to the total richness of lichens to avoid biases produced by differences in species abundance. To keep a reasonable test-wide Type I error, the alpha values were divided by the number of correlations (nine correlations) (Sebastião and Grelle, 2009). All analyses were carried out at plot level.

## 3. Results

A total of 307 epiphytic lichen species were recorded in 60 plots; for which nine functional traits were assessed. The richness of most functional trait categories were related with the gradient of disturbance (Figs. 1–4). Thus, lichen species with cyanobacteria and *Trentepohlia*

decreased with increasing forest disturbance (Fig. 1). A similar pattern was found in the growth forms, with crustose species with prothallus, foliose broadly lobed, filamentose and gelatinose species decreasing in secondary forests (Fig. 2), and the disappearance of foliose placodiod and squamulose species in the monospecific forests of *A. acuminata*. Species with apothecia and isidia also decreased in monospecific forests (Figs. 2 and 3). In contrast, foliose species with narrow lobes and those species with lirellate apothecia and soredia increased along the disturbance gradient (Figs. 2 and 3). In addition, lichens with acids as secondary compounds (atranorin, antrachinones, stictic and usnic acid) were more frequent in secondary forests, while lichens without acids (or with other compounds) increased in primary forests (Fig. 4).

The most relevant predictors for the richness of functional traits and CWM of epiphytic lichens were canopy cover and tree diameter, followed by altitude (Table 2). Aspect and slope had influence on very few traits (Table 2). Canopy cover had a positive and significant effect on cyanolichens, crustose species with prothallus, foliose placodioid, gelatinose species and lichens without secondary metabolites. Tree diameter had the same effect on lichens with *Chroococcoid* photobionts, foliose with broad lobes, fruticose, squamulose and isidiate species. On

**Table 2**
Results of the Generalized Linear Mixed Models of plot-scale variables on the richness and CWM of the considered functional trait categories of epiphytic lichens. Coefficients of the variables in the model and *P*-value (between parentheses) are indicated.
DBH = mean tree diameter, CWM = community weighted means of trait values.

| | Richness | | | | | CWM | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Canopy cover | DBH | Altitude | Aspect | Slope | Canopy cover | DBH | Altitude | Aspect | Slope |
| **Photobiont** | | | | | | | | | | |
| Chlorococcoid | | +13.69 (0.0006) | | | | | | | | |
| Cyanobacteria | +7.95 (0.0080) | | +8.09 (0.0074) | | | +11.41 (0.0014) | | | | |
| Trentepohlia | | | | | | −25.92 (0.0001) | | | | +4.35 (0.0456) |
| **Size** | | | | | | | | | | |
| Macrolichens | | | | | | | | | | |
| Microlichens | | | | | | | | | | |
| **Growth form** | | | | | | | | | | |
| Crustose | | | | | | | | | | |
| Crustose with prothallus | +11.56 (0.0013) | | | | | +8.54 (0.0075) | | | | |
| Foliose with broad lobes | | +7.16 (0.0100) | | | | | | | | |
| Foliose with narrow lobes | | | −6.93 (0.0110) | | | −6.19 (0.0177) | | | | |
| Foliose placodioid | +9.23 (0.0037) | | +7.14 (0.0155) | | | +4.55 (0.0378) | | | | |
| Filamentose | | | +5.13 (0.0456) | | | +5.05 (0.0317) | | | | |
| Fruticose | | +8.00 (0.0065) | | | | | | | | |
| Gelatinose | +12.08 (0.0010) | | +5.05 (0.0417) | | | +9.18 (0.0037) | | | | |
| Squamulose | | +5.45 (0.0233) | +4.12 (0.0473) | | | | | | | |
| **Reproduction** | | | | | | | | | | |
| Asexual | | +28.50 (< 0.0001) | | | | | +12.46 (0.0009) | | | |
| Sexual | | | | | | | −6.14 (0.0165) | | | |
| Asexual and sexual | | | | | | | | | | |
| None | | | | | | +4.27 (0.0444) | | | | +4.91 (0.0311) |
| **Reproductive structure** | | | | | | | | | | |
| Apothecia | | +9.48 (0.0033) | | | | | −7.28 (0.0106) | +4.40 (0.0434) | | |
| Isidia | | +18.47 (< 0.0001) | | | | | | | | |
| Lirellae | | | | | +4.46 (0.0393) | −7.20 (0.0097) | | | | |
| Perithecia | | | | | | +6.53 (0.0146) | | | | |
| Soredia | | +15.79 (0.0002) | +3.97 (0.0491) | | | −7.49 (0.0084) | +5.75 (0.0204) | | | |
| **Ascospores septation** | | | | | | | | | | |
| Simple | | +5.44 (0.0235) | | +4.81 (0.0381) | | | +4.07 (0.478) | | | |
| Septated | | | | | | | | | | |
| Muriform | | | | | | | | +4.78 (0.0476) | | |
| **Ascospores size** | | | | | | | | | | |
| Small | | +8.31 (0.0057) | | | | | | | −6.80 (0.0118) | |
| Medium | | | | | | | | | | |
| Large | | | | | | | | | | |
| **Thallus colour** | | | | | | | | | | |
| Dark | | +13.59 (0.0006) | +10.20 (0.0027) | | | | | | | |
| Light | | | | | | | | | | |
| **Chemistry** | | | | | | | | | | |
| Acids | | +12.96 (0.0007) | | | | −7.62 (0.0079) | | | | |
| Other compounds | | | | | | | | | | |
| No compounds | +10.04 (0.0025) | | +4.97 (0.0343) | | | +8.88 (0.0044) | | | | |

**Table 3**

Trait categories of epiphytic lichens with statistical significant values as indicators of forest type. *P*-values < 0.05 are considered significant. Trait categories with indicator value > 55% are considered as the best indicators. PF = primary forests; SF = secondary forests; MF = monoespecific forests of *Alnus acuminata*.

| Functional group | Forest type | Indicator value | *P*-value |
|---|---|---|---|
| **Photobiont** | | | |
| Chlorococcoid | MF | 49.7 | 0.0001 |
| Cyanobacteria | PF | 65.4 | 0.0001 |
| Trentepohlia | MF | 49 | 0.0001 |
| **Size** | | | |
| Macrolichens | PF | 36 | 0.1332 |
| Microlichens | MF | 43.6 | 0.0001 |
| **Growth form** | | | |
| Crustose | MF | 54.8 | 0.0001 |
| Crustose with prothallus | PF | 56.3 | 0.0001 |
| Foliose with broad lobes | PF | 50.1 | 0.0001 |
| Foliose with narrow lobes | MF | 59.6 | 0.0001 |
| Foliose placodioid | PF | 55.5 | 0.0001 |
| Filamentose | PF | 66 | 0.0001 |
| Fruticose | MF | 76.5 | 0.0001 |
| Gelatinose | PF | 55.4 | 0.0087 |
| Squamulose | PF | 63.9 | 0.0001 |
| **Reproduction** | | | |
| Asexual | SF | 38.4 | 0.0162 |
| Sexual | MF | 35.8 | 0.1131 |
| Asexual and sexual | MF | 38.7 | 0.0357 |
| None | MF | 54.8 | 0.0094 |
| **Reproductive structure** | | | |
| Apothecia | PF | 38.7 | 0.0003 |
| Isidia | SF | 46.3 | 0.0002 |
| Lirellae | MF | 80 | 0.0001 |
| Perithecia | SF | 40.5 | 0.2162 |
| Soredia | MF | 55.5 | 0.0001 |
| **Ascospores type** | | | |
| Simple | MF | 40.3 | 0.0229 |
| Septate | PF | 40.2 | 0.0005 |
| Muriform | PF | 43.6 | 0.0525 |
| **Ascospores size** | | | |
| Small | MF | 43.9 | 0.0016 |
| Medium | PF | 41.6 | 0.0001 |
| Large | MF | 49 | 0.0002 |
| **Thallus colour** | | | |
| Dark | PF | 53.3 | 0.0001 |
| Light | MF | 55.1 | 0.0001 |
| **Chemistry** | | | |
| Acids | MF | 55.5 | 0.0001 |
| Other compounds | MF | 36.6 | 0.5857 |
| No compounds | PF | 59 | 0.0001 |

the other hand, canopy cover had a negative effect on the species with *Trentepohlia*, foliose lichens with narrow lobes, species with lirellae, with soredia and with acids as secondary metabolites (Table 2).

Cyanolichens, species without secondary compounds, crustose with protallus, foliose placodiod, filamentose, gelatinose and squamulose growth forms, were the best indicators of sheltered habitats of montane undisturbed forests (PF), whereas, fruticose, foliose species with narrow lobes, lirellate and sorediate lichens and those species with light thallus colour and acids as secondary compounds were the best indicators of disturbed forest (Table 3).

Total species richness and diversity of epiphytic lichens were highly correlated with most growth form categories. The increase in the richness of gelatinose growth forms, filamentous, squamulose, foliose placodiod and crustose with prothallus was highly and significantly correlated with the increase in the total species richness. On the other hand, the richness of crustose and foliose species with narrow lobes were negatively correlated with the total richness of lichens (Table 4). Diversity was mainly related with gelatinose forms, crustose with prothallus and foliose species with broad lobes. Most growth forms were negatively correlated with Sørensen's and Bray-Curtis similarity indices except crustose, fruticulose and foliose species with narrow lobes (Table 4).

## 4. Discussion

Our results demonstrate that lichen traits and the CWM were related to the forest structural changes produced by disturbance and were mainly controlled by factors related with the canopy cover and tree diameter. In relation with these results, several trait categories have high indicator values of the forest conservation status and growth forms are related with the total lichen species richness and diversity in tropical montane forests.

The observed changes in functional groups (species with similar trait categories) in relation with the forest disturbance level may be caused by the similarity in the ecological and physiological requirements. Thus, the greater occurrence of three functional groups (*i.e.* cyanolichens, gelatinose and crustose species or foliose species with placodiod thalli) on primary forests, was mainly due to the presence of a closed canopy, sheltered and humid environments and inner parts of forests that remain unaltered (Belinchón et al., 2007; Kranner et al., 2008; Aragón et al., 2010; Normann et al., 2010; Rosabal et al., 2010; Marini et al., 2011; Benítez et al., 2012; Li et al., 2013). This is because these lichens are intolerant to excessive light and need liquid water to activate photosynthesis (Lange et al., 1986; Nash, 1996; Hedenås and Ericson, 2000; Sillet and Antoine, 2004). Crustose species with prothallus (*e.g. Cryptothecia* and *Herpothallon*) are more frequent in primary forests probably favoured by the hyphal projections from the medulla that create a hydrophobic layer and repels water excess as reported for *Cryptothecia rubrocincta* (Lakatos et al., 2006). Filamentose lichens (*e.g. Coenogonium*) are also related with old-growth and dense primary forests, and restricted to the low light environment of tropical shady understorey (Sipman and Harris, 1989; Lücking, 1999; Brodo et al., 2001). For them it has been reported high evaporation rates and rapid desiccation of the thallus (Lakatos et al., 2006).

The decrease in squamulose and foliose species with broad lobes in monospecific forests could be related with the size of the trunks which

**Table 4**

Pearson's correlation coefficients between growth forms and total richness and diversity of lichen species. *P*-value is indicated as * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ and ns = non-significant.

| Traits richness | Total Richness | Shannon index | Simpson inverse index | Sorensen index | Bray Curtis |
|---|---|---|---|---|---|
| Crustose | −0.61*** | -0.19 ns | -0.13 ns | 0.54*** | 0.53*** |
| Crustose with prothallus | 0.55*** | 0.40** | 0.15 ns | −0.77*** | −0.73*** |
| Foliose with broad lobes | -0.02 ns | 0.70*** | 0.53*** | −0.68*** | −0.78*** |
| Foliose with narrow lobes | −0.87*** | −0.31* | -0.04 ns | 0.78*** | 0.67*** |
| Foliose placodioid | 0.56*** | 0.30* | 0.04 ns | −0.73*** | −0.73*** |
| Filamentose | 0.70*** | 0.30* | 0.06 ns | −0.68*** | −0.63*** |
| Fruticulose | -0.24 ns | -0.01 ns | 0.07 ns | 0.42*** | 0.31* |
| Gelatinose | 0.74*** | 0.44*** | 0.17 ns | −0.73*** | −0.76*** |
| Squamulose | 0.64*** | 0.32* | 0.02 ns | −0.68*** | −0.63*** |

may provide less available substrate for lichens, therefore limiting their abundance (Esseen et al., 1996; Lie et al., 2009).

In contrast, fruticose, foliose species with narrow lobes, species with lirellate apothecia and those with acids as secondary metabolites were more abundant in secondary forests and negatively correlated with canopy cover. This is probably related to more light availability and a lower humidity promoted by canopy disruption. As a general pattern, foliose species with narrow lobes (*e.g. Heterodermia* and *Hypotrachyna*) and fruticose lichens are more heliophytic, occupying sites with high irradiance levels and water stress (Aragón et al., 2010; Rosabal et al., 2010; Marini et al., 2011; Benítez et al., 2012; Giordani et al., 2012; Koch et al., 2013; Li et al., 2015; Prieto et al., 2017).

Lichens with lirellate ascoma (*e.g. Graphis*) were also more abundant in secondary forests. This is probably related with the tolerance to high light intensities and dry habitats conferred by the black and closed lirellae (Kappen, 1988; Lücking, 1999; Koch et al., 2013). Lichens producing acids as secondary compounds were more common in secondary forests, due to the protection against excessive radiation conferred by these compounds as it has been previously showed (Cocchietto et al., 2002; Hauck and Huneck, 2007; Hauck et al., 2009, 2013). With increasing disturbance intensity the importance of *Chlorococcoid* green algae and *Trentepohlia* as lichen photobionts increased, while it decreased for cyanobacteria. Lichens with green algae are better adapted in open and intensively managed forests having a great capacity to avoid photoinhibition effects and being able to photosynthetize with minimum thallus water content and reactivate photosynthesis from air humidity (Lange et al., 1986; Demmig-Adams et al., 1990; Gauslaa and Solhaug, 2004; Hilmo et al., 2005; Ellis and Coppins, 2006; Stofer et al., 2006).

The analysis of indicator traits showed that photobiont type, growth form, reproductive structure and secondary metabolites can be used as a complement indicator to evaluate the conservation status (*i.e.* disturbance level) of tropical montane rainforests. Thus, crustose lichens with protallus, foliose placodioid, filamentose, gelatinose and squamulose growth forms can be used as indicators for primary forests, while foliose with narrow lobes and fruticose species, lirellate and soerdiate lichens were the best indicators of secondary forests.

Other studies also found lichen traits related with forests disturbance level. Thus, fruticose and foliose species with narrow lobes are more abundant in open or disturbed forests (Giordani et al., 2012; Koch et al., 2013; Li et al., 2013) and cyanobacterial and gelatinose lichens in undisturbed or primary forests (Rosabal et al., 2010; Aragón et al., 2010, 2013; Benítez et al., 2012; Li et al., 2013). Based on these results, we propose the use of functional traits as a complement to evaluate the conservation status of forests. Thus, lichen functional traits could be a cost-effective way to obtain spatially detailed information for the definition of conservation priority areas which can be crucial for environmental planning and biodiversity policies (Pinho et al., 2012; Giordani et al., 2012). This is especially important for tropical regions where the lack of knowledge in lichen diversity is apparent, together with the highest deforestation and loss rates of species diversity.

On the other hand, the great effort required for sampling and identification of lichens, especially the most inconspicuous species (*e.g.* crustose lichens), calls for developing alternative ways for rapid diversity surveys (Giordani et al., 2009). Growth forms of lichens and bryophytes are easier identifiable traits than taxa, and can be applied by non-specialists. In this context, previous papers have shown that growth forms of lichens and bryophytes could be used for infer total richness (Oishi, 2009; Pardow et al., 2012; Aragón et al., 2016). The results of our study, in accordance with those previously obtained by Aragón et al. (2016), show that the diversity of growth forms is highly correlated with the overall lichen richness and can be used to infer species richness and diversity in tropical montane forests. Here, we go a step forward given that we analyzed growth forms separately. Thus, we found several functional groups positively correlated with a higher species richness (*i.e.* crustose with prothallus, foliose placodioid,

squamulose, filamentose and gelatinose) meanwhile others were negatively correlated (*i.e.* crustose and foliose species with narrow lobes).

In conclusion, species traits and CWM of lichen communities responded significantly to structural forest changes related with disturbance as canopy cover and tree diameter. Those functional groups are proposed as complementary indicators of disturbance level of forests and can be used as a measure to manage tropical forests. We also found the richness of different growth forms as indicators of the total epiphytic lichen species richness and diversity in montane tropical forests. The use of certain growth forms can be used to infer total species diversity and richness (*e.g.* gelatinose or squamulose species). This approximation will provide an important step for conservation studies as it constitute a feasible and promising alternative for evaluating and monitoring environmental changes in tropical montane forests that can be applied by non-specialists because the easiness to identify traits of lichens.

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