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Effects of tropical montane forest disturbance on epiphytic macrolichens

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HIGHLIGHTS

- Tropical montane forest disturbance drastically reduced macrolichen diversity.
- Species loss was most severe for the "shade-adapted lichens" because high radiation is harmful to them.
- In secondary forests lichen diversity of native forests was not regenerated.
- The protection of remnants of primary tropical forest might help to preserve a diverse community of epiphytic macrolichens.

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ABSTRACT

The high diversity of epiphytes typical of undisturbed montane tropical forests has been negatively affected by continuous deforestation and forest conversion to secondary vegetation. Macrolichens are an important component of these epiphytes. Because their physiology is strongly coupled to humidity and solar radiation, we hypothesized that microclimatic changes derived from forest clearing and logging can affect the diversity of these poikilohydric organisms. In southern Ecuador, we examined three types of forests according to a disturbance gradient (primary forests, secondary forests, and monospecific forests of *Alnus acuminata*) for the presence/absence and coverage of epiphytic macrolichens that we identified on 240 trees. We found that total richness tended to decrease when the range of the disturbance increased. The impoverishment was particularly drastic for "shade-adapted lichens", while the richness of "heliophytic lichens" increased in the drier conditions of secondary growth. Epiphytic composition also differed significantly among the three types of forests, and the similarity decreased when the range of the disturbance was greater. We concluded that a span of 40 years of recovery by secondary vegetation was not enough to regenerate the diversity of epiphytic macrolichens that was lost due to forest disturbances.

1. Introduction

Montane tropical rain forests have been recognized as one of the most diverse ecosystems, being simultaneously one of the most threatened habitats in the world (Henderson et al., 1991; Gentry, 1995; Brummit and Nic Lughadha, 2003; Barthlott et al., 2005). Montane rain forests are disappearing at an incredibly high rate and currently cover a tiny fraction of their historical distributions (Henderson et al., 1991; Bruijnzeel and Hamilton, 2000; Wright, 2005; Laurance and Peres, 2006; Gibbs et al., 2010). Many natural forests have been reduced to small isolated remnants by deforestation and subsequent agricultural or livestock activities (Churchill et al., 1995; Asner et al., 2005; Gibbs et al., 2010). This scenario of forest alteration from logging and different land uses has serious consequences for epiphytes (Barthlott et al., 2001; Wolf, 2005; Nöske et al., 2008), which are important components of the diversity within montane rain forests (Barthlott et al., 2001; Nadkarni et al., 2001; Gradstein et al., 2003; Gradstein, 2008) and have important roles in the total biomass, water balance and nutrient cycling of the ecosystems (see Holz and Gradstein, 2005).

As a general pattern, epiphyte diversity tends to be higher in primary than in secondary vegetation (Barthlott et al., 2001; Gradstein, 2008). This matter has been recently studied in montane forests, but the results have been rather controversial; some studies supported the higher diversity in primary vegetation (Kappelle et al., 1995; Nöske et al., 2008), while others have found no relationship (Hietz, 1998; Holz and Gradstein, 2005; Nöske et al., 2008). This variation in the patterns observed might be related to differences in the studied taxa, the level of disturbance, the diversity of the host tree species, or the age of the secondary vegetation (Hietz et al., 2006; Gradstein, 2008). In addition to the epiphytic richness, forest disturbance also affects species composition of the epiphytes (Hietz et al., 2006). For instance, epiphytes characteristic of a shaded understory declined in more open vegetation than in primary forests, while "sun epiphytes" were lacking from the shady canopy strata of natural forests (Hietz et al., 2006; Gradstein, 2008).

Macrolichens (foliose and fruticose lichen species) are important epiphytic organisms in montane rain forest (Mandl et al., 2010), and

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the diversity and composition of the communities depend mainly on microclimatic factors associated with forest structure (tree age, canopy cover, management intensity, tree diversity) (Aragón et al., 2010). The physiology of macrolichens is strongly coupled to humidity, solar radiation and temperature conditions (Green et al., 2008), so their distributions at a local level are expected to be determined by changes in forest structure derived from natural or human disturbance of the forests (Bergamini et al., 2005; Werth et al., 2005; Nascimbene et al., 2007; Aragón et al., 2010). Within macrolichens, certain groups without cortical pigments (e.g., peltigeralean species) are more sensitive to environmental changes, because they suffer photoinhibition in excessive radiation and are strongly dependent on atmospheric moisture (Lange et al., 2004; Kranner et al., 2008). In this sense, we expect drastic changes in macrolichen composition between the natural rain forest and the more disturbed environment of secondary vegetation. In addition to microclimatic changes caused by the reduction in canopy in disturbed forests, forest logging also causes a loss in diversity of host tree species. This fact may affect the epiphytic diversity and composition because the establishment of a particular species of lichens is determined by several factors related to the host tree species such as bark roughness and pH and tree size (Fritz et al., 2008; Ranius et al., 2008; Belinchón et al., 2009; Aragón et al., 2010). Thus, we expect to find a higher diversity of epiphytic macrolichens in primary forests than in the young secondary vegetation, where the trees are younger.

Our main goal was to analyze differences in species richness and diversity of epiphytic macrolichens in relation with forest disturbance in tropical montane forests. The forest disturbance level considered included remnants of natural forests (primary forests), secondary forests that developed after selective logging of primary forest, and secondary vegetation that consisted of a monospecific forest of *Alnus acuminata*. We hypothesized that the reduction in canopy, the fewer species of host trees and the younger secondary vegetation with respect to primary forests would affect the diversity of the epiphytic macrolichens. Specifically, we addressed the following questions: do the macrolichen communities suffer an impoverishment when forest disturbance is increased? Which species contribute most to differences among the three forests disturbance levels?

2. Materials and methods

2.1. Study area

The study areas included six tropical montane forests located in southern Ecuador (Loja Province; 2200–2800 m asl) (Fig. 1). 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% (Instituto Nacional de Meteorología e Hidrología, INAMI).

In this study, we distinguished three types of vegetation according to a disturbance gradient: (1) relicts of primary forest area (PF) of evergreen montane tropical vegetation. The PFs are characterized by a dense canopy layer (ca. 80–85% coverage) with large trees (35–40 m tall). The upper canopy is composed of *Cinchona macrocalyx* Pav. ex DC., *Clusia elliptica* Kunth, *Myrica pubescens* Humb. and Bonpl. ex Willd, *Podocarpus oleifolius* D. Don and *Weinmannia pubescens* HBK. (2) Secondary forests (SF) that have regrown after selective or total logging events on primary vegetation that took place some 40 years ago (Brown and Lugo, 1990; Holz, 2003). The canopy layer is ca. 60–70% in coverage, mainly composed of species in the *Melastomataceae* and *Lauraceae*, up to 25–30 m tall. (3) Secondary vegetation dominated by young, monospecific forests (MF) of *A. acuminata* Kunth, a pioneer native species of the

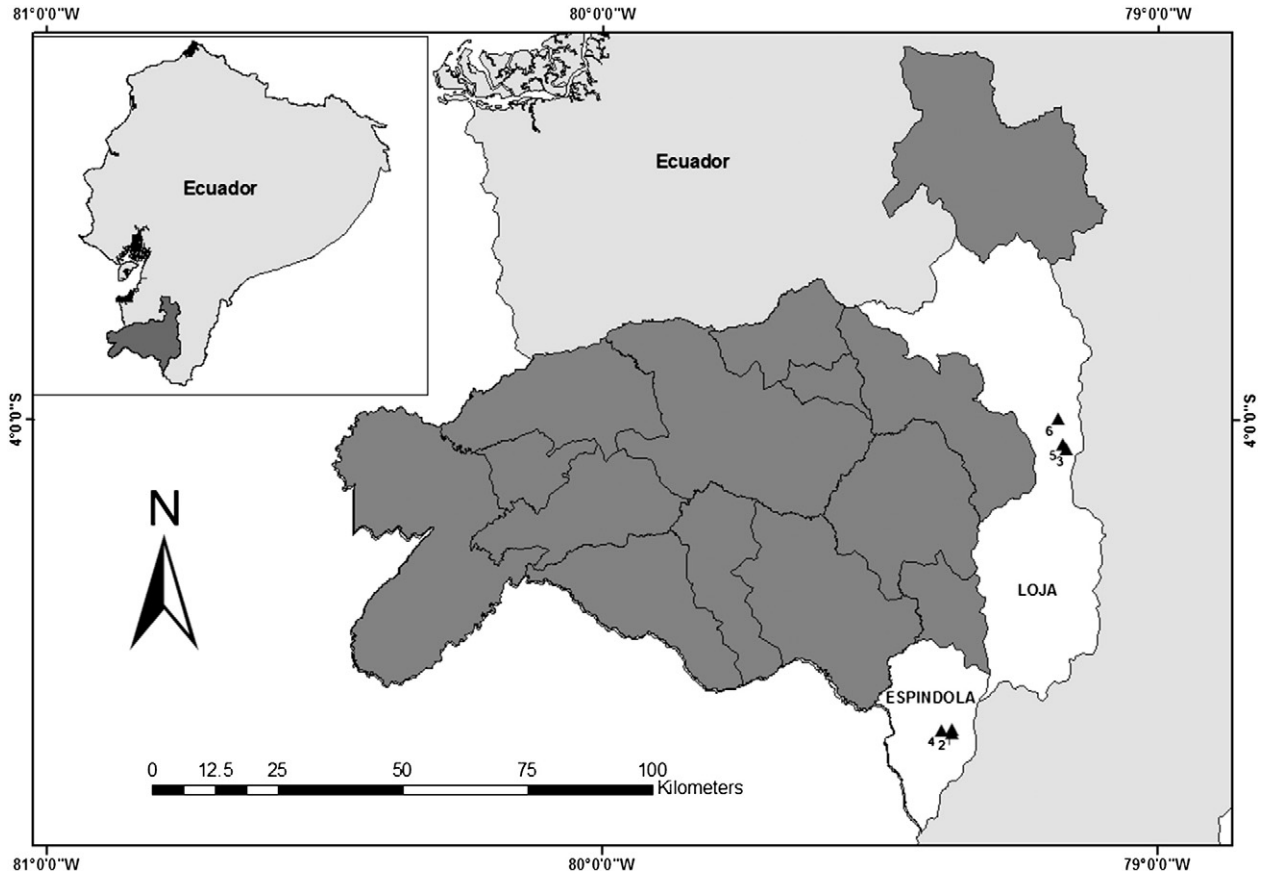

Fig. 1. Study area in Loja Province of southern Ecuador showing the location of the six tropical montane forest sites: 1 and 2, primary forests (PF); 3 and 4, secondary forests (SF); 5 and 6, monospecific forests of *Alnus acuminata* (MF).

Andes. The MFs were characterized by a very uniform structure, absence of understory, a canopy layer of ca. 50% coverage and trees up to 20 m tall.

2.2. Experimental design

Six forests were selected to span the disturbance gradient considered (2 PFs, 2 SFs and 2 MFs) (Fig. 1). Ten plots (5×5 m) at different elevations and orientations were selected within each forest, and four trees were sampled within the 10 plots. The distance between plots within a forest was over 50 m. Trees with the greatest and the smallest diameter and two other trees with a diameter at breast height (dbh) that was closest to the mean dbh within the plot were selected for a reliable representation of the epiphytic macrolichens of the stand. Additionally, we measured the elevation (m asl), slope (°), aspect (cosine transformed), and the canopy cover (%) at plot level, and the dbh of all trees (cm) within each plot. These variables are summarized in Appendix B.

We determined the species richness and composition of epiphytic macrolichens on 240 trees (40 in each forest). On the basis of our field experience in this type of community, we used 20×30 cm grids on the bark of each selected tree as monitoring units (Aragón et al., 2012). Six positions were chosen: three heights (0–50 cm, 51–150 cm, 151–200 cm) on the north and on the south aspects to obtain a good representation of the species growing in the different microenvironments of the tree trunks. We calculated the means of two data sets (macrolichen composition and species richness) for a given sample position. The total species richness was defined as the total number of species found in the six sites per tree. For the lichen composition, we calculated the mean estimated cover of each species (% of the site area) for the six sample sites. We calculated the total species cover per tree (as percentage of the grids) using the same methods.

2.3. Data analyses

The effects of microclimatic variables (slope, aspect, elevation, canopy cover, dbh) on the epiphytic richness at the tree and plot level was modeled by fitting generalized linear mixed models (GLMMs) (McCullagh and Nelder, 1989). This modeling approach was chosen because our data had a hierarchical structure with trees nested within plots, plots nested within forests and forests nested within disturbance level. We analyzed the data using a multilevel approach and, when necessary, considered plots and forests as random factors and applied mixed modeling (Verbeke and Molenberghs, 1997). Predictors were included as explanatory variables (fixed factors), and plot and forest were included as random sources of variation. Effects of random factors were tested using the Wald Z-statistic test. All GLMM computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX ver. 8 for SAS/STAT).

To test whether the three levels of disturbance had significantly different compositions of epiphytic species and to detect the effects of forest and plot variability, we performed a three-factor permutational multivariate analysis of variance (PERMANOVA) on the cover data (Anderson et al., 2008). In this analysis, the experimental design included three factors: disturbance level (three levels, fixed factor), forest (two levels, random factor nested within disturbance) and plot (10 levels, random nested within forest), with four replicate trees for each plot. The cover data (percentage cover by each macrolichen per tree) were $\log_{10}(x+1)$-transformed to account for contributions by both rare and abundant taxa. We used the Bray–Curtis distance measure. To assess species similarity among the different disturbance levels, we performed additional pairwise PERMANOVA tests (Anderson et al., 2008). We also computed a non-metric MDS (multidimensional scaling) ordination from the species cover values to reveal the degree of similarity among levels of disturbance. To identify the species that contributed most to the similarity and dissimilarity among the different disturbances levels, we used the SIMPER statistical routine (Clarke and Warwick, 1998). For all tests, we allowed 9999 random permutations under the reduced model.

3. Results

3.1. Species richness

We recorded a total of 119 species of epiphytic macrolichens on 240 trees. Results showed that the total number of macrolichens increased when forest disturbance decreased (Fig. 2). A total of 82 species were found in primary forests (PF), 64 species in secondary forests (SF) and 49 species in monospecific forests of *A. acuminata* (MF) (Appendix A). Moreover, species richness of shade species decreased when forest disturbance was higher (Appendix A). We found 36 exclusive species in PFs, but only 8 and 17 exclusive species in SFs and MFs, respectively (Appendix A).

Results of the mixed models showed that the most relevant predictors of the epiphytic communities at plot and tree levels were canopy cover and tree diameter (Table 1). The random variable forest was not significant in any case.

3.2. Species composition

Multivariate statistical analyses showed that epiphytic composition was structured according to the different spatial scales, and a large component of variation was associated with the disturbance level (Table 2). The non-metric MDS ordination showed a clear separation between trees in the different disturbance levels (Fig. 3). The subsequent pairwise test revealed significant differences in epiphytic composition between all three disturbance levels (Table 3). Results of the PERMANOVA test showed that the highest similarity values for species composition within a disturbance level were associated with the highest disturbance: PF (29.35%), SF (35.44%) and MF (41.59%). The SIMPER routine revealed that not all species contribute equally to establish the differences in the disturbance gradient. We observed that the largest contributions are due to differences in species cover of the genus *Sticta* (*Sticta* aff. *canariensis*, *Sticta tomentosa*) (Table 4).

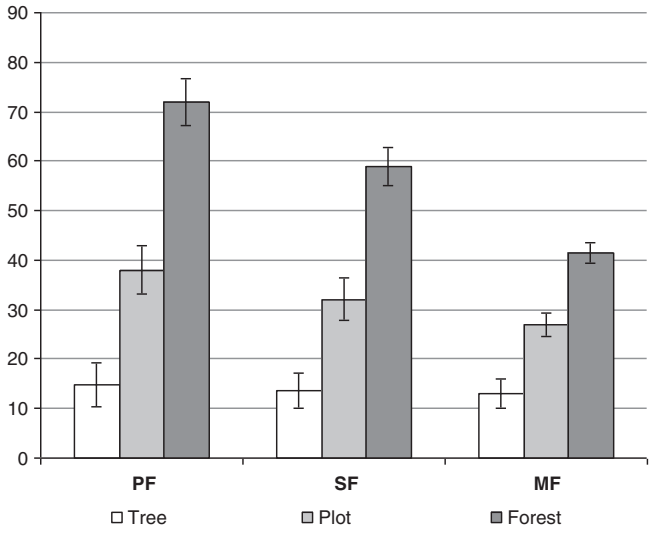

Fig. 2. Species richness of epiphytic macrolichens in the three types of vegetation (PF, SF and MF) at tree, plot and forest levels. Values represent means (±SD).

Table 1
Results of the generalized linear mixed models on some community traits. Coef.: coefficient of the variable in the model. S.E.: standard error. The random variable forest was non-significant in both cases, while plot variable at tree level was significant (Z-value = 2.67, Prob. Z = 0.0038). Tree diameter (cm) was at tree level, while elevation (m asl), slope (°), aspect (cosine transformed), canopy cover (%) and mean tree diameter (cm) were at plot level.

Richness	Coef. (S.E.)	*F*-value	*P*-value
Tree level			
Tree diameter	0.061 (0.022)	6.82	**0.0056**
Elevation	0.002 (0.001)	2.84	0.0969
Slope	−0.0085 (0.019)	0.19	0.6607
Aspect	0.289 (0.319)	0.82	0.3685
Canopy cover	0.052 (0.017)	8.73	**0.0031**
Plot level			
Mean tree diameter	0.231 (0.049)	21.52	<**0.0001**
Elevation	0.003 (0.002)	1.20	0.2783
Slope	−0.010 (0.021)	0.23	0.6325
Aspect	0.208 (0.371)	0.31	0.5781
Canopy cover	0.341 (0.0472)	46.72	<**0.0001**

P-values<0,05 are considered significant.

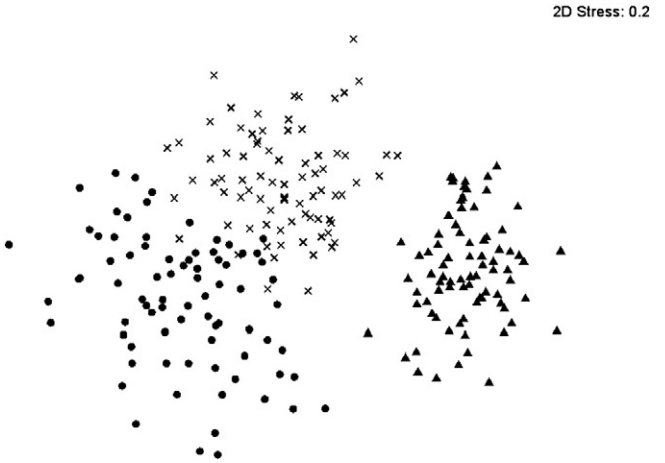

Fig. 3. Non-metric MDS ordination plot for the samples (trees) from the three types of vegetation according to a disturbance gradient. PF (●); SF (×); MF (▲).

4. Discussion

Our results demonstrated that deforestation in tropical montane rainforests resulted in major loss in the species diversity of epiphytic macrolichens. Secondary forests (SF and MF) had on average 25–45% fewer species than in the neighboring primary forests (PF). Similarly, Gradstein (2008) pointed out that deforestation is a major cause in the loss of all epiphytic species, especially those of the shaded understory of the forest, the so-called "shade epiphytes". In our case, the impoverishment of epiphytic macrolichens in the more disturbed forests was mainly due to the severe loss of the more shade-adapted species (Peltigerales). The most plausible explanation could be related to the efficiency in the physiological activity and the degree of desiccation tolerance in the latter group (Lange et al., 1993; Jovan and McCune, 2004; Kranner et al., 2008). The Peltigerales is composed mainly of lichens without cortical pigments that protect the thallus when it is exposed to excessive irradiation, and many of them possess cyanobacteria as the photobiont, which are strongly dependent on the amount of atmospheric moisture (Lange et al., 1993; Jovan and McCune, 2004; Kranner et al., 2008; Marini et al., 2011) because they need liquid water to activate photosynthesis (Lange et al., 1993).

Environmental conditions inside primary forests are optimal for the development of shade-adapted lichens because the high canopy cover favors the presence of more light-sheltered sites in the understory layer and a permanently moist environment where the air is constantly saturated (Sipman and Harris, 1989; Gradstein, 2008). On the contrary, the open canopy and stronger radiation in disturbed forests (SF and MF) create a drier microclimate than in natural forests (PF) (Gradstein, 2008). The consequent lower humidity negatively affects the shade-adapted lichens. When desiccation stress was induced for some macrolichens species, photosynthesis, respiration, morphology and growth were negatively affected, and the effects were greater for shade species (included in *Collema*, *Leptogium*, *Lobaria*, *Peltigera*, *Sticta*) growing in moist habitats (tropical climate) than for species adapted to more exposed areas and drier environments (see Kranner et al., 2008). However, heliophytic species (with green algae and cortical pigments, mainly included in Lecanorales, Caliciales and Teloschistales) were 13–16% more numerous in more disturbed forests than in the primary forests and were especially abundant in the monospecific forests of *A. acuminata*, representing 85% of the total species. The decrease in "shade-adapted lichens" vs. the increase in "heliophytic lichens" in the more disturbed forests provides a negative balance in the total number of the species and therefore an impoverishment of the macrolichen communities linked to the increased forest disturbance. Holz and Gradstein (2005) found a similar pattern in montane forests in Costa Rica, while Nöske et al. (2008) found that the number of epiphytic lichen species increased in secondary forests, suggesting that the number of species along a disturbance gradient does not follow a uniform pattern over time and that community composition might provide a more sensitive indicator of the human impact than species richness.

In addition to the changes in microclimate caused by the more or less open canopy, the impoverishment of epiphytic macrolichens in more disturbed forests might be explained by several factors related to differences in forest structure among the three types of vegetation considered (Fritz et al., 2008; Aragón et al., 2010; Soto-Medina et al., 2011). First, the larger tree size in primary forests involves more bark surface, formation of age-related specialized substrates and longer periods for colonization (Fritz et al., 2008; Ranius et al., 2008; Johansson et al., 2009). Second, since the establishment of lichens is linked to bark roughness and pH (e.g., Coppins and Wolseley, 2002; Rosabal et al., 2010), the species richness will decrease in secondary forests

Table 2
Results of three-factor PERMANOVA analysis of species composition by disturbance gradient, forest and plot.

Source	df	MS	Pseudo-*F*	*P*	CV (%)
Disturbance	2	1.1345	8.9826	0.0001	35.504
Forest (disturbance)	3	12633	3.9021	0.0001	15.326
Plot (forest (disturbance))	54	3237.4	1.9495	0.0001	19.833
Error	180	1664			40.793

Table 3
Results of pairwise PERMANOVA test between the types of vegetation according to disturbance gradient to show dissimilarity (%, according to Bray–Curtis index) and level of significance.

Source	Dissimilarity (%)	*P*
PF vs SF	76.94	0.0006
PF vs MF	91.43	0.0007
SF vs MF	82.15	0.0007

Notes: PF: primary forests; SF: secondary forests; MF: monospecific forests of *Alnus* acuminata.

Table 4
Results of the SIMPER analyses.

Species	CA			CA			CA		
	PF	SF	CD	PF	MF	CD	SF	MF	CD
Bulbothrix coronata				0.00	1.18	1.21	0.00	1.18	1.42
Coccocarpia palmicola	0.13	1.14	1.29						
Heterodermia aff. *diademata*				0.00	1.76	1.77	0.00	1.76	2.07
Heterodermia aff. *galactophylla*	0.00	2.11	1.96				2.11	0.22	2.42
Heterodermia galactophylla				0.00	1.03	1.05			
Heterodermia isidiophora	0.74	0.96	1.51	0.74	0.92	1.25	0.96	0.92	1.62
Heterodermia japonica	0.73	1.51	1.90	0.73	2.00	2.13	1.51	2.00	2.81
Heterodermia leucomela	0.90	1.15	1.54	0.90	2.38	2.09	1.15	2.38	2.67
Heterodermia spathulifera				0.00	3.30	3.10	0.48	3.30	3.56
Hypotrachyna revoluta	0.58	4.12	3.65	0.58	8.06	7.24	4.12	8.06	8.38
Hypotrachyna rocky				0.00	2.02	1.98	0.45	2.02	2.43
Leptogium azureum	1.64	3.00	3.50	1.64	0.31	1.69	3.00	0.31	3.44
Leptogium cochleatum	0.82	0.44	1.21						
Lobaria subdissecta	4.05	2.54	4.97	4.05	0.00	4.03	2.54	0.00	2.80
Parmeliella ecuadorense	0.38	0.90	1.23						
Parmotrema aff. *exquisitum*				0.00	1.28	1.33	0.29	1.28	1.69
Parmotrema aff. *peralbidum*	0.13	3.03	3.32				3.03	0.13	3.39
Parmotrema arnodii	1.60	4.13	4.92	1.60	0.28	1.67	4.13	0.28	4.69
Parmotrema rampoddense				0.45	6.39	6.14	0.40	6.39	7.07
Parmotrema zollongeri	0.00	1.67	1.92	0.00	1.41	1.22	1.67	1.41	2.64
Pseudocyphellaria aurata	0.51	0.86	1.21						
Punctelia aff. *crispa*	1.76	2.65	3.60	1.76	0.31	1.61	2.65	0.31	2.66
Punctelia aff. *reddenda*							0.62	1.09	1.50
Sticta aff. *canariensis*	13.47	3.21	14.05	13.47	0.00	11.66	3.21	0.00	3.26
Sticta andensis	2.13	0.38	2.11	2.13	0.00	1.98			
Sticta ferax	1.24	0.31	1.42						
Sticta humboltii	1.26	0.00	1.39	1.26	0.00	1.21			
Sticta laciniata	1.04	0.00	1.15	1.04	1.03	1.00			
Sticta tomentosa	11.16	4.83	10.56	11.16	0.00	10.28	4.83	0.00	5.40
Sticta sp.1	2.48	0.00	2.74	2.48	0.00	2.39			
Sticta sp.2	1.33	0.00	1.38	1.33	0.00	1.20			
Usnea sp. 1				0.36	7.19	6.23	0.80	7.19	7.08

Notes: CA: mean cover (%); CD: contribution of each species to the dissimilarity (%).

where trees have rather smooth bark and are more architecturally uniform than in primary forests (Gradstein, 2008). However, this trend might be mitigated by the high species diversity in the tropics, by the great water availability or by the interactions between other epiphytic organisms (angiosperms, mosses and ferns) (Cáceres et al., 2007; Soto-Medina et al., 2011). Third, the presence of a dense bryophyte cover provides a suitable substrate for the establishment of the biggest and the most shaded macrolichens (several species of *Lobaria* and *Sticta*) (Kranner et al., 2008; Belinchón et al., 2009).

Differences among management types are also corroborated by results on species composition. However, a large part of the variability in species composition is associated with forest, plot and trees, indicating that local factors contribute to shape lichen communities, independently by management regime. The differences between primary forests and the rest of the disturbed forests (SF and MP) were mainly attributed to the coverage of more shaded-adapted species (e.g., *Sticta* spp.). These species drastically reduced their presence and coverage with disturbance level. Similarly, Rivas Plata et al. (2008) showed that some genera of microlichens had preferences for undisturbed primary forests, fully shaded microhabitat and bark of mature trees. However, in the absence of shade lichens in drier habitats, the increased coverage by the more heliophytic lichens (e.g., *Heterodermia* spp., *Hypotrachyna* spp.) will be responsible for the dissimilarity.

The differences in species composition between the primary and secondary forests (SF and MF), which were not managed during the last 40 years since the last selective or total logging, might indicate that the epiphyte macrolichens had regenerated. Similarly, Gradstein (2008) found that the epiphytic composition in the natural forest was very different than in forests that had 50 years to recover, citing differences in the main variables that determine the response of the epiphytic organisms to habitat disturbance as possible causes: host tree characteristics, openness of the canopy and the microclimate in the forests (Gradstein, 2008; Nöske et al., 2008). In the same way, Holz and Gradstein (2005) suggested that at least 100 years are needed for the complete recovery of the floristic and community composition.

We therefore concluded that tropical forest disturbance significantly and drastically reduces macrolichen diversity. Disruption of the canopy leads to microclimatic changes that affect species richness of epiphytic macrolichens. Species loss is most severe for the "shade-adapted lichens" (included in Peltigerales) because in the disturbed habitats these epiphytes were not able to tolerate the high irradiation; therefore, these species may be useful indicators of forest conservation. In addition, change in the tree species composition and host tree characteristics play an important role. Actually, in this study there was evidence that in secondary forests lichen diversity of native forests was not regenerated; consequently, only the protection of remnants of primary tropical forest might help to preserve a rich and diverse community of epiphytic macrolichens.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2012.09.072.

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Appendix A. Number of trees on which each species appears in three types of vegetation according to a disturbance gradient. PF: primary forests, SF: secondary forests, MF: monospecific forests of *A. acuminata*.

Taxa	PF	SF	MF
Lecanorales			
Alectoria ochroleuca (Hoffm.) A. Massal.	9*		
Anzia parasitica (Fée) Zahlbr.	4*		
Bryoria sp.	1*		
Bulbothrix apophysata (Hale & Kurok.) Hale			6*
Bulbothrix coronata (Fée) Hale			45*
Bulbothrix isidiza (Nyl.) Hale		16*	
Bulbothrix suffixa (Stirton) Hale		14*	
Canomaculina cristobalii (L.I. Ferraro & Elix) Elix		3	14
Canomaculina pilosa (Stizenb.) Elix & Hale	1	1	
Cladonia coniocraea (Flörke) Sprengel	7	13	
Cladonia subradiata (Vainio) Sandst.	8	15	
Everniastrum cirrhatum (Fr.) Hale ex Sipman	7	2	
Everniastrum vexans (Zahlbr. ex W.L. Culb. & C.F. Culb.) Hale ex Sipman	5	4	2
Flavopunctelia flaventior (Stirt.) Hale			3*
Hypotrachyna aff. *degelii* (Hale) Hale	16	1	
Hypotrachyna bogotensis (Vain.) Hale	4*		
Hypotrachyna costaricensis (Nyl.) Hale	5	21	9
Hypotrachyna densirhizinata (Kurok.) Hale		6*	
Hypotrachyna eitenii (Hale) Hale			8*
Hypotrachyna rachista (Hale) Hale		4*	
Hypotrachyna revoluta (Flörke) Hale	14	46	64
Hypotrachyna reducens (Nyl.) Hale			9*
Hypotrachyna rockii (Zahlbr.) Hale		15	44
Hypotrachyna sp.			28*
Parmelinopsis miniarum (Vain.) Elix & Hale	5*		
Parmotrema aff. *exquisitum* (Kurok.) DePriest & B.W. Hale		8	31
Parmotrema aff. *peralbidum* (Hale) Hale	3	5	3
Parmotrema arnoldii (Du Rietz) Hale	27	55	8
Parmotrema austrosinense (Zahlbr.) Hale			9*
Parmotrema cristiferum (Taylor) Hale			17*
Parmotrema exquisitum (Kurok.) DePriest & B.W. Hale			12*
Parmotrema internexum (Nyl.) Hale ex DePriest & B.W. Hale		9	9
Parmotrema mellisii (Dodge) Hale	8*		
Parmotrema rampoddense (Nyl.) Hale	1	1	61
Parmotrema zollingeri (Hepp) Hale		31	26
Punctelia aff. *crispa* Marcelli, Jungbluth & Elix	39	34	
Punctelia aff. *reddenda* (Stirt.) Krog		17	27
Ramalina celastri (Spreng.) Krog & Swinscow			26*
Ramalina cochlearis Zahlbr.	2		2
Ramalina peruviana Ach.			2*
Ramalina sp.		5	25
Relicina abstrusa (Vainio) Hale	7*		
Rimelia subisidiosa (Müll. Arg.) Hale & A. Fletcher	2*		
Rimelia succinreticulata Eliasaro & Adler	5*		
Usnea sp. 1	16	3	65
Usnea sp. 2	1		17
Usnea sp. 3	3*		
Usnea sp. 4	2	1	
Peltigerales			
Coccocapia dissecta Swinscow & Krog	4*		
Coccocarpia erythroxyli (Spreng.) Swinscow & Krog	6	6	
Coccocarpia filiformis Arv.	4*		
Coccocarpia guimarana (Vain.) Swinscow & Krog	2*		
Coccocarpia microphyllina Lücking & Aptroot	7*		
Coccocarpia palmicola (Spreng.) Arv. & D.J. Galloway	8	39	
Coccocarpia pellita (Ach.) Müll. Arg.	12*		
Coccocarpia prostrata Lücking, Aptroot & Sipman	7	5	
Coccocarpia sp.	22*		
Coccocarpia stellata Tuck.	12	16	21
Leioderma glabrum D.J. Galloway & P.M. Jørg.		13*	
Leptogium austroamericanum (Malme) C.W. Dodge	6	4	
Leptogium azureum (Sw.) Mont.	49	32	12
Leptogium burgesii (L.) Mont.	7	17	
Leptogium burnetii Dodge	6*		
Leptogium chloromelum (Ach.) Nyl.	2		5
Leptogium cochleatum (Dicks.) P.M. Jørg. & P. James	28	14	
Leptogium coralloideum (Meyen & Flot.) Vain.	2	3	22
Leptogium corticola (Taylor) Tuck.	9	7	
Leptogium cyanescens (Rabh.) Körb.	13*		
Leptogium diaphanum (Sw.) Nyl.	3*		
Leptogium laceroides B. de Lesd.	5	2	
Leptogium marginellum (Sw.) Gray	4*		
Leptogium millegranum Sierk	6*		
Leptogium olivaceum (Hook.) Zahlbr.		8*	
Leptogium phyllocarpum (Pers.) Mont.	17	1	
Lobaria dissecta (Sw.) Raeusch.	8*		
Lobaria erosa (Eschw.) Nyl.	3	4	
Lobaria subdissecta (Nyl.) Vain.	51	39	
Lobaria tenuis Vain.	1*		
Lobariella crenulata (Hook. in Kunth) Yoshim.	8	7	8
Lobariella exornata (Zahlbr.) Yoshim.	3*		
Lobariella pallida (Hook.) Yoshim.	6	7	
Pannaria conoplea (Ach.) Bory	9	24	
Pannaria mosenii C.W. Dodge	6*		
Pannaria prolificans Vain.	1*		
Parmeliella andina P.M. Jorg. & Sipman	22*		
Parmeliella delicata P.M. Jørg. & Arv.	23*		
Parmeliella miradorensis Vain.	13*		
Parmeliella sp.	17	31	
Peltigera sp.	1*		
Pseudocyphellaria aurata (Ach.) Vain.	2	3	23
Pseudocyphellaria crocata (L.) Vain.	1	3	
Sticta aff. *canariensis* (Ach.) Bory ex Delise	47	28	
Sticta andensis (Nyl.) Trevis.	14	11	
Sticta ferax Müll. Arg.	5	7	
Sticta fuliginosa (Dicks.) Ach.	7*		
Sticta humboldtii Hook.	11*		
Sticta laciniata (Sw.) Ach.	12*		
Sticta tomentosa (Sw.) Ach.	61	51	
Sticta sp. 1	9*		
Sticta sp. 2	13*		
Caliciales			
Heterodermia aff. *diademata* (Taylor) D.D. Awasthi			54*
Heterodermia aff. *galactophylla* (Tuck.) W.L. Culb.		47	9
Heterodermia comosa (Eschw.) Follmann & Redón		1*	
Heterodermia corallophora (Taylor) Skorepa		9	11
Heterodermia galactophylla (Tuck.) W.L. Culb.		5	48
Heterodermia hypochraea (Vain.) Swinscow & Krog			9*
Heterodermia hypoleuca (Mühl.) Trevis.		2	25
Heterodermia isidiophora (Nyl.) D.D. Awasthi	25	28	32
Heterodermia japonica (M. Satô) Swinscow & Krog	23	39	46
Heterodermia leucomela (L.) Poelt	43	38	61
Heterodermia microphylla (Kurok.) Swins. & Krog	1*		
Heterodermia palpebrata (Taylor) Trass		2*	
Heterodermia sitchensis Goward & W.J.		7*	
Heterodermia spathulifera Moberg & Purvis		15	54
Heterodermia subcitrina Moberg			3*
Heterodermia sp.	2	8*	
Phaeophyscia aff. *limbata* (Poelt) Kashiw.			12*
Teloschistales			
Teloschistes flavicans (Sw.) Norman			41*

* denote exclusive species per vegetation type.

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