Biodivers Conserv (2015) 24:1239–1252
DOI 10.1007/s10531-014-0855-7

ORIGINAL PAPER

Epiphyte homogenization and de-diversification on alien *Eucalyptus* versus native *Quercus* forest in the Colombian Andes: a case study using lirellate Graphidaceae lichens

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Received: 1 September 2014 / Revised: 9 December 2014 / Accepted: 18 December 2014 /

Abstract In many tropical areas, monospecific tree plantations are replacing natural forest. The ecology of these plantations is quite different from that of natural forests, including the diversity and community structure of vascular and cryptogamic epiphytes. Few studies have looked at the ecology of guilds of epiphytes in plantations versus natural forest. Here, we investigated epiphytic, lirellate species of the family Graphidaceae, the largest family of tropical lichen fungi, which are widely distributed and abundant in tropical regions. We compared species richness and community structure in a monospecific plantation of the introduced tree species *Eucalyptus globulus* versus native oak forest dominated by *Quercus humboldtii*. Overall species richness was substantially higher in the natural oak forest (41 vs. 14 species, with eight shared between both stands, for a total of 47), whereas species abundance was significantly higher in the gum plantation. While species richness per tree (alpha diversity) was comparable between both stands, average species turnover between trees within each stand (beta diversity) was significantly higher in the natural oak forest, resulting in substantially higher overall species richness (gamma diversity). We conclude that the monospecific gum plantation exhibits both de-diversification (lower overall species richness) and homogenization (more similar communities between trees) of these epiphytic lichen guilds. This is not an effect of phorophyte diversity

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Communicated by Karen E. Hodges.

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since in both stands, only a single tree species each was considered. Among the lichens identified, we detected six new to the Neotropics and 29 new records for Colombia.

Keywords Monospecific tree plantations · Alpha diversity · Beta diversity · Gamma diversity · Lichen bioindicators

Introduction

Oak forests reach their natural southernmost limit in the Colombian Andes, where they form an important component of native subandine forest ecosystems, characterized by the dominance of *Quercus humboldtii* Bonpl. (Lozano and Torres 1974; Galindo et al. 2003; León et al. 2009). These forests are found in all three mountain ranges of the country, between 750 and 3,450 m altitude (Agudelo 2009; Muñoz and Camacho 2010). Fossil records suggests that these oak forests go back to the late Cretaceous (Lozano and Torres 1974). The combination of regional mesoclimate and microclimate generated by the canopy of these forests supports a high diversity of epiphytes, among them bryophytes, lichens, ferns, bromeliads, and orchids (Muñoz and Camacho 2010), which contribute substantially to their floristic richness (Lozano and Torres 1974). *Quercus humboldtii*, commonly known as Andean or Colombian oak, can reach up to 40 m height and a DBH of up to 45 cm (Lozano and Torres 1974; Agudelo 2009). Its fruits are eaten and dispersed by small mammals (Lozano and Torres 1974).

In many areas, these native oak forests are replaced by introduced *Eucalyptus* tree monocultures (FAO 1981; Kapelle 2006), mostly *E. globulus* Labill., but encompassing a large number of species originating from Australia. These adapt well to the conditions found in these areas, especially in the highlands of Cundinamarca, Boyacá, and Nariño, mostly between 1,900 and 3,000 m altitude (Hillis and Brown 1984; Muñoz et al. 2010). *Eucalyptus globulus*, also known as Tasmanian blue gum, was introduced approximately 200 years ago by Australian monks (Hofstede et al. 1998). Today, it is the economically most important tree species in the northern Andes, due to its rapid growth (Hillis and Brown 1984; Andrade 2008). It can reach up to 55 m height, under certain conditions in its native Australia (Tasmania) up to 100 m, and a massive DBH of up to 150 cm (Muñoz et al. 2010). Like many Myrtaceae, *Eucalyptus* trees have a flaking bark, making the colonization by epiphytes, especially lichens, difficult, and this bark structure appears to be contributing to the de-diversification of montane forests in the Andes and in other ecosystems (FAO 1981; Sanz et al. 2000; Fonseca et al. 2009).

Tropical montane forest ecosystems offer near-optimal growth conditions for epiphytes, among them lichens. Lichens are comparatively well-documented in Colombian montane forests, although most works focus on macrolichens (Aguirre-C 1982, 1985, 2008; Sipman and Aguirre 1982; Moncada 1998; Rivera and Córdoba 1998; Aguirre-C and Linares 2000; Linares and Pinzón 2001, 2006; Chaparro and Aguirre 2002; Sipman et al. 2008; Moncada et al. 2013a, b, c, 2014; Lücking et al. 2014). In contrast, few studies exist on crustose microlichens, focusing on the largest family of tropical crustose microlichens, Graphidaceae (Rincón-Espitia 2011; Soto-Medina et al. 2011; Soto-Medina and Bolaños 2012; Simijaca 2011; Peláez et al. 2014). Simijaca (2011) is the only study to report epiphytic lichens specifically from oak forest (*Q. humboldtii*). No data are available on epiphytic lichen diversity in *Eucalyptus* plantations, and studies on these introduced ecosystems focus entirely on their economic productivity (Andrade 2008; Muñoz et al. 2010). Little is known about how these introduced tree monocultures affect ecosystem diversity and function, in particular with respect to epiphyte communities, although studies from southern Brazil and Spain suggest that epiphytic lichen communities become depauperate on these trees (Fonseca et al. 2009; Käffer et al. 2009; Calviño-Cancela et al. 2012, 2013).

Here we use lirellate species of the family Graphidaceae to analyze the impact of *Eucalyptus* tree monocultures on epiphyte diversity and community structure, based on studies showing that general patterns of lichen diversity and community structure are correlated with that of other epiphytes at the stand level, even if there is variation at the microhabitat level (Wolf 1994; Hofstede et al. 2001; Kelly et al. 2004; Affeld et al. 2008; Mežka et al. 2008; Lõhmus and Lõhmus 2010). Graphidaceae is a dominant element of tropical lichen communities, with a total number of 2,500 currently accepted species (Wirth and Hale 1963; Staiger 2002; Staiger et al. 2006; Rivas Plata et al. 2013; Lücking et al. 2014). It contains both lirellate taxa formerly classified in Graphidaceae s.str., and taxa with rounded ascomata, formerly separated in the family Thelotremataceae (Rivas Plata et al. 2013). The latter are mostly characteristic of undisturbed forest ecosystems, whereas lirellate taxa colonize both pristine and disturbed vegetation (Rivas Plata et al. 2008). Furthermore, taxonomic treatments for their identification are now readily available (Rivas Plata et al. 2013), compared to other microlichens or tropical macrolichens whose taxonomy has recently been challenged substantially (Moncada et al. 2013a, b, c; Lücking et al. 2014). Lirellate Graphidaceae are therefore well suited to compare lichen community structure between forest stands of different disturbance levels.

Materials and methods

The study was carried out at Chicaque Natural Park, a private reserve situated on the western slope of the Eastern Cordillera in the Colombian Andes, in Cundinamarca and the municipality of San Antonio del Tequendama, between 74°18′25″ and 74°19′25″ western longitude and 4°36′21″ and 4°37′43″ northern latitude. The park is characterized by extensive forest areas with frequent cloud cover (Ojeda 2001; Armenteras et al. 2007), generating a vegetation ranging from montane cloud forest betwen 2,000 and 2,400 m (Rivera and Córdoba 1998) and subandine forest between 2,400 and 2,720 m, according to the classifications proposed by Cuatrecasas (1989) and Rangel (1997). The oak forest of the reserve is dominated by *Q. humboldtii* and is considered one of the last, well-preserved forests of its type near Colombia's capital, Bogotá. Bordering the reserve are various extensive plantations of *E. globulus*, providing a sharp contrast with the native oak forest inside the park.

We delimited one rectangular plot (100 × 10 m) each within an area of native oak forest inside and an area of gum plantation outside the reserve. Within each plot, we randomly chose 28 trees with a DBH of more than 30 cm. On each selected tree, we placed a vertical line in northern direction from 50 to 150 cm height (McCune et al. 1997) and recorded all lichen thalli touching or crossing the line and representing lirellate species of the family Graphidaceae.

The collected samples were curated in the herbarium Emilio Mahecha, cryptogamic section, of the Universidad Distrital Francisco José de Caldas (UDBC). Morphological and anatomical characters were studied and documented using a LEICA stereoscope connected to a CANON Powershot SX 10015 digital camera and, by means of thin hand sections, with a ZEISS compound microscope. Spot tests were performed on sections using solutions

Table 1 Species of lirellate Graphidaceae encountered in this study, their occurrence in each plot, with total number of trees on which species was found, and (in parenthesis) total number of specimens encountered, and indication of new reports for the Neotropics and Colombia

Species	*Quercus*	*Eucalyptus*	NEO	COL	Species	*Quercus*	*Eucalyptus*	NEO	COL
G. acharii	1 (1)	–			*G. seminuda*	1 (2)	–		New
G. angustata	1 (1)	2 (2)			*G. streblocarpa*	2 (2)	–		New
G. bettinae	1 (1)	–		New	*G. subasahinae*	1 (1)	–	New	New
G. carassensis	3 (4)	–		New	*G. subassimilis*	–	1 (1)	New	New
G. dolichographa	2 (3)	–			*G. subcelata*	1 (3)	–	New	New
G. elegans	–	2 (2)		New	*G. subcontorta*	1 (1)	–		New
G. elongata	2 (2)	10 (14)		New	*G. subdisserpens*	1 (1)	–	New	New
G. flavens	1 (1)	–		New	*G. subruiziana*	1 (1)	–		New
G. fujianensis	3 (4)	–	New	New	*G. tenella*	1 (1)	–		
G. furcata	2 (2)	–			*G. xylophaga*	1 (1)	–		New
G. glauconigra	–	1 (1)			*Graphis* sp.	1 (1)	1 (1)		
G. gomezii	2 (2)	–		New					
G. illinata	1 (1)	–			*Leiorreuma* sp.	–	1 (1)		
G. inmersicans	2 (2)	–		New	*P. caesiodisca*	3 (3)	–		New
G. lapidícola	1 (1)	–		New	*P. dendrítica*	8 (9)	27 (110)		
G. lourdesina	2 (2)	–		New	*P. fusca*	–	1 (1)		New
G. nanodes	1 (1)	–			*P. inusta*	2 (4)	15 (23)		
G. nuda	1 (1)	–		New	*P. kalbii*	1 (1)	–		New
G. pinicola	–	1 (1)			*P. lecanographa*	1 (1)	–		New
G. rhizocola	5 (5)	–			*P. major*	1 (2)	–		New
G. ruiziana	3 (3)	–			*P. nylanderi*	1 (1)	–		New
G. rustica	2 (2)	–		New	*P. scalpturata*	10 (22)	7 (7)		
G. sarawakensis	1 (1)	–	New	New	*P.* aff. *scalpturata*	8 (12)	3 (5)		
G. scaphella	1 (1)	–		New	*Phaeographis* sp.	4 (8)	2 (2)		

G. Graphis, *P. Phaeographis*, *NEO* Neotropics, *COL* Colombia of KOH (10 %) and PD (Lücking et al. 2009). For the identification of the species we used keys provided by Staiger (2002), Sipman (2006), Cáceres (2007), Lücking and Rivas Plata (2008), and Lücking et al. (2009).

We determined beta diversity between each pair of phorophytes and subsamples using Sørensen's (1948) coefficient of similarity as distance measure (Villarreal et al. 2006). The distance matrix was ordinated by means of non-metric multidimensional scaling (NMS) and also subjected to cluster analysis, employing flexible beta set to −0.25 as clustering algorithm. For NMS, we used a strategy starting with six axes, with reduction in dimensionality, using 1,000 runs with real data, a maximum of 500 iterations per run, a step length of 0.20, and 0.00001 as stability criterion. We then employed a randomization test with 500 runs with randomized data, to evaluate the recommended level of dimensionality of the NMS. The distance matrix was also subjected to a non-parametric Kruskal–Wallis ANOVA to compare pairwise distance values between the two plots. We also applied indicator species analysis based on a randomization approach, using the two plots as grouping variable. The analyses were performed in PC-ORD 6.0 (McCune and Mefford 1999; McCune and Grace 2002) and Statistica 6.0^{TM}.

Results

We sampled a total of 294 specimens of lirellate Graphidaceae, 128 in the oak forest and 166 in the gum plantation, representing 47 species. Of the 56 trees sampled, one in each plot had no lirellate Graphidaceae, leaving 27 each for the statistical analysis. Most of the samples in the oak forest (75 %) corresponded to the genus *Graphis*, with 32 species, followed by *Phaeographis* (25 %), with ten species (Table 1). In the gum plantation, the majority of the samples (50 %) belonged to *Phaeographis*, with six species, followed by *Graphis* (43 %), also with six species, and *Leiorreuma* (7 %), with a single species (Table 1). Thus, while lirellate Graphidaceae were more abundant in the gum plantation, overall species richness was substantially higher in the oak forest (41 versus 14 species). Among the 47 species recorded, six were new records for the Neotropics and 29 new for Colombia (Table 1).

NMS ordination resulted in a two-dimensional plot as best solution (Table 2). The stress of 25.883 for the first two axes was comparatively high, suggesting that additional community structure is contained on the third axis (combined stress 17.423). However, the

Table 2 Stress in relation to dimensionality as a result of the randomization test for the non-metric multidimensional scaling (NMS) ordination

Axes	Stress in real data (1,000 runs)			Stress in randomized data (500 runs)			p
	Min	Mean	Max	Min	Mean	Max	
1	39.648	47.296	57.056	41.310	47.947	56.855	0.0020
2	24.020	25.883	40.568	23.624	27.686	74.362	0.0040
3	17.069	17.423	21.184	15.924	19.997	75.822	0.0619
4	13.325	13.489	25.480	11.918	15.724	75.753	0.1357
5	11.039	11.450	13.688	9.037	12.827	73.237	0.2295
6	9.773	10.359	19.390	7.347	11.227	70.884	0.3932

primary intention of this analysis was to compare beta diversity patterns between the two plots, which remain the same in all three axis combinations (2–1, 3–1, 3–1); therefore only the two principal axes are displayed here. The diagram showed a rather dense grouping of the *Eucalyptus* trees, whereas the oak trees appeared scattered around the lower periphery of the *Eucalyptus* group (Fig. 1). However, two *Eucalyptus* trees fell within the oak trees, whereas three oak trees clustered with the *Eucalyptus* trees. This pattern was confirmed by the cluster analysis, which resulted in two groups largely corresponding to the two forest plots (Fig. 2).

Statistical comparison of pairwise Sørensen distance values within each plot showed significantly lower values for the *Eucalyptus* plot (average 0.46 ± 0.17, median 0.47, range 0–0.86) than for the *Quercus* plot (average 0.92 ± 0.17, median 1.00, range 0.20–1.00; Mann–Whitney U test: Z adjusted = 21.17, p = 0.0000). Thus, trees within the natural *Quercus* forest have nearly complete species turnover on average, whereas trees within the *Eucalyptus* plantation have over 50 % similarity on average. Richness (number of species per tree) was slightly but not significantly lower for the *Eucalyptus* plot (average 2.74 ± 1.29, median 2, range 1–6) than for the *Quercus* plot (average 3.07 ± 1.57, median 3, range 1–6; Mann–Whitney U test: Z adjusted = 0.74, p = 0.4623). On the other hand, abundance (number of thalli per tree) was significantly higher for the *Eucalyptus* plot (average 6.33 ± 2.97, median 6, range 1–12) than for the *Quercus* plot (average 4.37 ± 2.11, median 5, range 1–8; Mann–Whitney U test: Z adjusted = −2.27, p = 0.0231). As a consequence, overal higher species richness (gamma diversity) for the oak forest (41) as compared to the gum plantation (14) was chiefly determined by the higher species turnover (beta diversity) and not by higher species richness per tree (alpha diversity), with gamma diversity exceeding average alpha diversity by the factor 13.36. This effect was much reduced in the gum plantation, with a factor of 5.11 only.

Indicator species analysis did not detect any species with significant association with oak forest, possibly due to the overall low frequency and abundance of species in that plot (Table 3). Only *Graphis rhizocola* was found with marginal significance to associate with

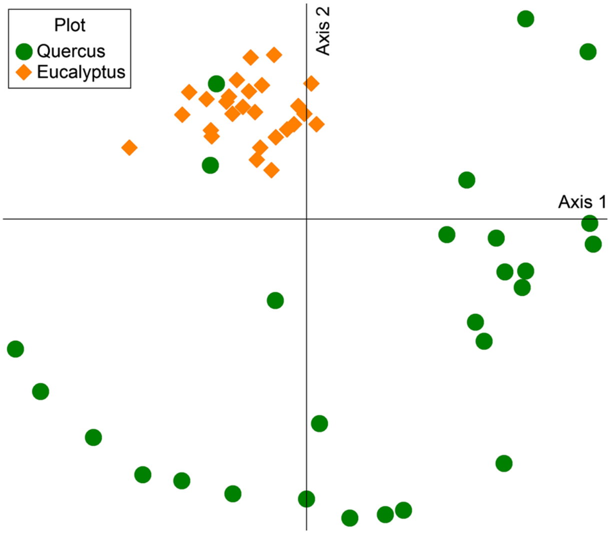

Fig. 1 Best NMS diagram for the ordination of tree samples between oak forest and gum plantation

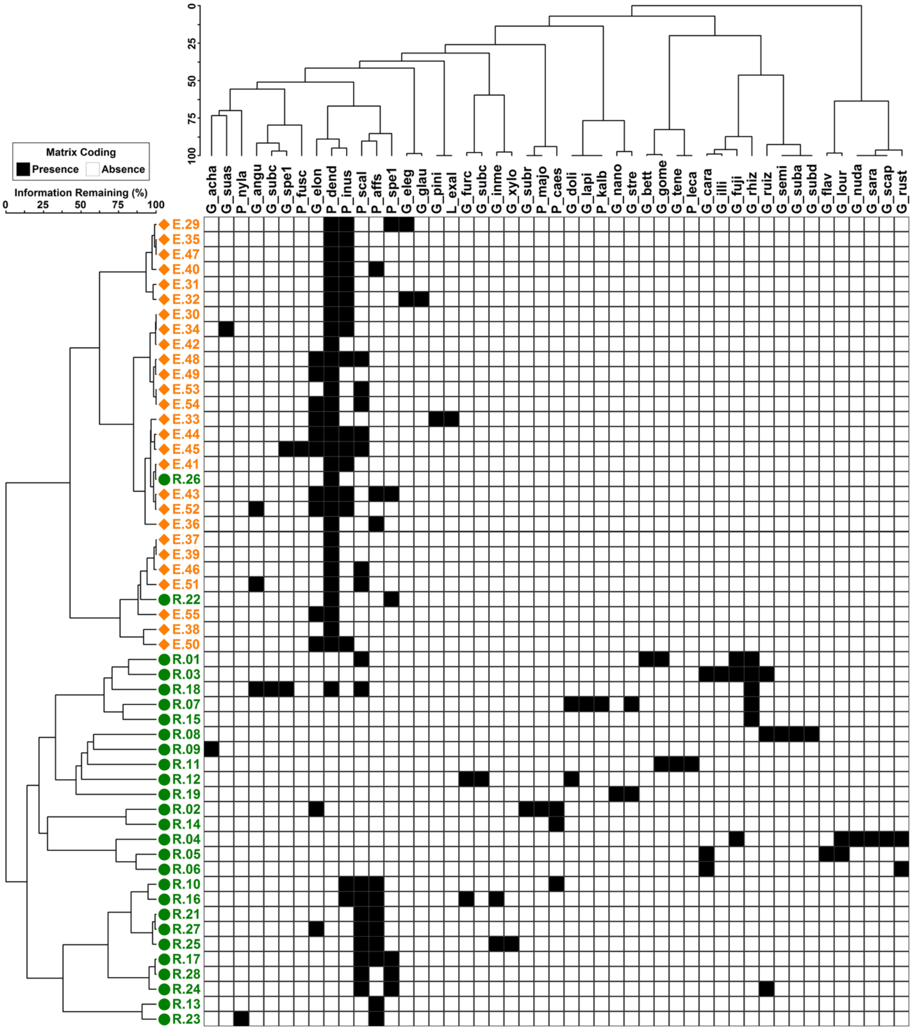

Fig. 2 Two-way cluster dendrogram of trees from the oak forest and gum plantation

Table 3 Results of the indicator species analysis for the two plots

Species	Plot	IV value	Mean	Std.Dev.	p value
Graphis rhizocola	*Quercus*	18.5	8.8	3.26	0.0524
Phaeographis dendrítica	*Eucalyptus*	92.4	34.1	5.07	0.0002
Phaeographis inusta	*Eucalyptus*	47.3	21.6	4.79	0.0006
Graphis elongata	*Eucalyptus*	32.4	16.6	4.42	0.0096

Only species with significant (or close to significant) p values shown natural oak forest. In contrast, three species were found to significantly associate with the gum plantation: *Phaeographis dendritica*, *P. inusta*, and *G. elongata* (Table 3).

Discussion

Effects of disturbed and secondary vegetation on epiphyte diversity and community structure have been demonstrated in various studies, generally showing a decrease in species richness, but sometimes also an increase in certain types of secondary forests due to a mixture of species characteristic of climax and pioneer vegetation (Hickey 1994; Sillett et al. 1995). These effects are mostly due to apparent adaptations of epiphytes to particular niches within native forest (Kelly 1985; ter Steege and Cornelissen 1989; van Leerdam et al. 1990; Zimmerman and Olmsted 1992; Wolf 1993, 1994; Hickey 1994; Hietz and Hietz-Seifert 1995; Andersson and Gradstein 2005). However, effects of monospecific tree plantations of epiphyte diversity and community structure have rarely been studied, and especially not much in tropical regions Sawyer (1993; Hietz and Hietz-Seifert 1995; Merwin et al. 2003; Hietz 2005; Brockerhoff et al. 2008; Käffer et al. 2009; Calviño-Cancela et al. 2012, 2013).

The results of our analysis showed a substantial effect on species richness and community structure in lirellate Graphidaceae lichens in *Eucalyptus* plantations compared to natural *Quercus* forest. While species richness per tree sample was not significantly affected, overall species richness or gamma diversity in the gum plantation decreased by 65 %. This de-diversification was mainly caused by a strong effect of homogenization, with beta diversity between tree samples reduced by approximately 50 % in the gum plantation compared to the oak forest and hence the lichen communities in the gum plantation becoming significantly more similar between individual trees. De-diversification and homogenization are thereby two partially independent effects, since homogenization does not necessarily mean de-diversification, if individual communities per tree retain high species richness. Likewise, de-diversification can occur without homogenization, if individual communities become species-poor but differ between individual trees. Thus, while lichens in terms of abundance did rather well in the *Eucalyptus* plot, in fact significantly better than in the *Quercus* plot, the lichen communities on individual trees were dominated by a few, abundant species, which basically repeated themselves on each tree. This effect is similar to what can be observed under the influence of air pollution, where lichen diversity dramatically decreases but a few species become abundant and even dominant, such as *Lecanora conizaeoides* in Europe (Cook et al. 1990; Wirth 1993; Bates et al. 2001; LaGreca and Stutzman 2006; Massara et al. 2009; Purvis et al. 2010; Lisowska 2011). The much fewer species found under anthropogenic conditions are then often a subset of the species found under natural conditions, with shifted abundance values. In the present case, seven out of 14 species where unique to the *Eucalyptus* plantation, but were all found in single samples only, so this suggested association with *Eucalyptus* has no statistical support. Although not found on the oak trees, these species are expected to occur on other trees in the natural oak forest, with similar bark characteristics as *Eucalyptus*, such as other Myrtaceae. On the other hand, the three dominant species in that plot, in particular *P. dendritica*, were also present in the natural oak forest, but became abundant only in the gum plantation. The high level of beta diversity in the oak forest detected here makes the characterization of an “oak forest community” based on the two-dimensional NMS diagram impossible, since it causes a comparatively high stress value for the first two axes. Hence, distinctive oak forest community can not be discerned; rather, the oak tree samples represent fragments of a hypothetical community with very low levels of species co-occurrences. The usefulness of the NMS ordination in this case lies in the powerful visualization of the very distinctive beta diversity patterns between the oak forest and the gum plantation.

The flaking bark of the *Eucalyptus* trees did not affect overall lichen abundance values, which were higher in the gum plantation than in the oak forest. We have two possible explanations for this: (1) the lichens found in the gum plantation grow faster or mature earlier than those in the oak forest, adjusting to the more dynamic substrate, or (2) the rhythm of bark shedding is not fast enough to prevent certain lichen communities from establishing. Cáceres et al. (2007) found similar result when comparing naturally occurring trees within a lowland rain forest preserve in northeastern Brazil: while lichen diversity was negatively correlated with bark shedding and species composition changed markedly, lichen abundance was not affected. These findings indicate that bark shedding has a filtering effect, allowing for fewer species, namely pioneer taxa that have low levels of competitivity under other circumstances, to colonize such substrates and increase their abundance values. The studies by Fonseca et al. (2009) and Käffer et al. (2009) in southern Brazil and by Calviño-Cancela et al. (2012, 2013) in Spain, comparing natural forest with tree plantations, also supports this point. The same effect is known under the influence of air pollution, with the aforementioned example of *L. conizaeoides* (Cook et al. 1990; Wirth 1993; Bates et al. 2001; LaGreca and Stutzman 2006; Massara et al. 2009; Purvis et al. 2010; Lisowska 2011).

Similar effects of reduced alpha and beta diversity in managed tree plots, with increased abundance of a few, otherwise rare species, were found for both vascular and non-vascular epiphytes in other studies. Thus, Hietz and Hietz-Seifert (1995) reported de-diversification and homogenization of vascular epiphytes in alder plantations (*Alnus acuminata*) versus native cloud forest in Mexico. Merwin et al. (2003) found monospecific tree cultured to be dominated by a few species of bromeliads, compared to a much higher diversity in natural forest. Studies in subtropical and extratropical areas in southern Brazil and northeastern Spain found substantial reduction of species richness and homogenization of community structure for *Eucalyptus* (and pine) plantations compared to natural forest (Fonseca et al. 2009; Käffer et al. 2009; Calviño-Cancela et al. 2012, 2013). Work on tropical herpetofauna and invertebrates discovered similar effects, including for *Eucalyptus* plantations in the Brazilian Amazon (Barlow et al. 2007, 2008; Gardner et al. 2007, 2008; Hung et al. 2008). These findings suggest a general pattern of changes in alpha and beta diversity in monospecific tree cultures, and our study demonstrates the same effect for *Eucalyptus* plantations in tropical montane areas. On the other hand, when monospecific tree plantations are formed by native tree species, this effect appears much less pronounced. For instance, monospecific shade tree stands in coffee plantations, mainly made up by trees of the native genus *Inga*, maintain a comparatively rich and well structured epiphyte community (Hietz 2005). Fonseca et al. (2009) and Käffer et al. (2009) demonstrated much higher lichen diversity for native *Araucaria* plantations compared to introduced *Eucalyptus* and *Pinus* monocultures in southern Brazil.

Many of the aforementioned studies suggest that the diversity of microhabitats generated by the diversity of tree species in natural forest is largely responsible for higher epiphyte diversity compared to monospecific tree plots, possibly due to subtle phorophyte preferences related to bark structure and bark pH (Cáceres et al. 2008). However, our results suggest that also the factor of forest management come into play. By selecting a single tree species in the natural forest, *Q. humboldtii*, we eliminated the factor of phorophyte diversity; hence, if phorophyte preferences alone would explain effects on lichen communities in tree plantations, we would expect the natural oak trees to display similar levels of low beta diversity as the *Eucalyptus* trees in the gum plantation. Yet, we found significant differences in terms of community structure, specifically beta diversity. Therefore, in addition to a reduction in tree species in monocultures, there must be other factors affecting epiphyte diversity. Among these are stand demography, with trees in monocultures having the same age whereas a natural forest, even if dominated by a single species, contains trees of a wide age range. Another factor is spatial structure, with trees in monocultures being evenly spaced whereas in a natural forest they follow a stochastic pattern determined by the interaction of dispersal and competition (Connell 1970; Janzen 1970; Clark and Clark 1984; Wright 2002; Nathan and Casagrandi 2004; Mangan et al. 2010). These factors affect canopy development and hence light regimes (Menalled et al. 1998), as well as the dispersal of epiphytes between trees. We therefore hypothesize that the lichen community structure in the natural oak forest is largely driven by the demography and spatial dispersion of the sampled oak trees and that a managed oak stand, with equally spaced trees of the same age, would have a community structure more similar to the gum plantation, albeit likely composed of different species.

In conclusion, our work supports findings from other studies that monospecific, standardized tree plots, especially those composed of alien tree species, affect diversity patterns of epiphytic communities and particularly lead to less diverse and more homogeneous assemblies. The present study appears to be the first to quantify this effect for *Eucalyptus* plantations replacing natural oak forest in tropical montane regions; our data also suggest that this effect is quite substantial. Analyzing these effects for other epiphytes and forest organisms should therefore be made a priority, considering that *E. globulus* is one of the most extensively planted alien tree species in the Andes (Hillis and Brown 1984).

Acknowledgments This study was partially supported through the following projects funded by the National Science Foundation: *Neotropical Epiphytic Microlichens—An Innovative Inventory of a Highly Diverse yet Little Known Group of Symbiotic Organisms* (DEB 715660 to The Field Museum; PI R. Lücking), and *ATM—Assembling a taxonomic monograph: The lichen family* Graphidaceae (DEB-1025861 to The Field Museum; PI T. Lumbsch, CoPI R. Lücking). The first and second author thank the Universidad Distrital Francisco José de Caldas, especially the Proyecto Curricular de Licenciatura en Biología, and the Herbario Forestal Gilberto Emilio Mahecha Vega (UDBC), Sección Criptógamas, for the logistic support. David Escobar, subdirector of the Parque Natural Chicaque, is thanked for authorizing the study within the limits of the natural reserve. Alejandra Suárez and the Grupo Colombiano de Liquenología (GCOL) assisted in various aspects of the project.

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