



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 succession (Koch et al., 2013), air pollution

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(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 (Kranter 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 µm ²); M = Medium (> 100 µm ²); L = Large (> 500 µm 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 (µm²).

^b Acids correspond to atranorin, parietin, fumarprotocetraric, stictic, norstictic and usnic. Other compounds refer to those that are exclusive in several species with an unknown function.

six 20 × 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 (Cocchiello et al., 2002; Hauck and Huneck, 2007; Hauck et al., 2009). Finally, the reproductive strategy is related with dispersion 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

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