

Diversity and rarity of epiphyllous bryophytes in a superhumid tropical lowland forest of Chocó-Colombia

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Abstract – Plant rarity is considered a useful predictor of the extinction risk of species. However, apparent rarity can emerge from incomplete data sets or incorrect sampling. Epiphyllous bryophytes are a poorly collected and taxonomically complicated group, with incompletely known distribution patterns. In this paper we explore the diversity patterns and meso- and micro-habitat specialization of common and rare epiphyllous bryophyte species, and evaluate the threat status of *Aphanolejeunea gracilis*, *Leptolejeunea tridentata*, and *Otolejeunea schnellii*. Epiphylls were collected from 240 samples (10 × 10 cm) in 30 plots of 5 × 5 m in superhumid lowland forest of the Chocó, Colombia. Our results indicate that epiphyll diversity and species composition is similar among palm and non-palm leaves. Disturbance had a negative effect on epiphyll cover, species richness, and diversity of rare species. Data on rare species did not correlate with global or national red lists, indicating that detailed surveys are necessary to accurately assess the threat status of “rare” species.

Bryophytes / Chocó / diversity / endangered species / epiphylls / range distribution / rarity

INTRODUCTION

Extinction processes driven by human factors is one of the main threats to global diversity in our time (Vitousek *et al.*, 1997). Evidence points to habitat loss and fragmentation as the main menace to organisms in tropical regions (Laurance and Useche, 2009). An important criterion to evaluate the extinction risk of a species is its rarity; higher extinction risks are usually associated with rare species. The patterns of rarity and the processes that cause rarity have been widely studied (Cleavitt, 2005). A species can be considered rare if its populations are small, its distribution range is limited, and its habitat is restricted (Rabinowitz, 1981; Söderström *et al.*, 2007). Rarity patterns in plants have been evaluated for many species using a wide arrange of data sets, from historic reports in the literature to specific population counts. Many of the rare species detected in these studies have been included in national or global red lists and incorporated into regional databases, as the primary sources for the conservation of endangered species (Andelman *et al.*, 2004; Broennimann *et al.*, 2005). In the case of tropical

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bryophytes, rarity patterns are particularly misleading because for many species their real distributions are unknown, and even less is known about their population sizes and microhabitat specialization (Hallingbäck *et al.*, 1998).

Global and national bryophyte red lists focus on species with decreasing populations or limited ranges. However inclusion of tropical species in red lists is usually based only on literature data and not on field surveys (IUCN, 2002; Linares & Uribe-M, 2002). Many tropical bryophytes have been poorly collected, especially epiphyllous ones, and their distribution ranges have been determined from herbarium collections only. Even though some inferences can be extracted from the available information: (1) most bryophyte species have widespread distributions with a smaller proportion of endemics than vascular plants (reviewed by Frahm, 2008); (2) epiphyllous bryophytes have a long history of taxonomical complexity and are generally avoided by bryologists; (3) epiphyllous bryophytes show a low specialization to host species or leaf type and communities are more or less constant through the same mesohabitat (Lucking, 1995; Zartman & Nascimento, 2006). This indicates that the understanding of the real distributions of epiphyllous bryophytes is far from complete and that more research is needed to arrive at a more accurate picture as to which species are endangered and how are they threatened by natural or human-induced processes.

This paper focuses on the diversity and rarity patterns of epiphyllous bryophytes in a superhumid tropical forest relative to their threaten status according to national and global red lists (Hallingbäck *et al.*, 1998; Linares & Uribe-M, 2002). We addressed the following questions: What are the main diversity trends of the epiphyllous bryophytes in the superhumid forest of the Chocó? What proportion of the local species is rare? Are the rare species listed in the red book of bryophytes? Are the rare species associated to a particular micro- or mesohabitat in the forest? We hypothesized that if the species are endangered: they will show small distribution ranges, restricted population size, reduced local frequencies, and a strong dependence on environmental factors or substrates (high specialization). We tested this hypothesis using three epiphyllous species previously designated as endangered (Hallingbäck *et al.*, 1998; Linares & Uribe-M, 2002): *Leptolejeunea tridentata* Bischl., *Aphanolejeunea gracilis* Jovet-Ast, and *Otolejeunea schnellii* (Tixier) R.L. Zhu *et M. L. So*.

METHODS

The study area is located in the Chocó superhumid forest, on the Pacific Coast of northwestern South America (Fig. 1). The Chocó forests receive their rainfall from the trade winds that cross the Pacific Ocean, and release their humidity in a narrow fringe between the coast and the Andes. The study site, Tutunendo area, is located at the center of the Chocó region (5°45'27" N, 76°31'13" W) covering an area of approximately 800 km², with an elevation of approximately 100 meters, and mean annual rainfall of 12,400 mm. The region is extremely rich in vascular plant species and is a center of endemism for several vascular plant families including Piperaceae and Araceae (Galeano *et al.*, 1998; Rangel, 2004; Quijano-Abril *et al.*, 2006). The area is covered with continuous forests but pressure from the expanding population is creating a noticeably disturbance pattern in the forests, with increasing rates of wood poaching and land

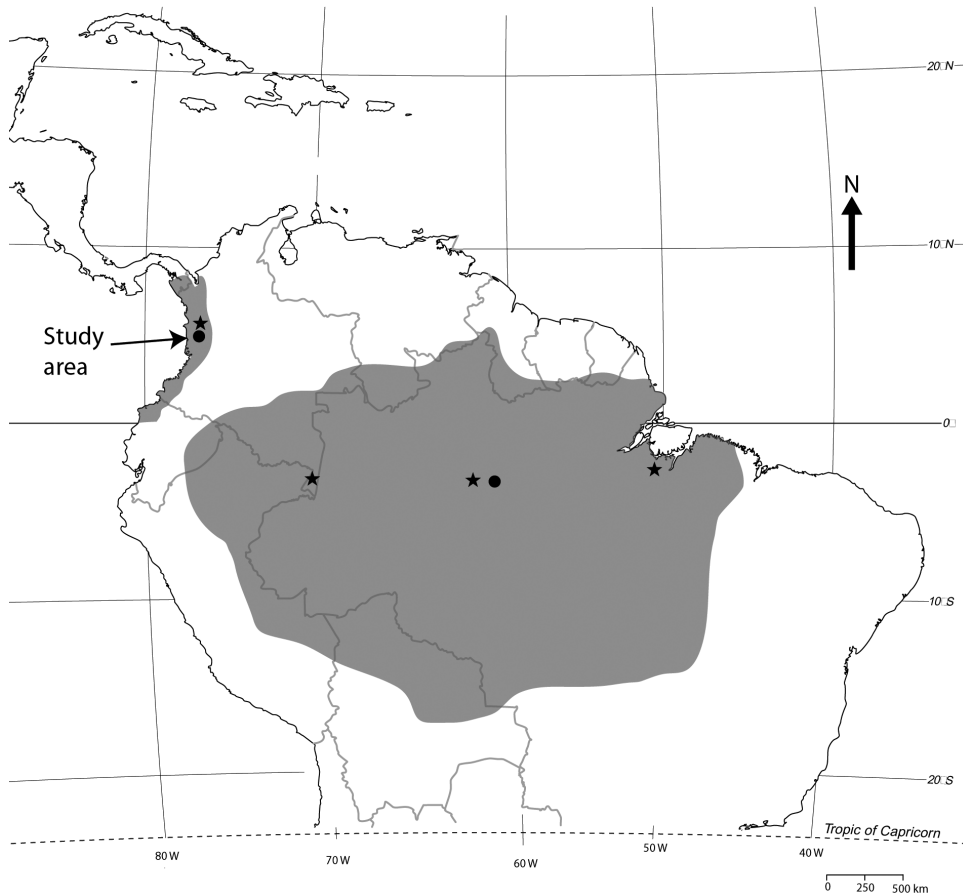


Fig. 1. Location of study site and reported localities of *Leptolejeunea tridentata* (stars) and *Otolejeunea schnellii* (dots), and the range of *Aphanolejeunea gracilis* in northern South America (shaded area).

use change. The occurrence of patches of secondary growth forest and man-made pastures has been increasing during the last 50 years, becoming a real threat to the natural wildlife (Brooks *et al.*, 2002).

Epiphyllous bryophytes were sampled in 30 square plots of 5×5 m. The plots were located in an area covering approximately 200 km^2 and were at least 200 m apart. Plots were selected by placing random points on trails and walking 15 meters inside the forest where the center of the plot was located. In each plot as many as 20 leaves from palms and other plants were collected and transported to the laboratory; leaves were collected up to 3 m height and leaves from epiphytes or recently fallen trees were excluded. Eight samples of 10×10 cm were randomly collected from the leaves at each plot for 240 samples total; four samples each were taken from palm leaves and non-palm leaves. To avoid biases in leaf selection, leaves were placed on tables with the abaxial surface facing up; thus, hiding epiphyll cover. To calculate the area covered by epiphylls, each

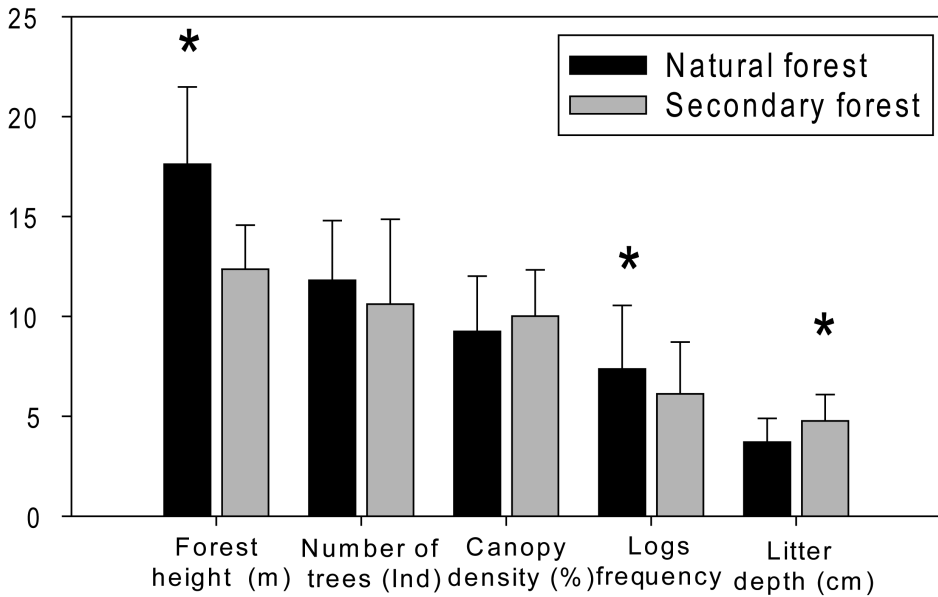


Fig. 2. Mean values for forest structural variables in natural and secondary forests. Significant differences between the forest types are denoted by a star (*) ($p < 0.05$). Bars correspond to one Standard Deviation.

selected leaf was photographed and analyzed using ArcMap v 9.01. The area was calculated for each morphologically recognizable species and values were later assigned after all the species in the sample were identified. The technique used to calculate the area was a digital process similar to the one used in the identification of different land cover classes from remote sensing sensors. The technique is based on the principle of clustering of pixels that have a similar variation pattern across the different bands (Benavides & Sastre-De Jesús, 2009).

We recorded forest structure from 30 10×10 m plots, each surrounding a 5×5 m sample plot. We measured forest mean height (measured based on trees > 10 cm and > 5 cm dbh), canopy density (using a semi-spherical mirror), number of decaying logs on the ground, leaf litter depth (taken as the average from four points), and presence of rocks and crevasses. Based on visual inspection and local reports, local forests were classified as natural forests with low human intervention (20 plots) and secondary growth forests (10 plots). Forest height in natural forest was 17 m and was significantly higher than secondary forest (12 m) ($F_{1,28} = 57.1$, $p < 0.001$). The same trend was observed for the number of logs, with higher values in natural (7.4) than in secondary forests (6.1) ($F_{1,28} = 4.3$, $p = 0.03$), and litter depth, with shallower litter deposition in natural (3.7 cm) than in secondary forests (4.8 cm) ($F_{1,28} = 4.10$, $p = 0.05$) (Fig. 2). A PCA analysis of tree height, litter depth, and log numbers showed that those variables were related with forest type and disturbance (results not shown).

Bryophyte species were identified using general treatments of neotropical epiphylls (Gradstein & Costa, 2003) and papers on *Aphanolejeunea* (Jovet-Ast, 1947), *Leptolejeunea* (Bischler, 1969), and *Otolejeunea* (Grolle & Reiner-Drehwald, 2000). Voucher specimens were deposited in the “Universidad

de Antioquia" (HUA) Herbarium under the series JCB 3100-3500. Distribution ranges of *Leptolejeunea tridentata*, *Aphalanolejeunea gracilis* and *Otolejeunea schnellii* were determined based on literature and herbarium collections (COL, GOET, HUA), with collections from the study site added.

DATA ANALYSIS – We compared the number of rare species and total species richness between natural and secondary forest, and between palm and non-palm substrates, using a two-way ANOVA. The same analysis was performed for species frequency and epiphyll percent cover for rare and all species. Groups were identified using the Tukey test for multiple mean comparisons (Sokal & Rohlf, 1994). ANOVA was performed using SAS statistical software (SAS Institute Inc, 2004). Relative frequency of species was estimated from the 10 × 10 cm subsamples and the stability of their relative frequency was calculated using bootstrap re-sampling with 1000 reruns to obtain 95 percent confidence intervals of the estimates. The bootstrap procedure was applied using the Boot library of the R statistical software (R Development Core Team, 2008).

We also explored the possibility of rare and endangered species being related to a specific group of epiphyllous species (Faith *et al.*, 1987; Faith & Walker, 1996). To this purpose we analyzed the changes in bryophyte composition between forest type and substrate using non metric multidimensional scaling (NMDS) based on the Bray-Curtis similarity index. NMDS is an ordination method that preserves the rank of the similarities between samples, preserving the multidimensional space where the samples are located according to the differences in species composition among sampling units. We selected a two dimensions solution in the NMDS, with a stress of 0.19 (compared to a stress of 0.15 in a three dimensions solution). NMDS was performed with DECODA (Minchin, 2006).

RESULTS

We found 72 epiphyllous bryophyte species in 240 10 × 10 cm leaf samples and 14.5 on average (max. 23, min. 6) in the 5 × 5 m plots. Twenty nine species (40%) were recorded only once and considered locally rare. The mean number of species per leaf sample (10 × 10 cm) was of 3.95 (max. 11, min. 0).

Natural and secondary forests had 61 and 45 species, respectively; these differences were not reflected in the species mean number, as determined by a two-way ANOVA ($F_{1,28} = 1.25$, $p = 0.25$; Fig. 3). The overall number of rare species was similar in natural (26 spp., 42%) and secondary forests (20 spp., 43%), and the same trend was observed for the mean number of rare species per sample and forest type ($F_{1,22} = 0.74$, $p = 0.39$). The total number of species found on palm leaves (52) was almost identical to the number found on non-palm leaves (53); however, the mean number of species per sample was higher on palms than on non-palms leaves ($F_{1,201} = 5.9$, $p = 0.01$) (Fig. 3).

Epiphyll cover was 27.1%, and epiphylls occurred in 92% of the samples collected. Epiphyll mean cover per sample was higher in natural forests (30%) than in secondary forests (19%) ($F_{1,28} = 6.1$, $p = 0.02$). Cover was also higher on palm leaves in natural forest (34%) than in secondary forest (16%) ($F_{1,201} = 5.9$, $p = 0.01$; Fig. 3).

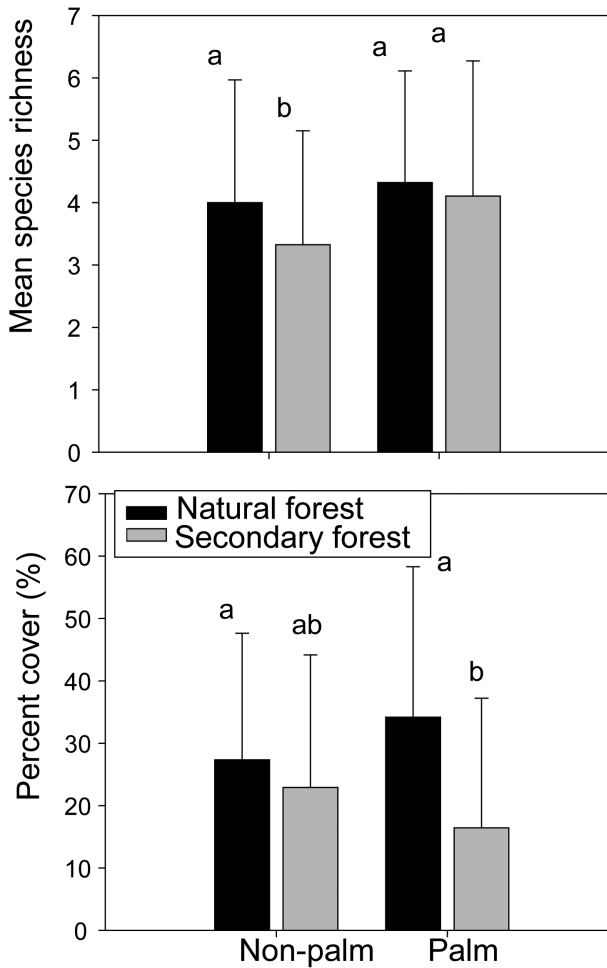


Fig. 3. Mean number of species per sample (top) and mean epiphyll cover (bottom) comparing forest type (natural vs. secondary) and substrate type (palm vs. non-palm leaves). Letters above the bars indicate groups as calculated by Tukey's multiple range test. Bars correspond to one Standard Deviation.

NMDS analysis revealed distinct species groups for natural and secondary forests, but not for palm and non-palm leaves. Vector fitting showed that changes in species composition were related to changes in forest type ($r = 0.45$, $p = 0.001$), forest height ($r = 0.44$, $p = 0.001$), and mean litter depth ($r = 0.33$, $p = 0.019$) (Fig. 4).

As to the three focal species, *Aphanolejeunea gracilis* was present in 106 of the 240 leaf samples and in 23 of the 30 5×5 plots, *Leptolejeunea tridentata* in 73 leaf samples (30%) and 29 plots, and *Otolejeunea schnellii* in 3 leaf samples and 2 plots (Table 1, Fig. 5). *Aphanolejeunea gracilis* showed a preference for natural forest ($F_{1,33} = 5.18$, $P = 0.029$; Fig. 4). In contrast, *Leptolejeunea tridentata* showed no preference for forest type ($F_{1,33} = 0.17$, $P = 0.68$) and was found across the whole study area inhabiting leaves in forest interior and edge, and also in man-made environments such as trails and borders of agricultural fields. *Otolejeunea schnellii* was only found in natural forest (Fig. 6).

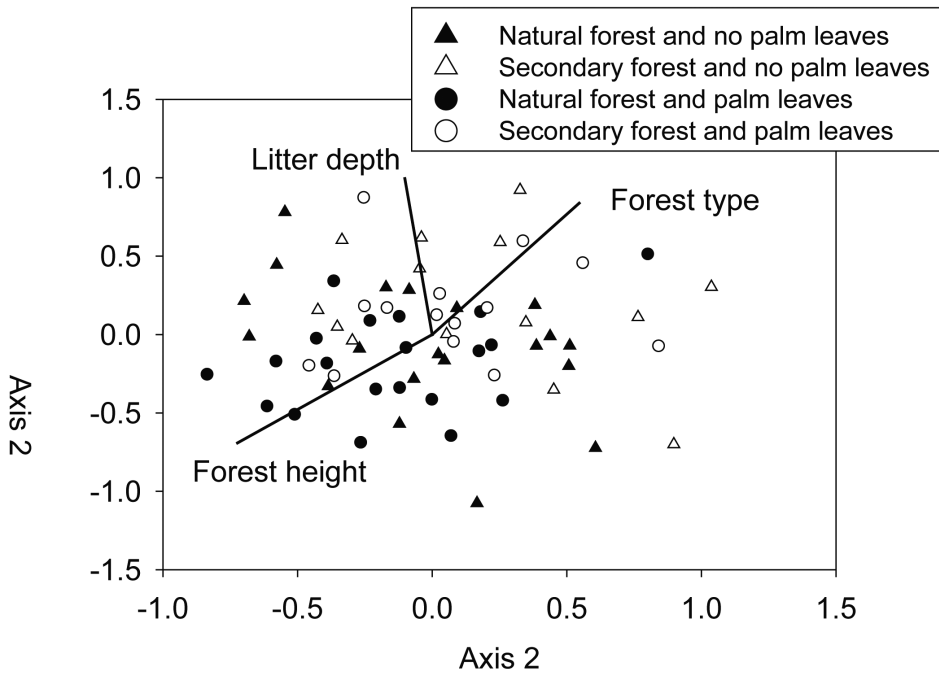


Fig. 4. NMDS biplot diagram of epiphyllous bryophyte composition in natural and secondary forest, and on palm and non-palm leaves. Vectors represent mean litter depth, mean tree height and a dummy variable of forest type (coded 0 for secondary and 1 for natural). For correlation and stress values see text.

Table 1. Species frequencies of epiphyll bryophytes in 240 leaf samples between two forest types, natural versus secondary, and between two substrate types, palm versus no-palm leaves

Forest type Substrate	Natural forest		Second-growth forest	
	No-Palm	Palm	No palm	Palm
Marchantiophyta (Liverworts)				
Lejeuneaceae				
<i>Aphanolejeunea gracilis</i> Jovet-Ast	34	38	14	20
<i>Aphanolejeunea longifolia</i> Jovet-Ast	10	9		1
<i>Aphanolejeunea</i> sp1	4			
<i>Aphanolejeunea</i> sp2		3		1
<i>Arachniopsis diacantha</i> (Mont.) Howe	1			
<i>Archilejeunea parviflora</i> (Nees) Schiffn.	5	1		
<i>Ceratolejeunea coarina</i> (Gottsche) Steph.	13	28	3	11
<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	18	18	9	13
<i>Cheilolejeunea holostipa</i> (Spruce) Zhu & Grolle	1			
<i>Cheilolejeunea rigidula</i> (Mont.) Schust.	1			
<i>Cololejeunea hildebrandii</i> (Aust.) Steph.	2			
<i>Cololejeunea obliqua</i> (Nees et Mont.) Schiffn.	1	2		
<i>Cololejeunea planiuscula</i> Tixier	2			

Table 1. Species frequencies of epiphyll bryophytes in 240 leaf samples between two forest types, natural versus secondary, and between two substrate types, palm versus no-palm leaves (*suite*)

Forest type Substrate	Natural forest		Second-growth forest	
	No-Palm	Palm	No palm	Palm
<i>Cololejeunea platyneura</i> (Spruce) S. W. Arnell		1		
<i>Cololejeunea surinamensis</i> Tixier	2	6	5	5
<i>Colura cylindrica</i> Herzog			2	
<i>Colura</i> sp.	1			
<i>Colura tortifolia</i> (Nees et Mont.) Steph.	2	7		7
<i>Cyclolejeunea accedens</i> (Gottsche) A. Evans	2	4		1
<i>Cyclolejeunea convexistipa</i> (Lehm. et Lindenb.) A. Evans	15	15	9	7
<i>Cyclolejeunea peruviana</i> (Lehm. et Lindenb.) A. Evans	3	7		1
<i>Cyclolejeunea</i> sp1	26	21	14	18
<i>Cyclolejeunea</i> sp2	23	39	6	12
<i>Cystolejeunea lineata</i> (Lehm. et Lindenb.) A. Evans		1		
<i>Diplasiolejeunea brunnea</i> Steph.	7	13	4	12
<i>Diplasiolejeunea cavifolia</i> Steph.	20	14	10	10
<i>Diplasiolejeunea pellucida</i> (Meissn.) Schiffn.	7	7		2
<i>Drepanolejeunea crucianella</i> (Tayl.) A. Evans	28	33	19	21
<i>Diplasiolejeunea</i> sp.			2	
<i>Drepanolejeunea evansii</i> Bischl.	2	5	1	3
<i>Drepanolejeunea inchoata</i> (Meissn.) Steph.	7	13		1
<i>Drepanolejeunea infundibulata</i> (Spruce) Steph.	5	5	1	
<i>Drepanolejeunea polyrhiza</i> (Nees) Grolle et Zhu	11	8	10	7
<i>Drepanolejeunea</i> sp.	1			
<i>Drepanolejeunea subdissitifolia</i> Herz.	2	6		1
<i>Harpalejeunea oxyphylla</i> (Nees et Mont.) Steph.				2
<i>Harpalejeunea stricta</i> (Lindenb. et Gottsche) Steph.	2	2	2	
<i>Harpalejeunea tridens</i> (Besch. et Spruce) Steph.	1			
<i>Lejeunea asperrima</i> Spruce		1		
<i>Lejeunea subspathulata</i> Spruce	1	3		
<i>Lepidolejeunea involuta</i> (Gottsche) Grolle	3	1	3	1
<i>Leptolejeunea elliptica</i> (Lehm. et Lindenb.) Schiffn.	10	10	2	4
<i>Leptolejeunea maculata</i> (Mitt.) Schiffn.	3	2	2	1
<i>Leptolejeunea obfuscata</i> (Spruce) Steph.			1	
<i>Leptolejeunea serratifolia</i> Schiffn.		3		
<i>Leptolejeunea tridentata</i> Bischl.	20	22	10	21
<i>Metalejeunea cucullata</i> (Reinw. et al.) Grolle		1		
<i>Microlejeunea</i> sp1	1	1	2	1
<i>Microlejeunea</i> sp2	1	4	2	1
<i>Odontolejeunea lunulata</i> (Weber) Schiffn.	6	4	2	1
<i>Odontolejeunea rhomalea</i> (Spruce) Steph.	3	2	4	

Table 1. Species frequencies of epiphyll bryophytes in 240 leaf samples between two forest types, natural versus secondary, and between two substrate types, palm versus no-palm leaves (*suite*)

Forest type Substrate	Natural forest		Second-growth forest	
	No-Palm	Palm	No palm	Palm
<i>Otolejeunea schnellii</i> (Tixier) Zhu et So	1	2		
<i>Pictolejeunea picta</i> (Gottsche ex Steph.) Grolle			1	
<i>Prionolejeunea denticulata</i> (Weber) Schiffn.				1
<i>Prionolejeunea microdonta</i> (Gottsche) Steph.	3			
<i>Prionolejeunea muricato-serrulata</i> (Spruce) Steph.	1	3		
<i>Prionolejeunea</i> sp.	1			
<i>Pycnolejeunea contigua</i> (Nees) Grolle		1	1	
<i>Rectolejeunea berteriana</i> (Gott.) A. Evans	2	1	4	
<i>Stictolejeunea squamata</i> (Willd.) Schiffn.	3			1
<i>Symbiezidium transversale</i> (Sw.) Trevis.	1	1		
<i>Xylolejeunea crenata</i> (Nees et Mont.) X.-L. He et Grolle		1		1
Plagiochilaceae				
<i>Plagiochila stricta</i> Lindenb.	1		1	
<i>Plagiochila</i> sp.	2		1	
Radulaceae				
<i>Radula episcia</i> Spruce	9		4	1
Bryophyta (Mosses)				
Calymperaceae				
<i>Syrrophodon incompletus</i> Schwägr.		1		
<i>Syrrophodon prolifer</i> Schwägr.	1			
Hookeriaceae				
<i>Crossomitrium epiphyllum</i> (Mitt.) Müll. Hal.				1
<i>Crossomitrium patrisiae</i> (Brid.) Müll. Hal.	22	9		3
Pilotrichaceae				
<i>Callicostella pallida</i> (Hornsch.) Ångström	1			
Sematophyllaceae				
<i>Trichosteleum papillosum</i> (Hornsch.) A. Jaeger	1			

The combined literature, herbarium and field data showed that *Aphanolejeunea gracilis* is widely known in tropical America, from Mexico to Bolivia and from the Pacific coast of Colombia in the West where it is locally very common, to the Atlantic coast of Brazil in the East (Gradstein & Costa, 2003). *Leptolejeunea tridentata* shows a wider distributional range than previously considered (Linares & Uribe-M, 2002) and occurs along the Colombian Pacific coast where it was originally described and is locally common, the southern Colombian Amazon region (Ruiz-Agudelo & Aguirre, 2004), the middle Amazonian basin of Brazil (Zartman, 2003), and the eastern Amazon area, (Ilkiu-Borges, 2000), spanning more than 3000 km. Finally, *Otolejeunea schnellii* is reported here for the first time in Colombia (collection JCB 3150, HUA) and is otherwise known from the Manaus region in the central Amazon basin (Fig. 1).

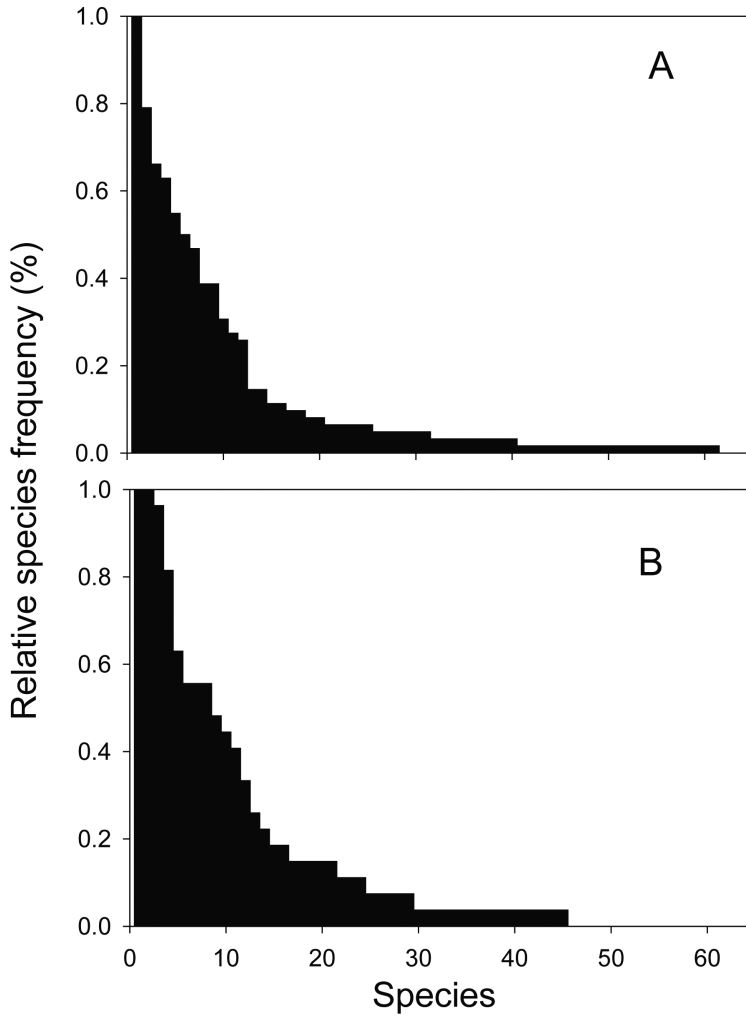


Fig. 5. Relative frequency of 72 epiphyllous bryophyte species in the superhumid forest of the Chocó, in natural forest (top), and in secondary forest (bottom). Frequency was calculated from presence in 240 10×10 cm samples.

DISCUSSION

The superhumid forests of the Chocó have a rich epiphyllous flora. As compared with other epiphyllous studies in neotropical lowland areas, our study usually shows higher species richness in fewer samples. Presumably, this is due to the exceptionally humid local climate, with annual rainfall over 10,000 mm. For example, a study in central Amazonia (Zartman, 2003)

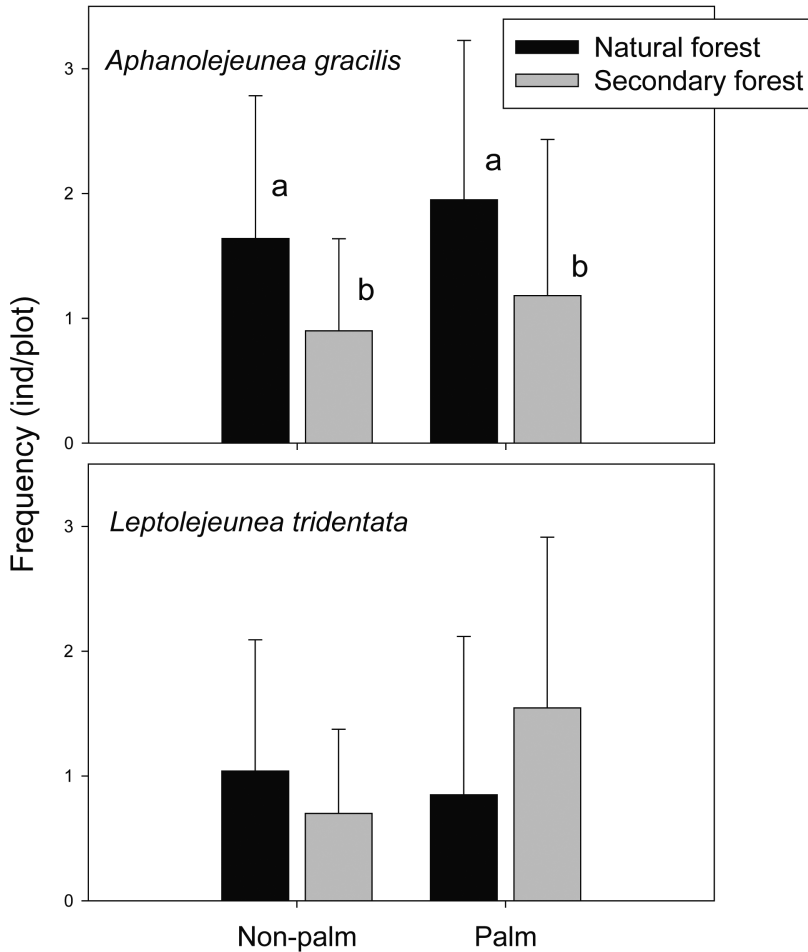


Fig. 6. Mean species frequency for *Aphanolejeunea gracilis* (A) and *Leptolejeunea tridentata* (B). For further explanation see Fig. 3.

recorded 65 species sampled in more than 718 leaves in 16 1-ha plots. Mean annual rainfall in central Amazonia is around 1,900 mm. A rather similar number (60 spp.) was reported from 12 0.1-ha plots in the Atlantic forest of Brazil (Pereira-Alvarenga & Pôrto, 2007) where mean annual rainfall was 2450 mm. For a study in Costa Rica, Sonnleitner *et al.* (2009) reported 60 species from 114 leaves of 57 phorophytes; at this location mean annual rainfall was 6,000 mm (Wanek & Pörtl, 2005). And only 15 species were reported from 200 leaves in a forest in Panamá with mean annual rainfall of 2,600 mm (Windsor, 1990; Marino & Allen, 1992). However, higher species numbers were found by Lücking (1995, 1997) who recorded 86 epiphyllous species in 0.1 ha of submontane forest (*ca* 500 m) of Costa Rica, with mean annual rainfall over 7000 mm (Lücking, 1995).

Epiphyllous communities are considered to respond swiftly to changes in microclimatic conditions (e.g. Richards, 1984; Lucking, 1999; Sonnleitner *et al.*, 2009). In the Amazon forest species composition and richness changed according to forest fragment size, with common species appearing more sensitive to fragmentation than rare ones (Zartman, 2003). Our results recorded species richness, cover, and composition changed between disturbed and natural forests; highlighting the relevance of microclimate on epiphyllous communities. In contrast, in terms of species richness non-epiphyllous liverworts have shown a weaker response to changes in microhabitat conditions; for example similar numbers of species occurred in 10 year old fallows and natural forest in Bolivia (Acebey *et al.*, 2003). However, species composition and abundance of non-epiphyllous liverwort species may change significantly from natural to disturbed forest (Ariyanti *et al.*, 2008; Gradstein & Sporn, 2009).

As to the three focal species, we found that two species previously reported from only a few localities and a handful of collections are fairly common in the investigated Colombian forests. Therefore, their status of being rare and endangered, assigned by Linares & Uribe-M (2002), was not supported. The wide distribution of *A. gracilis* is indicative of the limited exploration of many tropical forests by trained bryologists (Gradstein & Costa, 2003). At the same time, species long considered endemic are found in more and distant localities, such is the case in *L. tridentata*, previously known only from the Chocó of Colombia but recently reported from all across the Brazilian Amazon (Linares & Uribe-M, 2002). The new report from the Chocó of *Otolejeunea schnellii*, a species described from the Manaus region in the central Amazon region, also indicates a much wider distributional range.

We propose that *L. tridentata* and *A. gracilis* should be excluded from the national red list of Colombia for two reasons. First, the collections from the Chocó and the Amazon Colombian rain forests, two different biogeographical areas of Colombia (Olson *et al.*, 2001), indicate broader distribution ranges than previously thought. Second, the high frequency observed in these two species support the hypothesis that they have populations that are large enough to be self sustainable in the long term, even with increasing forest disturbance. Fragmented landscapes have shown to have a low effect on the genetic diversity of epiphyllous liverworts, at least in neutral markers, indicating that small populations can have enough genetic variability to guarantee the viability of local populations (Zartman *et al.*, 2006; Zartman & Nascimento, 2006)

Bryophyte rarity has been related to substrate rarity, meaning that substrates that are not frequent in a landscape will have larger proportion of rare species than common substrates (Newmaster *et al.*, 2005). In this scenario, epiphyll rarity can be considered a result of dispersal constraints and microhabitat limitations more than substrate availability, provided that suitable habitats are available (forested areas). Epiphylls were collected only on non-haired leaves since previous studies have shown a significant lower diversity of epiphylls in haired leaves. On the other side palm leaves have been found to support up to 24 species (Lucking, 1995). We found no difference in the frequency of species on palm or non-palm leaves indicating a low substrate preference and thus supporting our hypothesis. Therefore, some predictions concerning the factors controlling the local abundance of these species can be formulated. *Aphanolejeunea gracilis* and *O. schnellii* showed a preference for natural over secondary forest, indicating a particular microhabitat and mesohabitat preferences for these two species. On the other hand, *Leptolejeunea tridentata* was found in almost all the forest microhabitats, even in the forest edge exposed to full

sunshine (field observation). We therefore predict that dispersal limitations have a stronger effect on its local abundance than microhabitat conditions.

In this study more epiphyllous bryophyte species and higher covers were found in natural than in secondary forests, indicating possible effects of the stable conditions; that is, higher canopy development, and low perturbation rate, on epiphyll colonization and growth. In contrast, non-epiphyllous bryophytes seem to be more affected by microhabitat availability than mesohabitats, and rare species are concentrated in rare microhabitats (Newmaster *et al.*, 2005). In our case, epiphyll rarity was more related to a particular mesohabitat (natural and secondary forest) than to microhabitat rarity. We suggest that the conditions for epiphyllism are so stressful that once the climatic barrier for epiphyll development is crossed, the species tolerant to these particular mesohabitats will arrive and thrive regardless of microhabitat characteristics such as phorophyte species or micro-topography (but large topographic differences such as position in ridges or ravines cause changes in species composition; (Sonnleitner *et al.*, 2009). Sonnleitner and collaborators (*l.c.*) also reported a low relationship between epiphyllous bryophyte composition and canopy cover or light intensity: a pattern that we also observed in the present study. Compared with trunk epiphytic liverworts, epiphylls are considered to have smaller distribution ranges and environmental tolerances (Acebey *et al.*, 2003).

Our study indicates that, apart from substrate limitations, epiphyllous bryophytes can be found across large areas and under a wide arrangement of environmental conditions. They only require enough moisture and shade. We emphasize that future conservation efforts addressed to preserve bryophyte populations should evaluate the current status of the populations, since information in herbaria and taxonomical literature may not reflect the real distributions and abundances of the species. In turn, herbaria and taxonomical literature should be used to select or guide which species require further ecological evaluation (Hallingbäck *et al.*, 1998; Hallingbäck, 2007). Finally, this study shows that whole epiphyllous communities are more affected by small scale human disturbances in the forests, such as selected timber extraction, than individual species. However, since the ecology and demography of many species remains unknown, the scientific basis for the conservation of epiphylls still remains weak.

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