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Large trees and dense canopies: key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests

Á. Benítez[1], M. Prieto[2] and G. Aragón[2]*

[1]*Sección de Sistemática y Diversidad, Departamento de Ciencias Naturales, Universidad Técnica Particular de Loja, San Cayetano s/n, Loja, Ecuador*
[2]*Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, Móstoles E-28933, Madrid, España*

*Corresponding author. E-mail: gregorio.aragon@urjc.es

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The high richness of epiphytes in moist tropical montane forests is continuously decreasing due to deforestation and habitat loss. Lichens and bryophytes are important components of epiphyte diversity on trunk bases and play an important role in the water balance and nutrient cycling of tropical montane forests. As lichens and bryophytes are very sensitive to microclimatic changes, we hypothesized that their species richness and composition would change with forest alteration. We also expected their response patterns to be different given the capability of lichens to photosynthesize using water vapour. In this study, we assessed the richness and composition of epiphytes (lichens and bryophytes) on the trunk bases of 240 trees in primary and secondary forests of southern Ecuador. We found that diversity was higher in primary forests and lower in monospecific secondary forest stands. Total diversity was negatively affected by habitat loss and by the reduction of canopy cover for bryophytes. Shade epiphytes were replaced by sun epiphytes in open secondary forests. We conclude that lichen and bryophyte diversity of tropical montane forests are negatively affected by the removal of large trees and canopy disruption. The different species compositions of primary and secondary forests and the high number of species exclusive to primary forests indicate that secondary forests are of limited importance in compensating for the loss of non-vascular epiphyte species associated with primary forests.

Introduction

Neotropical montane rain forests are considered 'hot spots' of global biodiversity and are a high conservation priority (Gentry, 1995; Myers *et al*., 2000; Dirzo and Raven, 2003). Epiphytes constitute an important floristic, structural and functional component in these forests (Barthlott *et al*., 2001; Gradstein, 2008; Köster *et al*., 2009); however, this exceptional diversity is threatened by continued deforestation and habitat loss (Churchill *et al*., 1995; Bruijnzeel and Hamilton, 2000; Gibbs *et al*., 2010). Forest conversion produces changes that directly influence epiphyte diversity: abiotic conditions are altered, habitat complexity (i.e. tree size, tree species and canopy structure) is reduced, and dispersal is constrained (Werner *et al*., 2005, 2011; Hietz *et al*., 2006). In fact, several authors have found a loss of epiphytic diversity (including vascular plants, bryophytes and lichens) in secondary forests and a higher diversity in primary forests (PFs) (Barthlott *et al*., 2001; Acebey *et al*., 2003; Krömer and Gradstein 2003; Wolf, 2005; Gradstein 2008; Gradstein and Sporn, 2010).

Non-vascular epiphytes (i.e. bryophytes and lichens) constitute an important fraction of epiphytic organisms in tropical montane forests in terms of diversity, biomass and nutrient cycling (Pócs, 1982; Sipman, 1995; Holz and Gradstein, 2005; Mandl *et al*., 2010; Gehrig-Downie *et al*., 2011). Due to their poikilohydric nature, these organisms are tolerant to desiccation (Pardow and Lakatos, 2013), even though their degree of desiccation tolerance varies greatly among species (Proctor *et al*., 2007; Kranner *et al*., 2008). In particular, lichens and bryophytes in humid sites in tropical forests, mainly the forest understory and inner parts of the canopy, are highly sensitive to desiccation (Kranner *et al*., 2008; Pardow and Lakatos, 2013) and may experience photoinhibition when exposed to a small rise in solar radiation (Sillett and Antoine, 2004; Green *et al*., 2008; Pardow and Lakatos, 2013). As the physiology of these organisms is strongly linked to ambient moisture, solar radiation and temperature (Gignac, 2001; Sillett and Antoine, 2004; Green *et al*., 2008), forest logging and land use may greatly affect the diversity of non-vascular epiphytic communities.

The canopy disruption caused by forest logging can affect the humidity, temperature and light conditions inside forests, making them unsuitable sites for shade-adapted species (Gradstein, 2008; Gradstein and Sporn, 2010; Normann *et al*., 2010; Benítez *et al*., 2012). Open forests are generally drier, warmer and windier compared with closed forests, where moisture content is higher and less variable (Gradstein, 2008). However, these microclimate changes do not necessarily involve a decrease in species

richness, but rather a replacement in community composition (Holz and Gradstein, 2005; Nöske *et al*., 2008). The more shade-adapted lichens and bryophytes that are intolerant to desiccation are often replaced by heliophytic species (Ariyanti *et al*., 2008; Gradstein, 2008; Gradstein and Sporn, 2010; Benítez *et al*., 2012).

Forest logging may also have immediate negative effects on the persistence of bryophytes and lichens due to the removal of host tree species (Gradstein, 2008). Host tree characteristics, especially tree size, play an important role in lichen and bryophyte colonization (Benítez *et al*., 2012; Rosabal *et al*., 2013), probably due to greater bark surface available for colonization on large trees and the creation of additional microhabitats (Fritz *et al*., 2008; Ranius *et al*., 2008). Epiphytic diversity may also be influenced by bark roughness, humus and moss cover on the bark surface, stochastic effects of species dispersion, and to lesser extent, bark pH (Sipman and Harris, 1989; Cáceres *et al*., 2007; Gradstein and Culmsee, 2010; Soto *et al*., 2012).

As a result of human activities in Ecuador, PFs have often been replaced by secondary vegetation, creating forests with a less-developed canopy structure, smaller trees and less tree diversity. Benítez *et al*. (2012) found that the diversity of 'shade epiphytes' decreased drastically as a result of such forest disturbance. This could be due to the high percentage of the macrolichen species belonging to the order Peltigerales (∼50 per cent), as these species are adapted to within forest conditions, have high water demands and are sensitive to high solar radiation. However, as macrolichens represent less than one-third of all poikilohydric epiphytic species in tropical montane forests, these results should be interpreted with caution when considering epiphytic communities as a whole (bryophytes and lichens). Knowledge of the differences in epiphytic diversity in primary and secondary forests is crucial to evaluate the conservation status of these forests and to design conservation strategies.

The goal of this study was to explore the response of the non-vascular epiphytic community to forest logging in tropical montane rain forests. We hypothesized that differences in species diversity and community composition would be related to differences in forest structure and microclimate caused by the intensity of forest logging. Another objective was to compare the response patterns between bryophytes and lichens, as lichens prefer relatively high light levels (excluding some cyanolichens) (Sillett and Antoine, 2004; Green *et al*., 2008; Normann *et al*., 2010) and are generally less negatively affected by drought than bryophytes (Perhans *et al*., 2009).

Materials and methods

Study area

This study was carried out at two sites in southern Ecuador and included six remnants of tropical montane forests along a disturbance gradient (Table 1). The climate is humid tropical with a mean annual temperature of 20°C, an annual rainfall of ∼1900 mm and a relative humidity of ∼80 per cent (National Institute of Meteorology and Hydrology, INAMI). The altitude of the studied plots ranged from 2200 to 2800 m a.s.l.

Field work was carried out in three types of forest vegetation varying in age, species composition and tree cover: (1) remnant PF fragments of evergreen tropical montane forests characterized by a dense canopy layer (∼75–85 per cent cover) and large trees (35–40 m tall). The main canopy trees were *Cinchona macrocalyx* Pav. ex DC., *Clusia elliptica* Kunth, *Myrica pubescens* Humb. & Bonpl. ex Willd., *Podocarpus oleifolius* D. Don ex Lamb. and *Weinmannia pubescens* Kunth. (2) Secondary mixed forest fragments (SF) regrown after selective logging events which took place ca. 40 years earlier (Brown and Lugo, 1990; Holz, 2003). Canopy cover was ∼60–70 per cent, and the main canopy trees were *Melastomataceae* and *Lauraceae* species (25–30 m tall). (3) Secondary monospecific forests of *Alnus acuminata* Kunth (MF; 35–40 year old) regrown by natural regeneration after forest clearing (Hofstede and Aguirre, 1999). This tree is a pioneer and native species of the Andes. Monospecific forests are characterized by their uniform structure, absence of understory plants, ∼50 per cent canopy cover and trees up to 20 m tall. Logging and firewood extraction were the main contemporary human activities in MF, whereas there were no human activities in PF and SF.

Species identification

For species identification, we used >200 taxonomic and floristic papers (e.g. Gradstein *et al*., 2001; Gradstein and Costa, 2003; Frisch *et al*., 2006; Cáceres, 2007; Aptroot *et al*., 2008; Timdal, 2008; Lücking, 2009; Moncada *et al*., 2013). For species nomenclature, we followed mainly Tropicos.org for bryophytes and MycoBank for lichens.

Experimental design

We sampled two stands of each forest type (PF, SF and MF). We established ten 5 × 5 m plots in each stand for a total of 60 plots. The distance between the plots in each forest stand was >50 m. In each plot, epiphytic lichens and bryophytes were sampled on the bases of 4 mature trees (total of 240 trees) using 20 × 30 cm grids. Samples were taken on each tree at three different heights (0–50, 51–150, and 151–200 cm) on the northern and southern exposure for a total of six samples per tree. Species richness was defined as the total number of species found in each plot. For epiphytic composition, we estimated the mean cover of each species (per cent of grid area) per tree

Table 1 Means of the environmental variables in the studied primary and secondary montane forests (two stands of each forest type) in Ecuador

Forest	Location	Canopy cover (%)	Tree diameter (cm)	Elevation (masl)	Slope (°)	Aspect
PF1	4° 33′ 27″ S, 79° 22′ 9″ W	78.0	33.1	2848	26.6	E–SW
PF2	4° 33′ 54″ S, 79° 22′ 13″ W	76.5	34.4	2586	32.8	SW–N
SF1	4° 3′ 9″ S, 79° 9′ 55″ W	67.5	28.2	2688	38.2	NW–NE
SF2	4° 33′ 35″ S, 79° 23′ 21″ W	66.0	26.5	2393	32.6	E–SW
MF1	4° 2′ 36″ S, 79° 10′ 20″ W	51.5	16.2	2377	26.4	E–SW
MF2	3° 59′ 53″ S, 79° 10′ 46″ W	54.0	19.6	2196	18.1	NE–SW

PF, primary forest; SF, mixed secondary forest; MF, monospecific secondary forest of *A. acuminata*.

and per plot (as the percentage of four trees). We also measured the following variables at the plot level: canopy cover (per cent), elevation (m a.s.l.), slope (°), aspect (cosine transformed) and mean tree DBH (cm) of the four trees analysed per plot as a proxy for stand structure.

Data analyses

Richness and diversity

We determined the effect of the environmental variables (canopy cover, mean DBH, elevation, aspect and slope) on the following community traits: total species richness, lichen richness, bryophyte richness and species diversity (Simpson inverse and Shannon indices). The Simpson and Shannon indices allow data on species richness and relative abundance to be combined (Gorelick, 2006). The Simpson index was determined by the predominant species, and the Shannon index was based on the assumption that individuals were randomly selected and that all species were represented in the sample (Magurran, 2004). Although host trees have a great influence on epiphyte diversity in temperate regions, the effect of host tree was not explored, as host-specificity does not seem to play an important role in tropical forests with a relatively high diversity of tree species (Sipman and Harris, 1989; Cáceres *et al*., 2007; Rosabal *et al*., 2013).

The effects of slope, aspect, elevation, canopy cover and mean tree diameter on species richness, the Shannon index and Simpson inverse index were analysed at the plot level using generalized linear mixed models (GLMMs) (McCullagh and Nelder, 1989; Verbeke and Molenberghs, 1997). Because forest stands were quite far apart (Benítez *et al*., 2012), stand distance was initially included in the models, but it was later removed as no significant differences were detected. Predictors were included as explanatory variables (fixed factors), and forest and plot were included as random sources of variation. Effects of random factors were tested using the Wald Z-statistic test. We fitted the mixed models using a normal distribution with an 'identity' link function. All GLMM computations were performed using SAS (GLIMMIX version 8 for SAS/STAT).

We measured total species richness, lichen richness and bryophyte richness at the forest level, as the total species identified on 40 trees in each forest. Sampling completeness at the forest level was estimated with *Chao2* species richness estimator, using EstimateS 9.1.0 (Colwell, 2013).

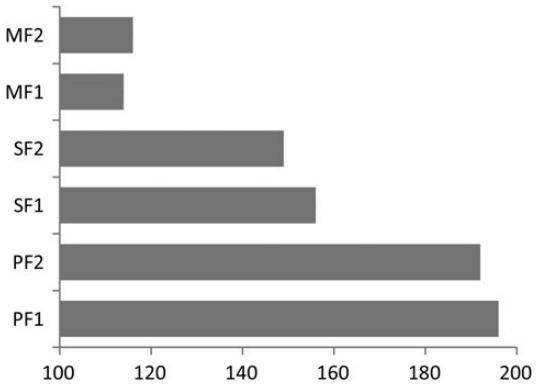

Figure 1 Species richness of epiphytic lichens and bryophytes in primary and secondary montane forests in Ecuador. PF, primary forest; SF, mixed secondary forest; MF, monospecific secondary forest of *A. acuminata*. Axis X, epiphytic species richness; Axis Y, forest types.

Species composition and community structure

Non-metric multidimensional scaling (NMDS) ordination was performed to detect the main factors influencing epiphytic composition. NMDS analyses were carried out using CRAN software R (R Core Team 2013) with vegan package (Oksanen *et al*., 2013). For the NMDS analyses, the Bray-Curtis distance was used, as it is one of the most effective measures for community data (McCune *et al*., 2002). The coefficients of determination (r^2) for the predictor variables were calculated with ordination axes to interpret the relationships between the variables and community composition (1000 permutations).

Bray-Curtis dissimilarity between plots within a forest was calculated as a measure of species replacement. A pairwise PERMANOVA test using Bray-Curtis distance was also performed to assess species similarity among the three types of forest vegetation. Statistical analysis was performed using version 6.1.11 of PRIMER multivariate statistical analysis software (Anderson *et al*., 2008), allowing 9999 random permutations under the reduced model.

Results

Richness and diversity

A total of 374 epiphytic species (307 lichens and 67 bryophytes) were collected in the 60 plots (Supplementary data) The highest number of species was observed in PFs with 234 species, followed by secondary mixed forests (SF) with 191 species and monospecific secondary forests with 134 species (Figure 1; Table 2). A similar pattern was observed for the richness estimator (*Chao* 2), confirming the occurrence of the highest species richness in PF (Table 2). Fifty-four species were exclusive to PF, exceeding the number of species exclusive to SF (Supplementary data). Species replacement

Table 2 Species richness and dissimilarity of bryophytes and lichens at the forest level

	Bryophytes		Lichens	
	Observed species (*Chao 2*; *SE*)	Bray-Curtis dissimilarity (%)	Observed species (*Chao 2*; *SE*)	Bray-Curtis dissimilarity (%)
PF1	44 (46; 3.42)	70.79	152 (173; 9.25)	76.53
PF2	42 (44; 2.53)	72.51	150 (157; 5.16)	73.26
SF1	35 (36; 1.17)	67.83	121 (128; 5.05)	68.79
SF2	31 (32; 2.13)	69.22	118 (132; 7.71)	67.41
MF1	23 (23: 0.04)	58.04	91 (93: 2.06)	57.85
MF2	26 (27; 2.04)	49.8	86 (92; 3.86)	59.34

Chao 2 estimates of total richness are shown in brackets.
SE, standard error; PF, primary forest; SF, mixed secondary forest; MF, monospecific secondary forest of *A. acuminata*.

Table 3 Results of the generalized mixed linear models on community traits at the plot level including beta coefficients (Coef.) and associated SEs

Plot level	Coef. (SE)	*F*-value	*P*-value
Total richness			
Mean tree diameter	0.009 (0.002)	14.46	**0.001**
Canopy cover	0.002 (0.002)	1.45	0.235
Elevation	0.032 (0.016)	3.95	0.054
Slope	<−0.001 (0.001)	0.09	0.771
Aspect	<0.001 (0.000)	2.04	0.179
Bryophytes richness			
Mean tree diameter	0.208 (0.070)	8.74	**0.005**
Canopy cover	0.146 (0.062)	5.62	**0.021**
Elevation	0.121 (0.501)	0.06	0.811
Slope	0.018 (0.027)	0.42	0.522
Aspect	0.002 (0.004)	0.30	0.591
Lichen richness			
Mean tree diameter	0.430 (0.137)	9.88	**0.003**
Canopy cover	−0.039 (0.113)	0.12	0.732
Elevation	0.061 (0.053)	3.60	0.052
Slope	−0.019 (0.051)	0.13	0.721
Aspect	0.005 (0.004)	1.63	0.207
Shannon index			
Mean tree diameter	0.017 (0.006)	7.54	**0.008**
Canopy cover	<−0.001 (0.005)	0.01	0.934
Elevation	0.046 (0.042)	1.17	0.285
Slope	<0.001 (0.002)	0.02	0.901
Aspect	<−0.001 (0.000)	0.01	0.922
Simpson inverse index			
Mean tree diameter	0.445 (0.173)	6.60	**0.013**
Canopy cover	0.008 (0.151)	0.01	0.957
Elevation	1.252 (1.230)	1.04	0.313
Slope	0.027 (0.067)	0.16	0.690
Aspect	−0.007 (0.008)	0.73	0.406

Significant values are in bold.

(as a measure of dissimilarity) was also higher in PF for both lichens and bryophytes (Table 2). Analysis of environmental variables showed that tree diameter was the most relevant predictor of species richness at the plot level (Table 3). Canopy cover had a significant effect on bryophyte richness. The random variable forest was non-significant in all cases.

Species composition and community structure

NMDS ordination resulted in a two-dimensional pattern with an average stress of 13.22 and showed a clear separation of the three different forest types. Most of the variability was explained by Axis 1 ($r^2 = 0.69$), followed by Axis 2 ($r^2 = 0.12$, Figure 2). Axis 1 was associated with changes in canopy cover (Axis 1 = −0.926, Axis 2 = +0.378, $r^2 = 0.712$, $P = 0.001$) and tree diameter (Axis 1 = −0.8333, Axis 3 = +0.553, $r^2 = 0.539$, $P = 0.001$). The pairwise test revealed significant differences in epiphytic composition between the three types of forest vegetation: PF *vs* SF (66.40 per cent dissimilarity, $P = 0.025$), SF *vs* MF (75.00 per cent dissimilarity, $P = 0.034$) and PF *vs* MF (84.18 per cent dissimilarity, $P = 0.015$).

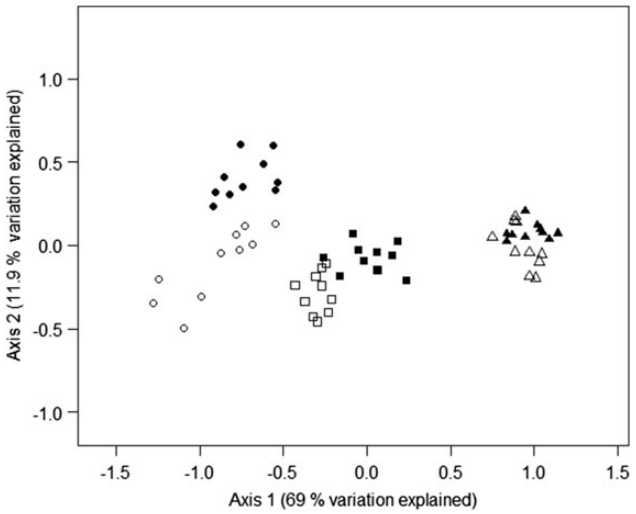

Figure 2 Non-metric multidimensional scaling analysis of species composition for the samples (plots) in the studied primary and secondary montane forests (two stands of each forest type) in Ecuador. PF, primary forest (circle); SF, mixed secondary forest (square); MF, monospecific secondary forest of *Alnus acuminata* (triangle).

Herbertus divergens, *Coccocarpia filiformis*, *C. pellita*, *Coenogonium eximium* and *Cryptothecia exilis* correlated with a dense canopy and large trees as found in PF, whereas *Frullania brasiliensis*, *F. gibbosa*, *Metzgeria lechleri*, *Graphis anfractuosa*, *G. cinerea*, *Heterodermia diademata* and *H. hypochraea* correlated with a more open canopy and smaller trees, characteristic of SF and MF (Supplementary data).

Discussion

Our results showed significant changes in non-vascular epiphytic diversity (lichens and bryophytes) related to forest alteration in montane tropical forests. Major shifts in species diversity were caused by changes in canopy cover and tree size. Thus, epiphytic diversity was higher in PF than in the forests with more altered vegetation. In these two forest types, diversity was higher in mixed (SF) than in monospecific (MF) secondary forests. These results are consistent with other studies on epiphyte diversity in tropical montane forests (e.g. Acebey *et al.*, 2003; Wolf, 2005; Werner and Gradstein, 2009) and support the notion that forest alteration leads to species loss in these communities. These data further indicate that species loss is related to the degree of forest alteration (i.e. selective logging, clear-cut, plantation) (Ariyanti *et al.*, 2008; Sporn *et al.*, 2009; Gradstein and Sporn, 2010) and the time since disturbance (Holz and Gradstein, 2005; Gradstein, 2008). As at least one hundred years are needed for the complete recovery of epiphyte diversity in montane forests (Holz and Gradstein, 2005), the maintenance of PFs is crucial in the conservation of tropical rain forest biodiversity (Gibson *et al.*, 2011).

We also found that lichens and bryophytes responded differently to forest disturbance. Species loss in lichens mainly correlated with reduced tree size, whereas species loss in bryophytes was also significantly related to climatic changes (i.e. increase in solar radiation, decrease in air humidity) induced by lower canopy cover in SF and MF. A high, dense canopy promotes optimal climatic

conditions inside forests for the growth of shade epiphytes which have higher water demands and are very sensitive to solar radiation (Sillett and Antoine, 2004; Gradstein, 2008; Benítez *et al*., 2012; Pardow and Lakatos, 2013). The irradiation in closed forests is converted into heat at the interface of the atmosphere and the canopy, maintaining moist and cool conditions in the forest understory (Hohnwald, 1999, cited in Werner and Gradstein, 2009). Canopy disruption caused by selective logging produces small openings in the canopy (5–10 per cent), which can significantly affect ambient moisture (Zimmerman and Kormos, 2012) and lead to a decrease in the diversity of shade epiphytes, adapted to the moist, shaded interior of the forest (Sipman and Harris, 1989; Acebey *et al*., 2003; Gradstein, 2008; Gradstein and Sporn, 2010). However, while bryophytes experienced species loss due to high irradiation and evaporation stress in more open habitats (Perhans *et al*., 2009), total lichen richness was not reduced by these factors. This may be because some of the more shade-adapted species (shade epiphytes) were replaced by light-demanding species (sun epiphytes) especially in MF where canopy openness was the highest (∼50 per cent). Thus, open secondary montane forests can support a high richness of epiphytic lichens, even though there are fewer shade epiphytes (Hietz *et al*., 2006; Nöske *et al*., 2008).

Species composition of both bryophytes and lichens was severely altered by the increase in canopy openness, indicating that community composition is a more sensitive indicator of human impact than species richness (Nöske *et al*., 2008). In general, shade epiphytes are more sensitive to environmental changes, because they are strongly dependent on atmospheric moisture and experience photoinhibition when exposed to greater sunlight than in their normal environment (Gauslaa *et al*., 2001; Green *et al*., 2008; Kranner *et al*., 2008). Ariyanti *et al*. (2008) found that microclimatic changes related to the loss of shaded cover were responsible for shifts in bryophyte composition. In our study, differences in species composition between the three forest types were particularly noticeable in the higher number of species of the liverwort genus *Plagiochila* and the lichen genera *Coccocarpia*, *Coenogonium*, *Herpothallon*, *Leptogium* and *Sticta* in PFs vs. species of the lichen genera *Graphis, Heterodermia* or *Parmotrema* in secondary forests. Biological characteristics of lichens exclusive to PFs are the predominance of the photobiont with a reduction of the mycobiont (*Coenogonium*) or the presence of cyanobacteria as photobionts, constituting the so-called cyanolichens (*Leptogium*, *Coccocarpia*, *Sticta*) (Green *et al*., 2008; Benítez *et al*., 2012). However, some cyanolichen species (e.g. *Coccocarpia stellata*, *Leptogium azureum*, *L. chloromelum* and *Sticta weigelii*) may also occur in open, relatively dry habitats (Normann *et al*., 2010; Rosabal *et al*., 2010). In this sense, and focusing on these cyanolichens, we observed a contrasted vertical and horizontal zonation along the trunks. In the drier and more open sites along our gradient (*A. acuminata* forests), these species were more common on tree bases (<50 cm) and on northern exposures where light incidence was lower. However, these species in PFs were located at higher elevations (151–200 cm) on both exposures (north and south).

One of the major problems faced by tropical forests is the harvesting of large, long-lived and slow-growing trees (Zimmerman and Kormos, 2012), as they have the greatest bark surface area and the greatest formation of specialized aged bark substrates (e.g. Fritz *et al*., 2008; Johansson *et al*., 2009; Király *et al*., 2013). We suggest that these features, which are absent on younger, smaller trees, are preferred by epiphyte species, which might explain the high species replacement (measured as dissimilarity) between PF and MF.

Conclusion

Species diversity of non-vascular epiphytes (lichens and bryophytes) growing on the trunk bases of tropical montane forests is negatively affected by forest alteration in two ways: (1) removal of hosts, especially large trees and (2) environmental changes caused by canopy disruption. Opposite to Dent and Wright (2009), who pointed the importance of secondary forests in terms of supporting tropical biodiversity, our analyses showed different species composition of primary and secondary forests and a high number of species found exclusively in PFs, thus suggesting that secondary forests are of limited importance in compensating for the loss of epiphytic species in PFs. Although this study contributes to the knowledge of these organisms and their dynamics in tropical ecosystems, we should consider the constraints related to the number of replicates per forest type. Since the response of lichens and bryophytes to new environmental conditions caused by the increase in canopy openness is related to their morphological and anatomical characteristics (e.g. growth form, thallus thickness, type of photobiont and cortical pigments), more studies on the functional traits of epiphytes are needed to better understand their response to forest disturbance.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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