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Bryophyte communities along horizontal and vertical gradients in a human-modified Atlantic Forest remnant

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Abstract: We compared the richness, diversity, and composition of epiphytic bryophytes in a Brazilian Atlantic Forest remnant along zones of height within host trees (vertical gradient) and edge to interior (horizontal gradient). We established five classes of edge distance, and within each one, three host trees were selected (15 in total). Samples were collected in five height zones within host trees from the base to the top. The highest average values of richness and diversity were found in the trunk zone. There was no significant difference of bryophyte total richness and diversity along edge distance and vertical zones. However, the guilds of light tolerance displayed particularities regarding vertical zonation. Shade epiphytes decreased significantly along vertical gradients, whereas sun epiphytes increased, demonstrating a compositional vertical stratification within host trees. Thus, bryophyte distribution in both understories and canopies is more related to microenvironmental conditions than landscape characteristics such as edge distance. Moreover, the features of the Atlantic Forest associated with the environmental heterogeneity of the remnant may play an important role in the lack of gradient in species' composition from the edge to the interior of the forest.

Key words: Brazil, canopy, community ecology, edge effects, tropical forest, vertical stratification.

Résumé : Les auteurs ont comparé la richesse, la diversité et la composition des bryophytes épiphytes dans une forêt vestigiale du Brésil Atlantique selon les zones en hauteur (gradient vertical) et de la bordure vers l'intérieur (gradient horizontal) sur les arbres-hôtes. Ils ont établi cinq classes de distances par rapport à la bordure et à l'intérieur de chacune, ils ont sélectionné trois arbres-hôtes (15 au total). Ils ont récolté des échantillons dans cinq zones de hauteur sur chaque arbre-hôte de la base vers le sommet. Ils ont observé les valeurs moyennes les plus élevées pour la richesse et la diversité dans la zone du tronc. Il n'y a pas de différence significative dans la richesse et la diversité en bryophytes totales selon la distance des bordures et les zones verticales. Cependant, les regroupements selon la tolérance à la lumière montrent des particularités en ce qui a trait au zonage vertical. Les épiphytes d'ombre diminuent significativement le long des gradients verticaux alors que les épiphytes de lumière augmentent, ce qui démontre la présence d'une stratification verticale de la composition en espèces à l'intérieur de l'arbre-hôte. Ainsi, la distribution des bryophytes à la fois en sous-étages et dans la canopée montre une relation plus étroite avec les conditions micro environnementales qu'avec les caractéristiques du paysage, comme la distance de la bordure. De plus, les caractéristiques de la forêt atlantique associées avec l'hétérogénéité environnementale du vestige pourraient jouer un rôle important dans l'absence de gradient dans la composition en espèces, de la bordure vers l'intérieur de la forêt.

Mots-clés : Brésil, canopée, écologie des communautés, effet de bordure, forêt tropicale, stratification verticale.

Introduction

Bryophytes with epiphytic habits reach a peak occurrence in tropical rainforests, inhabiting trees from the base to the outer canopy (Richards 1984; Uniyal 1999). The differences in air temperature, relative humidity, and quantity of light from understories to canopies and the age, diameter, angle, and bark texture of twigs, branches, and trunks promote a microclimatic gradient that can influence the vertical distribution of bryophytes (Frahm 1990; Whitmore 1998; Lowman and Rinker 2004; Sillett and Antoine 2004; Sporn et al. 2010).

Several authors have documented a clear species' turnover in community composition, richness, and life forms along vertical gradients (Cornelissen and ter Steege 1989; Cornelissen and Gradstein 1990; Montfoort and Ek 1990; Gradstein 1995; Wolf 1994, 1995; Acebey et al. 2003; Mota de Oliveira et al. 2009). Moreover, some of these authors (e.g., Montfoort and Ek 1990; Gradstein 1995; Acebey et al. 2003) have proposed that an approximate representation of the epiphyte group can be obtained by

sampling only 4–5 host trees, from the base to the outer canopy, and that the richness of an area can be underestimated when only studying and exploring the understory. At least this is the case in a reasonably conserved forest.

The importance of the canopy changes according to the structure of the vegetation. Acebey et al. (2003) compared the bryophyte flora of a primary forest with the flora found in an area undergoing different regeneration stages in Bolivia. The authors found that species' richness in the primary forest was higher in the canopy, whereas forests undergoing regeneration presented higher species' richness in an understory mainly composed of sun-tolerant and generalist bryophyte species with a growth strategy more resistant to drought, presumably because the forest was much more open.

A recent study of the Atlantic Forest, Brazil (Alvarenga et al. 2010), showed a clear alteration in vertical stratification of bryophytes within host trees between conserved and nonconserved fragments. Bryophytes failed to colonize lower trunks (2.1–10 m)

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Fig. 1. Location of the forest remnant and sampled host trees in the Murici Ecological Station, Alagoas, Brazil (reproduced with permission; Silva and Pôrto 2010).

and higher zones in most of the nonconserved fragments; they were restricted to the base (0–2 m) and with a greater proportion of generalists and sun-tolerant species compared with conserved fragments, i.e., with lower rates of habitat loss and fragmentation.

Indeed, habitat loss and fragmentation, and consequently edge effects, are considered the most harmful effects for the flora found in forest environments and can result in considerable species' loss (50% or more), especially those with low tolerance to desiccation (Gradstein 1992; Sillett et al. 1995; da Costa 1999).

The edges of remnant forests have been considered a distinctive biotic and abiotic gradient (Harper et al. 2005) in which species and microclimatic factors are distributed linearly in edge–interior directions (Wiens et al. 1985; Forman 1995; Moen and Jonsson 2003). Recent studies of bryophyte species' richness along edge–interior gradients (0–100 m) in Atlantic Forest fragments showed no significant observable edge influences. However, a holistic analysis of environmental factors in the Atlantic Forest, which included its historical use, better explained the bryophyte distribution (Alvarenga et al. 2009; Silva and Pôrto 2009, 2010; Oliveira et al. 2011). The authors attributed this to the highly complex environment of the Atlantic Forest, where the edge effects would be diffuse along the edge–interior directions.

In light of these issues and considering the importance of Atlantic Forest conservation and the bryophyte sensitivity to environmental changes, this is the first study that aims to determine whether species' distribution patterns in both the vertical (0–1000 m) and horizontal (base–canopy) gradients are modified in an Atlantic Forest landscape currently under anthropogenic pressure. Previous studies on how edge effects affect bryophytes, conducted in the Atlantic Forest, used a range of 0 to 100 m of edge distance (Alvarenga et al. 2009; Silva and Pôrto 2009, 2010; Oliveira et al. 2011) and showed that the edge effect was not an important variable. In the present study, we tested whether the edge effect could be detected in a wider range (an interval of 200 m) to see if the nucleus of the fragment or the vertical gradient would be more effective in explaining the distribution of bryophytes in the study area. The following questions were investigated. (i) Does the sampling of a small number of host trees (4–5, as recommended in literature) provide a representative estimate of the epiphytic bryophyte richness of the area? (ii) Does bryophyte richness and diversity respond better to the vertical (zones within host trees) or horizontal (edge-distance) gradients or do they respond to both factors together? (iii) Is the bryophyte flora of host trees near the edge predominated by species naturally adapted to dry sites (sun-tolerant) such as those occurring in the canopy of the remnant core? Is the canopy community the only one to persist near the edge while the understory community disappears? (iv) On the other hand, is the bryophyte flora in the understory of the remnant core mainly populated by shade-tolerant species?

Materials and methods

Study site

The study was carried out in the largest fragment of the Murici Ecological Station (EsEc Murici) (09°11'05"N–09°16'48"N, 35°45'20"W–35°55'12"W), located in the municipalities of Murici and Messias, Alagoas, Brazil (Fig. 1). The area consists of 6116.00 ha in the Atlantic Forest Domain and is classified as Lowland Open Broadleaf Forest (Veloso et al. 1991). It is considered of high biological importance and a priority for the conservation of plant groups, invertebrates, reptiles, amphibians, birds, and mammals (Conservation International do Brasil et al. 2000).

The area has a mountainous relief, with elevation varying between 100 and 643 m. The climate is hot and humid, with rainy and dry seasons. The average annual rainfall and temperature

throughout the fragment are ca. 2200 mm and 24 °C, respectively (National Institute of Meteorology Information (INMET), Pernambuco, Brazil, average calculation based on data from 1961 to 1990).

The selected fragment in which the study occurred covers 2628.00 ha, with a maximum width of approximately 2000 m, and is surrounded by a matrix of pastures and sugar cane fields. The average density, diameter at breast height (DBH), and height of trees are, respectively, 1926.7 individuals/ha, 15.17 cm, and 14.52 m (Oliveira et al. 2011). Dominant host tree species include Anacardiaceae (*Tapirira guianensis* Aubl.), Annonaceae (*Anaxagorea dolichocarpa* Spreng. & Sandw.), Euphorbiaceae (*Sapium glandulatum* Pax), Fabaceae (*Parkia pendula* (Willd.) Benth. ex Walp.), Moraceae (*Brosimum guianense* (Aubl.) Huber), and Sapotaceae (*Mannikara salzmännii* (A. DC.) H.J. Lam, *Pouteria bangii* (Rusby) T.D. Penn.).

Sampling

To sample from the edge towards the interior of the forest, five classes of distance from the edge were established: 0–200 m, 201–400 m, 401–600 m, 601–800 m, 801–1100 m. Using a digitized map of the fragment, obtained through a 2003 satellite image (SPOT 4 Datum SAD 69), three geographical points per distance class (distant from each other by at least 100 m and 10 m from the clearing area) were randomly drawn with the “animal movement” tool of Arcview 3.2a software. Subsequently, these geographical points were found in the field with the help of a GPS unit (Garmin 60CSX) and guided the selection of host canopy trees, with heights between 15 and 30 m and with a visually great diversity of bryophytes.

The host trees were climbed using a single-rope technique (Perry 1978; Moffet and Lowman 1995). Five height zones (Pócs 1982, with modifications) were established: Z1, base (soil level to 2 m elevation); Z2, trunk (2–8 m elevation); Z3, 1st ramification; Z4, 2nd ramification; and Z5, outer canopy or last ramifications and thinner branches (Fig. 2). To obtain the greatest possible bryophyte diversity, one sample of all bryophytes species present in each height zone per host tree was collected. From the total number of points that we collected from trees, five did not have bryophyte samples. When collections in loco were not possible, the thinner branches were cut with a pruner, knocked down, and picked up from the soil. It is important to state that the term canopy here is defined as the combination of all foliage, twigs, fine branches, and their attending flora (Parker 1995). In this context, the “canopy” here denotes forest community architecture from the first ramification to thinner twigs, i.e., the top of trees.

All samples were documented and deposited at the UFP – Geraldo Mariz Herbarium in the Botany Department of the Federal University of Pernambuco.

Data analysis

Completeness of sampling was assessed through the Chao2 index (Chao 1984) and computed using EstimateS 7.5 (Colwell 2005):

$$(1) \quad S1 = Sobs + \left(\frac{a^2}{2b} \right)$$

where $S1$ is the estimated number of species, $Sobs$ is the observed number of species, a is the number of singletons, and b is the number of doubletons. Host trees were treated as independent samples.

Diversity was calculated according to the Shannon index (H') (Ricklefs 2001). In this calculation, relative abundance is represented by the frequency of each species within the total of samples and not the number of individuals, as bryophytes occur in groups of small and ramified individuals, which hampers their counting (Mägdefrau 1982).

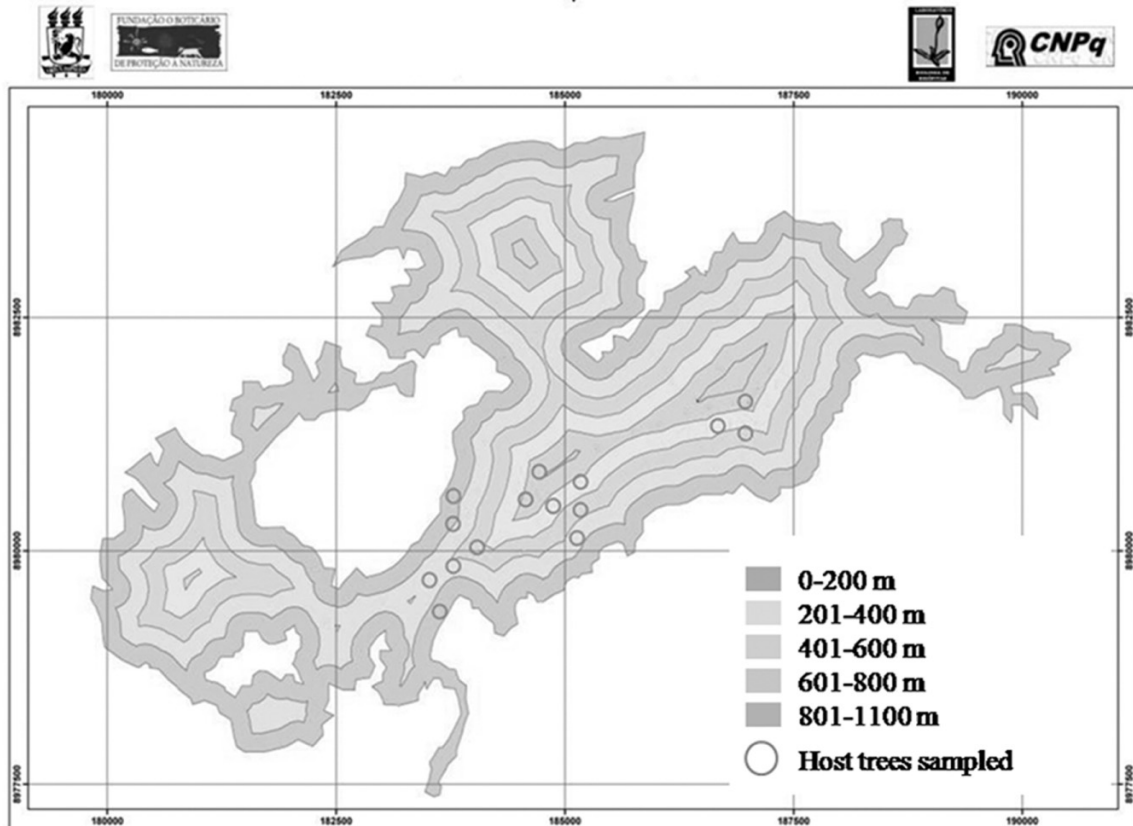
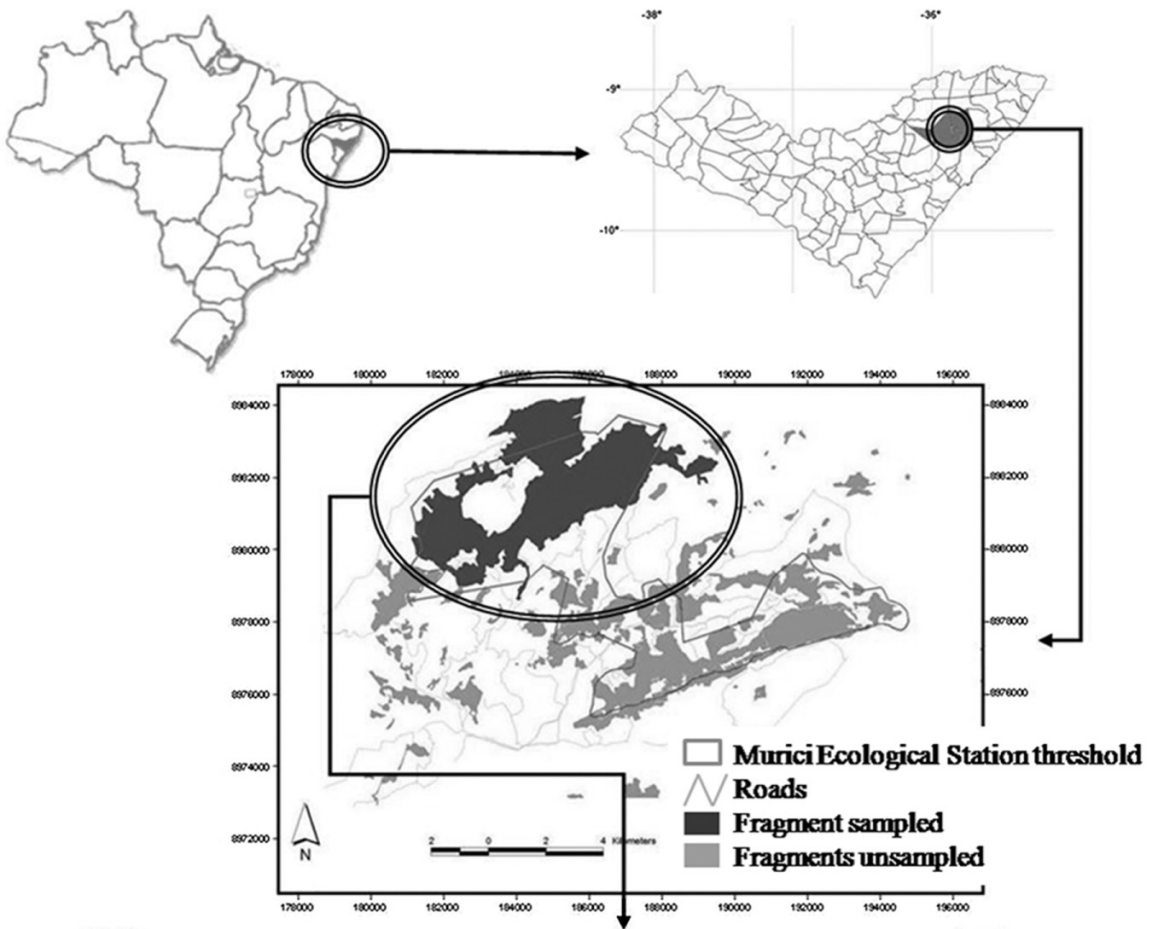
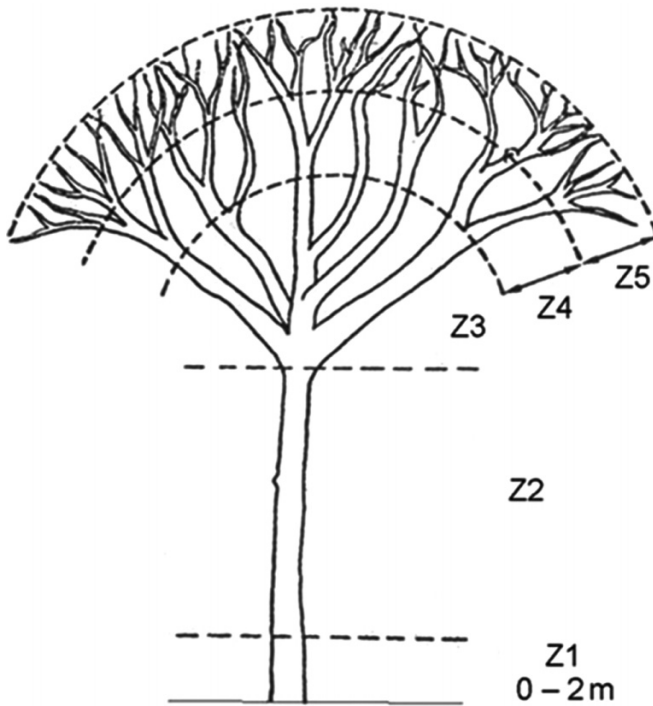


Fig. 2. Height zone scheme (Pócs 1982 with modifications) in a canopy tree. Scheme modified by ter Steege and Cornelissen (1989). Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy.



An analysis of covariance (ANCOVA) was carried out to test the principal effect and interaction among the independent variables' distance from the edge (covariable) and the height zone on bryophyte diversity and total and tolerance of guilds' richness.

The exploratory ordination technique detrended correspondence analysis (DCA) excluding singletons was applied to the communities of the different height zones and to communities of the different distance classes using PC-ORD 5. We calculated the explained variation (R^2) as the correlation between Euclidean distances among sample units in the ordination and relative Euclidean distances in the original space. The congruence in community similarity along the first DCA axis was tested with a Spearman rank correlation (using a Statistica 8 package).

Analysis of similarity (ANOSIM) was carried out using the software Primer 6 (Clarke and Gorley 2006) to test whether bryophyte communities differ among height zones in the host trees and whether they differ according to distance from the edge.

The Mantel test was applied using the Fitopac 1 program to determine whether floristic composition could be related to geographical distance between the studied host trees (Mantel 1967).

We used indicator species analysis (ISA) to verify whether species show preferences for a given height zone or a given distance from the edge (Dufrene and Legendre 1997). This method combines abundance and frequency values of species in each group, represented by height zone or distance class, and produces an indicator value for each species. The results obtained for each species were tested for statistical significance through the Monte Carlo regression test (Dufrene and Legendre 1997).

Results

Floristics and completeness of sampling

We found 78 species in 19 families and 44 genera: 53 species (68%) belonged to Marchantiophyta (liverworts) and 25 species (32%) belonged to Bryophyta (mosses) (Appendix A). A total of 345 occurrences of epiphytic bryophytes were recorded from the sam-

Table 1. Number of epiphytic bryophyte species observed (Sobs), singletons, and doubletons, estimated species (Chao2), and percentage of species collected from host trees in the forest remnant located at the Murici Ecological Station, Alagoas, Brazil.

Host tree	Sobs	Singletons	Doubletons	Chao2	% Species sampled
1	13.5	9.1	3.0	114.3	11.8
2	23.5	13.0	5.8	105.1	22.4
3	30.9	15.0	7.6	74.6	41.5
4	37.2	15.9	9.1	72.8	51.1
5	42.4	16.3	10.1	74.7	56.9
6	46.9	16.6	10.9	75.0	62.6
7	50.9	16.6	11.3	77.5	65.6
8	54.3	16.5	11.7	78.9	68.8
9	57.3	16.4	11.9	79.7	71.9
10	60.0	16.0	12.2	79.9	75.0
11	62.4	15.7	12.4	80.3	77.7
12	64.6	15.2	12.4	80.8	79.9
13	66.5	14.8	12.5	80.6	82.5
14	68.3	14.3	12.7	80.5	84.9
15	70	13.8	12.7	80.4	87.1

pled host trees. The most frequent species were *Cheilolejeunea rigidula* (Mont.) R.M. Schust., *Ceratolejeunea cornuta* (Lindenb.) Schiffn., *Symbiezidium barbiflorum* (Lindenb. & Gottsche) A. Evans, *Sematophyllum subpinnatum* (Brid.) E. Britton, and *Syrrophodon parasiticus* (Sw. ex Brid.) Paris; the first four are considered generalists and the last species is sun-tolerant. Forty species were classified as generalists, 15 as sun epiphytes, and 23 as shade epiphytes.

The Chao2 index showed that in our sampling, carried out in 15 host trees, 87% of the expected number of species in the area were found; a lower number of host trees (4–5) would provide only 51%–57% of the expected number of species, which is not sufficient for a good representation of extant species (Table 1).

Vertical stratification

Along the vertical gradient, the number of species per sample varied between 0 and 15 species, and both of these extreme values were recorded in the outer canopy (Z5). The highest overall richness and diversity were found on the trunk (Z2) (40 species, 5.1 bits/individual), and the lowest values were recorded in the middle canopy (Z4) (31 species, 4.5 bits/individual). We found little variation among height zones and no significant difference in total richness ($F_{[4,70]} = 5$, $P = 0.2$) and diversity ($F_{[4,70]} = 0.6$, $P = 0.6$) (Fig. 3).

However, the three guilds displayed particular characteristics regarding the vertical distribution on host trees. Generalist epiphytes were predominant, with $\geq 50\%$ of richness in all zones within host trees. The richness of shade epiphytes was always higher than that of sun epiphytes, except on Z5 (Fig. 4). The shade species reached higher values in Z1, whereas generalist and sun species did so in Z5. The shade species decreased significantly ($F_{[4,70]} = 2.34$, $P = 0.05$) along the vertical gradient, the sun epiphytes increased ($F_{[4,70]} = 10.1$, $P < 0.001$) with height on host trees, and generalist epiphytes showed no pattern ($F_{[4,70]} = 1.54$, $P = 0.19$) (Fig. 5).

Indicator species' analysis and ANOSIM confirmed these patterns. Nine species (13%) showed significant preference for a particular height zone, among which eight are indicative of Z5 (sun epiphytes or generalists) and one is indicative of Z1 (shade epiphyte) (Table 2). Furthermore, zones 1 and 5 were significantly different in bryophyte composition ($R = 0.3$, $P = 0.04$), indicating a slight gradient within host trees, at least between the first and last zones.

The DCA ordination of 52 samples (14 had fewer than three species and were excluded from this analysis) and 39 species

Fig. 3. Bryophyte total richness and diversity (H' (\log_2 transformed)) for each height zone studied: Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy.

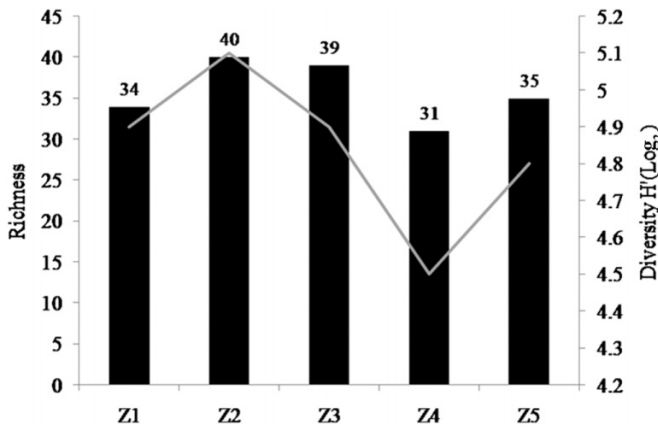


Fig. 4. Relative contribution (%) of tolerance guilds' richness for each height zone studied. Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy.

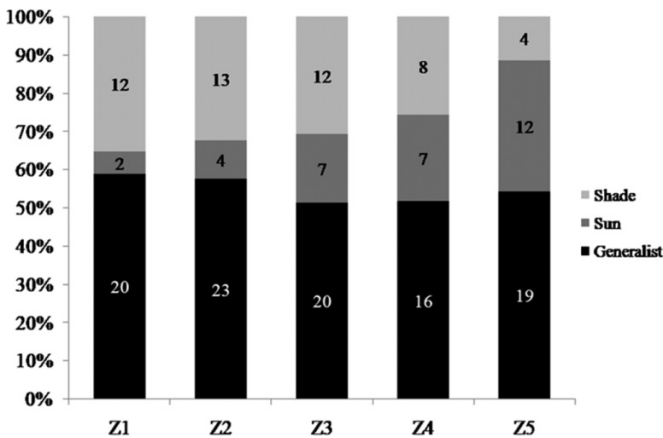
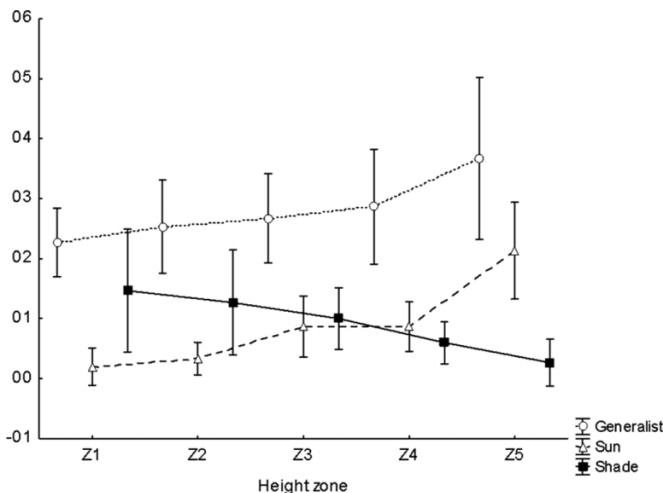


Fig. 5. Mean \pm 0.95 confidence interval of richness of generalist, sun, and shade epiphytes for each height zone studied: Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy.



(singletons and doubletons were excluded) resulted in two informative axes ($k_1 = 0.667$, explained variation = 25%; $k_2 = 0.427$, explained variation = 16%) for a total explained variation of 41% (Fig. 6a). The scores of the first axis were not significantly corre-

lated with height zone (Spearman's rank correlation $r_s = 0.24$, $P = 0.07$); however, the species composition shows a gradient, although not a very remarkable one, along height zones. Therefore, we ran another DCA of the whole dataset (excluding singletons) with each zone as one sample and the five zones lined up in exactly the order expected (1-2-3-4-5) (Fig. 6b). The total explained variation of the second DCA was 90% ($k_1 = 0.399$, explained variation = 90%; $k_2 = 0.030$, explained variation = 0.5%), and the scores of the first axis were highly correlated with height zone (Spearman's rank correlation $r_s = 0.96$, $P < 0.01$), demonstrating that community species' composition is explained mainly by height zone at landscape level.

Horizontal zonation

Edge distance did not influence total (generalists, $F_{[1,70]} = 1.44$, $P = 0.24$; sun, $F_{[1,70]} = 0.99$, $P = 0.32$; shade, $F_{[1,70]} = 0.59$, $P = 0.38$) and relative richness (generalists, $F_{[1,70]} = 0.001$, $P = 0.98$; sun, $F_{[1,70]} = 0.20$, $P = 0.65$; shade, $F_{[1,70]} = 0.001$, $P = 0.98$) of guilds and diversity ($F_{[1,70]} = 0.097$, $P = 0.33$) (Fig. 7; Table 3). Moreover, there was no significant difference in bryophyte assemblage among edge distance classes (ANOSIM $R = 0.1$, $P = 1$). The highest but not statistically significant similarity was recorded between distance classes I (0-200 m) and V (800-1.100 m) ($R = 0.1$, $P = 0.1$), which shows the lack of a defined horizontal gradient in the studied environment. Geographical distance between the samples did not explain species assemblage either ($r_M = 0.25$, $P = 0.13$).

A total of nine species (13%) showed significant preference for a given distance from the edge class (Table 2), one species in distance class II, three in distance class III, and five in distance class IV. Distance classes I and V showed no specialist species.

Discussion

Floristics and completeness of sampling

Several authors suggest that a satisfactory inventory of epiphytic bryophytes in tropical forests (although area scale is not provided) can be carried out through the sampling of 4 to 5 host trees, from the base to the outer canopy, regardless of the host tree species (Wolf 1995; Gradstein et al. 1996, 2003). According to our results, however, this proposition is not supported. For the whole study area, the sampling effort needed to arrive at the same percentage of species found by the above-mentioned studies (ca. 86%) was three times larger (15 host trees), which suggests a high beta diversity in the study area, i.e., high turnover of species from one microhabitat to the next. On the other hand, we were not able to find an explicit gradient of species' composition along the edge distance. Thus, for the whole study area, there seems to be a high turnover between habitats but not in a linear gradient towards the edge-nucleus. Our results mirror the environmental heterogeneity of the remnant caused by random disturbance within it. Scattered habitat perturbation such as selective logging, a common practice in the area, creates a complex habitat that can open opportunities for the establishment and development of a higher number of species due to the degree of support that the environment can provide (Andow 1991; Tonhasca 2005), therefore increasing the sampling effort demanded.

Regarding species' richness, we found 78 species (53 liverworts and 25 mosses) in the study area. Previous studies regarding vertical stratification of bryophyte species used similar sampling methodologies, dividing host trees in 4-6 height levels, which facilitate richness value comparisons. For instance, our richness values were close to those reported for 11 trees in a dry forest in Guyana by Cornelissen and ter Steege (1989): 81 taxa (28 mosses and 53 liverworts). Acebey et al. (2003), sampling only six host trees, recorded richness values similar to those that we recorded in 15 host trees at EsEc Murici: 80 species, among which were 48 liverworts and 32 mosses.

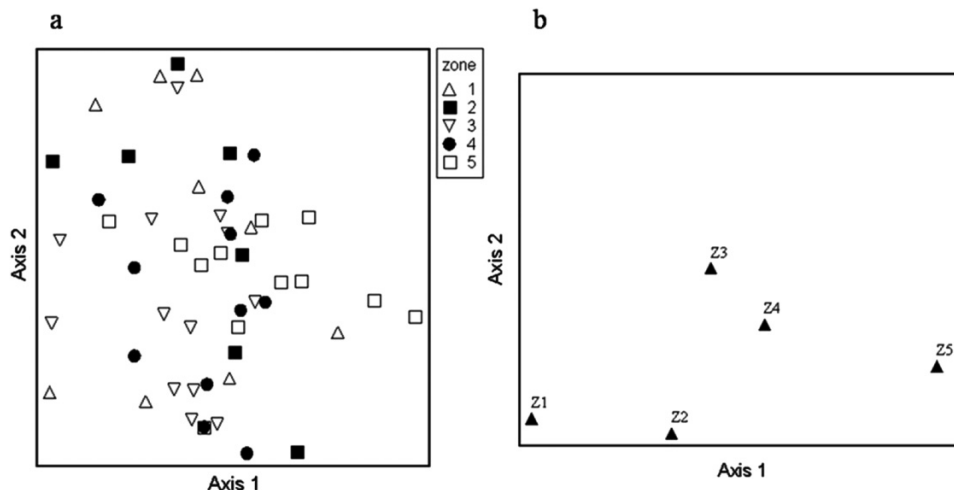
However, on the other hand, Montfoort and Ek (1990) recorded a greater number of species: 154 (66 mosses and 88 liverworts) in

Table 2. Indicator value given by indicator species analysis (ISA) for edge distance class and height zone.

Taxa	Edge distance class	Height zone	Indicator value	P
<i>Bryopteris filicina</i> (Sw.) Nees	IV	—	19	0.05
<i>Cheilolejeunea adnata</i> (Kunze) Grolle	III	—	22.3	0.03
<i>Cheilolejeunea rigidula</i> (Mont.) R.M. Schust.	II	—	26.5	0.03
<i>Frullania apiculata</i> (Reinw. et al.) Nees	III	—	28.6	0.007
		Z5	25.0	0.01
<i>Lejeunea cerina</i> (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees	IV	—	22.9	0.02
<i>Leucoloma serrulatum</i> Brid.	IV	—	50.0	0.001
<i>Metzgeria albinea</i> Spruce	III	—	22.3	0.03
<i>Phyllogonium viride</i> Brid.	IV	—	35.7	<0.001
<i>Squamidium brasiliensis</i> (Hornsch.) Broth.	IV	—	22.9	0.02
<i>Diplasiolejeunea brunnea</i> Steph.	—	Z5	25.0	0.005
<i>Drepanolejeunea fragilis</i> Bischl.	—	Z5	25.3	0.01
<i>Frullania caulisequa</i> (Nees) Nees	—	Z5	20.4	0.02
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	—	Z5	15.5	0.05
<i>Groutiella mucronifolia</i> (Hook. & Grev.) H.A. Crum & Steere	—	Z5	15.4	0.05
<i>Lejeunea flava</i> (Sw.) Nees	—	Z5	25.3	0.01
<i>Microlejeunea epiphylla</i> Bischl.	—	Z5	27.8	0.007
<i>Syrrhopodon incompletus</i> Schwägr.	—	Z1	20.0	0.03

Note: Edge distance class: I, 0–200 m; II, 201–400 m; III, 401–600 m; IV, 601–800 m; V, 801–1084 m. Height zone: Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy.

Fig. 6. Ordination biplot of the DCA analysis with 52 samples and 39 species (samples with fewer than three species and singletons and doubletons were excluded). Each point in the graph represents one sample. The biplot is given twice with different labels for the samples: (a) symbols indicate the height zone (see key); (b) symbols indicate each zone as one plot.



28 host trees (22 species) in a tropical rainforest in French Guiana, where a single *Protium* sp. tree could harbour 106 bryophyte species. Wolf (1995), studying bryophytes and macrolichens in 21 host trees in a montane forest in Colombia, also found high degrees of richness: 120 species. Concerning the study in French Guiana, the high richness value could be due to the environment, an extremely wet Cloud Lowland Forest, even when compared with other areas in the Amazon Forest (Mota de Oliveira et al. 2009). Furthermore, the high species' richness in Colombia may be related to the vegetation, which was montane forest. It is well known that this type of forest offers suitable conditions for the establishment of many bryophytes due to high precipitation, rich soils, topographic variation, constant high air humidity, low temperatures, and high light intensity (Gradstein et al. 2001; da Costa and Lima 2005).

When comparing bryophyte richness between those researches cited above, another point that should be taken into account is the type of host trees species studied. Indeed, several authors demonstrate that the bryophyte species' richness and composition change with host tree species (Schmitt and Slack 1990; González-Mancebo et al. 2003; Patiño et al. 2009; Patiño and

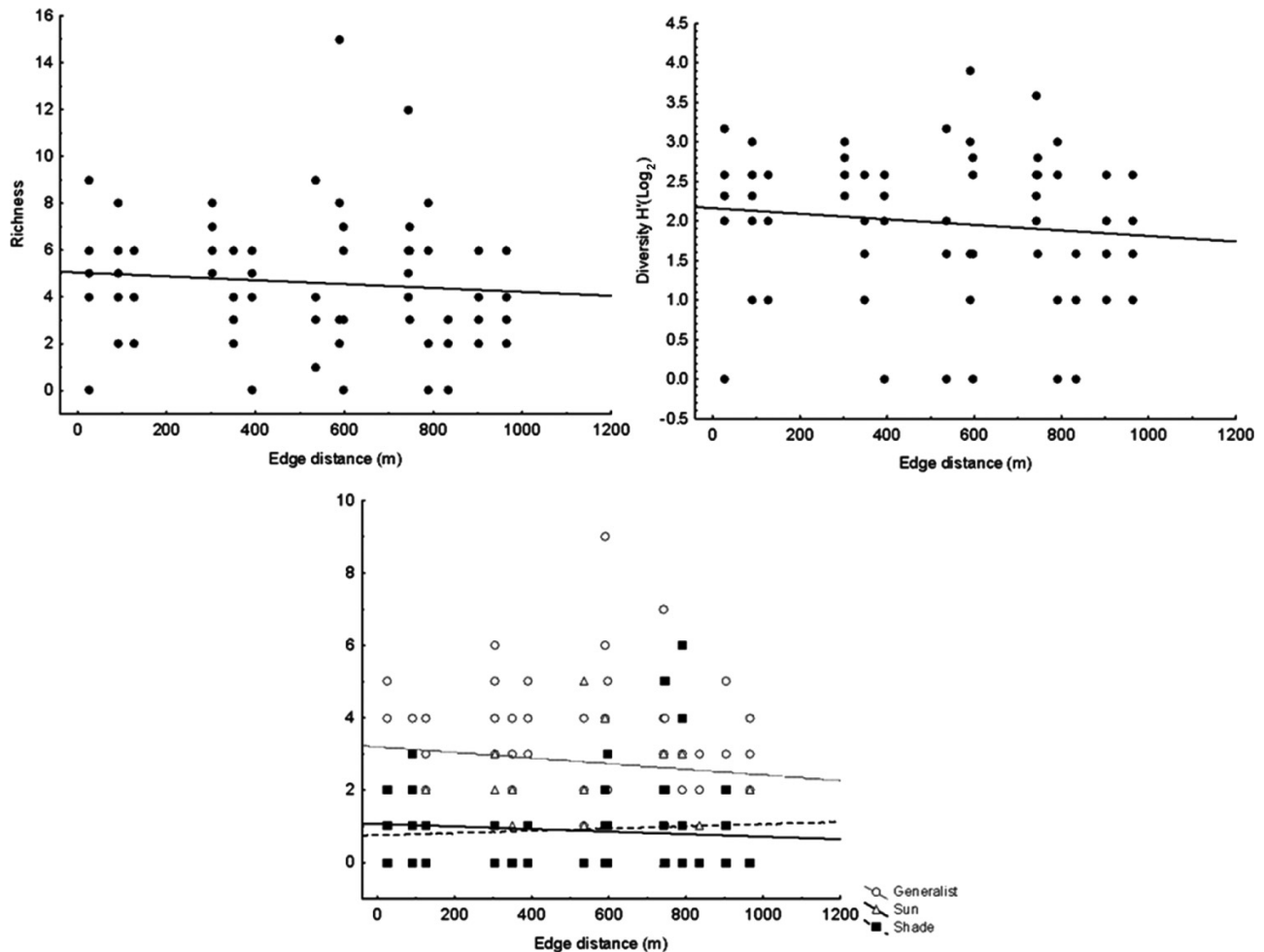
González-Mancebo 2011), and this should be considered in further studies.

Vertical stratification

We found little variation of overall richness and diversity among height zones. Contrary to what was expected, the number of species found in the outer canopy was practically the same as the number at the base, which points to the importance of the zones under the canopy to local diversity. The important role played by the understory in species' richness was also proposed for vascular epiphytes (Krömer et al. 2007). The authors compared the sampling of the vertical zonation with samples in the understory and showed that 20% of the flora was restricted to the understory, including pteridophytes and the Araceae and Piperaceae families.

Although the bryophyte composition of the study area responded to a vertical gradient, the stratification was not as remarkable as that reported for other forest areas (Cornelissen and ter Steege 1989; Acebey et al. 2003). In fact, the ANOSIM analysis defined only two height levels, understory and outer canopy. According to Krömer and Kessler (2006), a predictable vertical distri-

Fig. 7. Scatterplot of (a) total richness, (b) diversity (H' (\log_2 transformed)), and (c) richness of generalist, sun, and shade epiphytes in relation to edge distance. The best-fit line is shown for illustrative purposes only.



bution is mainly recorded for closed canopy forests, where microenvironmental conditions change markedly along height zones, rather than for open-canopy habitats, where the gradient is less steep (Werneck and Espírito-Santo 2002). Thus, considering that the local type of vegetation studied is an open broadleaf forest, which is also affected by current hunting and selective logging (Silva and Pôrto 2010), it seems reasonable that a slightly vertical gradient on composition was found.

Variations of bryophyte composition along vertical stratification were more apparent when considering the tolerance guilds. The number of sun-tolerant epiphytes showed an increasing trend toward the base canopy and reached their peak in the outer canopy, whereas shade-tolerant bryophytes demonstrated exactly the opposite pattern. Furthermore, generalist epiphytes were predominant in all zones and showed no linear relation with height zone. In fact, we found many of the species considered sun-tolerant (e.g., *Frullania caulisequa* (Nees) Nees, *Groutiella mucronifolia* (Hook. & Grev.) H.A. Crum & Steere, and *Diplasiolejeunea brunnea* Steph.) as indicative of species in height zone 5 (outer canopy). Cornelissen and ter Steege (1989) also reported well-defined bryophyte communities along the vertical gradient of the host trees. The authors found the base of the trunk covered by *Leucobryum* and other species sharing with the assemblage of dead logs, as well as the outer canopy inhabited by *Sematophyllum subpinnatum* (Brid.) E. Britton and *Frullania apiculata* (Reinw. et al.) Nees.

Horizontal zonation

The expectation that host trees closer to the edge would show more sun-tolerant species instead of shade specialists, regardless of the height zone, was not supported. In our studied area, we noticed that the understory community biomass may persist in disturbed areas, here referred to as edge proximity. Accordingly, there was no significant difference in composition, richness, and diversity along edge distance, not even at a distance of 1.000 m.

Studies dealing with edge effects in tropical rainforests attest to the lack of edge effect in the first 100 m both in the Amazon Forest (Zartman and Nascimento 2006) and in the Atlantic Forest (Alvarenga et al. 2009, 2010; Silva and Pôrto 2009; Oliveira et al. 2011), yet they proposed that the size of the forest fragment was the driving factor for bryophyte diversity. Especially in the Atlantic Forest, to grasp the ecological processes underlying bryophyte assemblages, several other variables were analyzed such as size, proximity to other forest fragments, and percentage of secondary vegetation, and all of them were more significant than edge effect (Alvarenga et al. 2009; Silva and Pôrto 2009, 2010). The authors suggest that the results obtained are due to complex environmental conditions and spatially random human disturbances, which hamper the expected linearity of the edge effect. It seems to be the case that in our highly impacted study area, the bryoflora spatial distribution is probably influenced by landscape characteristics and human disturbance events, rather than edge distance per se (Espírito-Santo et al. 2002; Dixo and Martins 2008).

Table 3. Richness of tolerance guilds for height zone and edge distance class.

Sample	Generalist	Sun	Shade
IZ1	5	0	5
IZ2	7	1	3
IZ3	10	4	4
IZ4	6	2	2
IZ5	8	7	1
IIZ1	10	0	0
IIZ2	11	1	1
IIZ3	7	2	1
IIZ4	6	2	1
IIZ5	5	3	0
IIIZ1	6	1	2
IIIZ2	6	2	3
IIIZ3	8	3	3
IIIZ4	11	2	2
IIIZ5	11	8	2
IVZ1	6	2	8
IVZ2	5	1	8
IVZ3	4	1	4
IVZ4	5	2	3
IVZ5	12	7	3
VZ1	6	0	1
VZ2	4	0	1
VZ3	3	1	2
VZ4	4	3	0
VZ5	6	2	0

Note: Edge distance class: I, 0–200 m; II, 201–400 m; III, 401–600 m; IV, 601–800 m; V, 801–1084 m. Height zone: Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy.

Microclimatic conditions in given areas of the forest probably act as refuges for bryophytes and other groups (Christianini and Galetti 2007). Indeed, Silva and Pôrto (2010) showed that factors specific to microclimatic conditions spread across the forest remnant such as higher altitude and canopy closure explain the bryoflora distribution in the understory more efficiently than edge distance. The result is probably due to the fact that areas found at higher altitude are less affected by human disturbance, plantations, and logging. This result was repeated for the communities studied in the vertical gradient, confirming that bryophyte distribution in both the understory and canopy is more related to microenvironmental conditions than landscape characteristics such as edge distance.

Therefore, other variables and factors such as the history of land use in the fragment probably need to be addressed for a better understanding of the distribution of the bryoflora in this remnant.

Conclusion

Based on our results, it is possible to conclude that a representative sampling of the epiphytic bryoflora along the vertical gradient demands a greater number of host trees than previously proposed for inventories in tropical rainforests. Moreover, in this environment, an efficient bryofloristic inventory can only be obtained through sampling from the understory to the canopy and can be independent of edge distance, as no horizontal zonation was identified. Finally, we conclude that the environmental characteristics of the Atlantic Forest and the environmental heterogeneity of the remnant may be important factors in the lack of horizontal gradient in community composition.

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Appendix A

Table A1 appears on the following pages.

Table A1. List of species of epiphytic bryophytes in the forest remnant located at the Murici Ecological Station, Alagoas, Brazil, total occurrence and occurrence by height zone and edge distance class.

Taxa	Tolerance guild	Total	Height zone					Edge distance class				
			Z1	Z2	Z3	Z4	Z5	I	II	III	IV	V
Marchantiophyta												
Cephaloziellaceae (1/1)												
<i>Cylindrocolea rhizantha</i> (Mont.) R.M. Schust.	Shade	2	—	—	1	1	—	2	—	—	—	—
Frullaniaceae (1/6)												
<i>Frullania apiculata</i> (Reinw. et al.) Nees	Sun	9	—	1	2	1	5	1	—	6	2	—
<i>Frullania caulisequa</i> (Nees) Nees	Sun	7	—	—	1	1	5	1	4	1	1	—
<i>Frullania dusenii</i> Steph.	Sun	1	—	—	—	—	1	—	—	—	1	—
<i>Frullania kunzei</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	Sun	5	—	—	—	2	3	—	1	1	2	1
<i>Frullania riojaneirensis</i> (Raddi) Ångstr.	Sun	1	—	—	—	—	1	—	—	1	—	—
<i>Frullania setigera</i> Steph.	Sun	4	1	1	1	1	—	—	—	3	1	—
Lejeuneaceae (19/39)												
<i>Anoplolejeunea conferta</i> (Meissn.) A. Evans	Generalist	4	—	1	—	—	3	1	2	—	1	—
<i>Archilejeunea fuscescens</i> (Hampe ex Lehm.) Fulford	Generalist	1	1	—	—	—	—	—	1	—	—	—
<i>Bryopteris filicina</i> (Sw.) Nees	Shade	6	3	2	—	1	—	2	—	—	4	—
<i>Ceratolejeunea ceratantha</i> (Nees & Mont.) Steph.	Generalist	2	—	1	1	—	—	—	—	1	1	—
<i>Ceratolejeunea coarina</i> (Gottsche) Steph.	Generalist	1	—	1	—	—	—	—	—	1	—	—
<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn.	Generalist	23	1	4	3	7	8	4	3	4	8	4
<i>Ceratolejeunea cubensis</i> (Mont.) Schiffn.	Generalist	13	3	2	3	3	2	1	10	2	—	—
<i>Ceratolejeunea laetefusca</i> (Austin) R.M. Schust.	Generalist	1	1	—	—	—	—	1	—	—	—	—
<i>Cheilolejeunea adnata</i> (Kunze) Grolle	Generalist	8	3	2	1	1	1	—	1	5	—	2
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R-L. Zhu	Generalist	1	1	—	—	—	—	—	—	—	—	1
<i>Cheilolejeunea rigidula</i> (Mont.) R.M. Schust.	Generalist	27	4	4	8	7	4	4	10	4	3	6
<i>Cheilolejeunea trifaria</i> (Reinw. et al.) Mizut.	Generalist	10	1	2	2	2	3	2	4	3	1	—
<i>Cololejeunea diaphana</i> A. Evans	Shade	1	—	1	—	—	—	—	1	—	—	—
<i>Colura tortifolia</i> (Nees & Mont.) Steph.	Sun	1	—	—	—	—	1	1	—	—	—	—
<i>Diplasiolejeunea brunnea</i> Steph.	Sun	3	—	—	—	—	3	1	—	1	—	1
<i>Diplasiolejeunea rudolphiana</i> Steph.	Sun	1	—	—	—	—	1	—	—	—	1	—
<i>Drepanolejeunea fragilis</i> Bischl.	Generalist	13	—	2	1	2	8	2	3	3	2	3
<i>Drepanolejeunea mosenii</i> (Steph.) Bischl.	Generalist	3	—	1	1	—	1	—	2	—	1	—
<i>Harpalejeunea stricta</i> (Lindenb. & Gottsche) Steph.	Sun	8	—	—	2	3	3	2	—	1	3	2
<i>Harpalejeunea tridens</i> (Besch. & Spruce) Steph.	Generalist	1	1	—	—	—	—	1	—	—	—	—
<i>Lejeunea caespitosa</i> Lindenb.	Generalist	1	—	—	—	—	1	—	—	—	1	—
<i>Lejeunea caulicalyx</i> (Steph.) M.E. Reiner & Goda	Generalist	3	1	—	1	1	—	—	—	2	1	—
<i>Lejeunea cerina</i> (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees	Generalist	5	1	2	2	—	—	1	—	—	4	—
<i>Lejeunea controversa</i> Gottsche	Generalist	1	—	—	—	1	—	—	—	—	—	1
<i>Lejeunea filipes</i> Spruce	Shade	1	—	—	1	—	—	—	—	—	1	—
<i>Lejeunea flava</i> (Sw.) Nees	Generalist	6	—	—	—	1	5	—	1	1	3	1
<i>Lejeunea grossitexta</i> (Steph.) E. Reiner & Goda	Generalist	3	1	—	1	1	—	—	—	2	1	—
<i>Lejeunea laetevirens</i> Nees & Mont.	Generalist	1	—	—	1	—	—	—	—	—	1	—
<i>Lejeunea oligoclada</i> Spruce	Generalist	2	—	1	1	—	—	2	—	—	—	—
<i>Lepidolejeunea involuta</i> (Gottsche) Grolle	Shade	6	—	2	3	1	—	—	1	3	2	—
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.	Sun	1	—	—	—	—	1	—	—	1	—	—
<i>Microlejeunea epiphylla</i> Bischl.	Generalist	5	—	—	—	—	5	1	2	1	1	—
<i>Omphalanthus filiformis</i> (Sw.) Nees	Generalist	2	—	—	1	1	—	—	—	—	2	—

Table A1 (continued).

Taxa	Tolerance guild	Total	Height zone					Edge distance class				
			Z1	Z2	Z3	Z4	Z5	I	II	III	IV	V
<i>Prionolejeunea aemula</i> (Gottsche) A. Evans	Shade	1	1	—	—	—	—	—	—	—	1	—
<i>Prionolejeunea denticulata</i> (Weber) Schiffl.	Generalist	6	4	2	—	—	—	2	1	—	2	1
<i>Prionolejeunea scaberula</i> (Spruce) Steph.	Shade	1	—	1	—	—	—	—	—	—	1	—
<i>Symbiezidium barbiflorum</i> (Lindenb. & Gottsche) A. Evans	Generalist	17	4	2	3	3	5	7	—	5	1	4
<i>Taxilejeunea obtusangula</i> (Spruce) A. Evans	Generalist	2	1	1	—	—	—	—	—	2	—	—
<i>Vitalianthus bischlerianus</i> (Pôrto & Grolle) R.M. Schust. & Giancotti	Shade	1	—	—	1	—	—	—	—	—	—	1
Metzgeriaceae (1/2)												
<i>Metzgeria albinea</i> Spruce	Generalist	8	1	2	1	2	2	—	—	5	3	—
<i>Metzgeria ciliata</i> Raddi	Generalist	1	—	—	—	—	1	—	—	—	1	—
Plagiochilaceae (1/4)												
<i>Plagiochila aerea</i> Tayl.	Shade	6	3	2	—	1	—	—	—	3	3	—
<i>Plagiochila disticha</i> (Lehm. & Lindenb.) Lindenb.	Shade	3	1	1	1	—	—	2	—	—	1	—
<i>Plagiochila distinctifolia</i> Lindenb.	Shade	1	—	—	—	—	1	—	—	—	1	—
<i>Plagiochila montagnei</i> Nees	Shade	4	—	1	2	—	1	1	—	1	—	2
Radulaceae (1/1)												
<i>Radula kegelii</i> Gottsche ex Steph.	Shade	4	2	1	1	—	—	3	—	—	1	—
Bryophyta												
Brachytheciaceae (2/2)												
<i>Squamidium brasiliensis</i> (Hornsch.) Broth.	Shade	5	1	1	2	—	1	—	—	1	4	—
<i>Zelometeorim patulum</i> (Hedw.) Manuel	Generalist	2	—	1	—	—	1	1	—	—	1	—
Calymperaceae (3/6)												
<i>Calymperes palisotii</i> Schwägr.	Generalist	1	—	1	—	—	—	—	1	—	—	—
<i>Octoblepharum albidum</i> Hedw.	Generalist	12	1	2	5	4	—	1	5	1	—	5
<i>Syrrhopodon incompletus</i> Schwägr.	Shade	3	3	—	—	—	—	2	—	1	—	—
<i>Syrrhopodon ligulatus</i> Schwägr.	Shade	3	—	1	1	1	—	2	1	—	—	—
<i>Syrrhopodon parasiticus</i> (Sw. ex Brid.) Paris	Sun	14	2	2	3	5	2	4	5	2	1	2
<i>Syrrhopodon prolifer</i> Schwägr.	Generalist	1	1	—	—	—	—	—	1	—	—	—
Dicranaceae (1/1)												
<i>Leucoloma serrulatum</i> Brid.	Shade	7	2	3	1	1	—	—	—	—	7	—
Fissidentaceae (1/1)												
<i>Fissidens guianensis</i> Montagne	Shade	1	1	—	—	—	—	—	—	—	—	1
Hookeriaceae (1/1)												
<i>Crossomitrium patrisae</i> (Brid.) Müll. Hal.	Generalist	2	—	1	—	—	1	1	—	1	—	—
Hypnaceae (1/1)												
<i>Ectropothecium leptochaeton</i> (Schwägr.) W.R. Buck	Generalist	1	—	—	—	—	1	1	—	—	—	—
Neckeraceae (1/1)												
<i>Porotrichum substriatum</i> (Hampe) Mitt.	Shade	2	1	1	—	—	—	—	—	—	2	—
Orthotrichaceae (2/3)												
<i>Groutiella apiculata</i> (Hook.) Crum & Steere	Sun	2	—	—	1	—	1	2	—	—	—	—
<i>Groutiella mucronifolia</i> (Hook. & Grev.) H.A. Crum & Steere	Sun	2	—	—	—	2	—	1	—	—	—	1
<i>Macromitrium punctatum</i> (Hook. & Grev.) Brid.	Sun	3	—	1	2	—	—	1	—	—	2	—
Phyllogoniaceae (1/1)												
<i>Phyllogonium viride</i> Brid.	Shade	5	2	1	1	1	—	—	—	—	5	—

Table A1 (concluded).

Taxa	Tolerance guild	Total	Height zone					Edge distance class				
			Z1	Z2	Z3	Z4	Z5	I	II	III	IV	V
Pilotrichaceae (2/2)												
<i>Lepidopilidium brevisetum</i> (Hampe) Broth.	Shade	2	—	—	—	1	1	1	1	—	—	—
<i>Lepidopilum scabrisetum</i> (Schwägr.) Steere	Shade	1	1	—	—	—	—	1	—	—	—	—
Pterobryaceae (1/1)												
<i>Jaegerina scariosa</i> (Lorentz) Arzeni	Generalist	3	—	1	1	—	1	2	—	1	—	—
Pylaisiadelphaceae (2/2)												
<i>Isopterygium tenerum</i> (Sw.) Mitt.	Generalist	2	—	—	—	2	—	—	1	1	—	—
<i>Taxithelium planum</i> (Brid.) Mitt.	Generalist	1	—	1	—	—	—	—	1	—	—	—
Sematophyllaceae (2/3)												
<i>Acroporium estrellae</i> (Müll. Hal.) W.R. Buck & Schäf.-Verw.	Shade	1	—	—	1	—	—	—	—	1	—	—
<i>Sematophyllum subpinnatum</i> (Brid.) E. Britton	Generalist	16	1	2	3	6	4	3	4	2	—	7
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.	Generalist	4	3	—	1	—	—	2	1	—	—	1
No. of occurrences		345	59	62	69	67	88	70	68	74	86	47

Note: Numbers in parentheses reflect the number of genera and species, respectively. Height zone: Z1, base; Z2, trunk; Z3, 1st ramification; Z4, 2nd ramification; Z5, outer canopy. Edge distance class: I, 0–200 m; II, 201–400 m; III, 401–600 m; IV, 601–800 m; V, 801–1084 m.