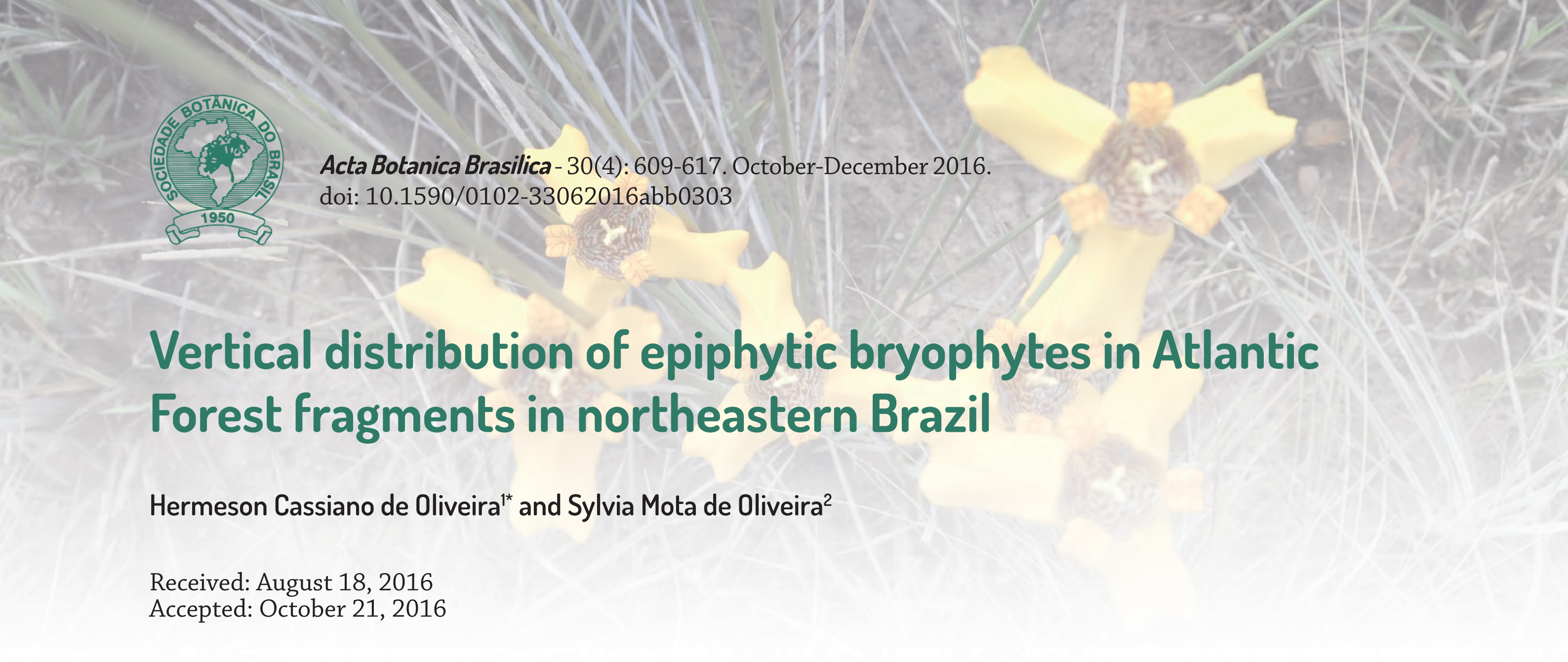

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Vertical distribution of epiphytic bryophytes in Atlantic Forest fragments in northeastern Brazil

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ABSTRACT

The microclimatic gradient established from the forest understory to the canopy provides a range of different conditions for the establishment of bryophytes along the height of a tree. We investigated epiphytic bryophyte communities of four fragments of Atlantic Forest with the aim of describing their vertical zonation and assessing differentiation among the communities of the different fragments. In each fragment, five host trees were selected from which bryophyte samples were collected in four height zones from the base to the canopy. Furthermore, 10 plots were demarcated in each fragment where bryophytes were collected from the understory. In total, 114 bryophyte species were found on the 20 sampled phorophytes, plus an additional 51 species in the understory, for a total of 165 species. Species composition of height zones differed significantly between communities of the trunk base and the canopy. The samples from the understory included 77% of all species. Among all species found, 10 showed a significant preference for a specific height. Around 70% of the bryophyte species grew as mats; this life form occurred in all trees and height zones. The results showed a weak, yet significant, vertical gradient, which differs from what is usually found in the Atlantic Forest.

Keywords: canopy, ecology, liverworts, mosses, tropical rain forest

Introduction

In tropical forests, the epiphytic habit is clearly the most important for bryophytes, where communities colonize trees from the base to the outermost canopy twigs (Richards 1984). This pattern of colonization is facilitated by the elevated moisture in tropical environments, which provides ideal microclimatic conditions for the development of these plants (Frahm 2003). The variety of microhabitats and the constantly moist microclimates facilitate the cooccurrence of numerous species, which results in high species diversity (Gradstein *et al.* 2008).

The microclimatic gradient from the forest understory to the canopy, with significant variation in air temperature, relative humidity, light availability and CO2 concentration, is well documented in the literature (Whitmore 1998; Lowman & Rinker 2004). A clear turnover in bryophyte species composition along this vertical gradient on host trees has been documented in tropical rainforest sites (Sporn *et al.* 2010). In the Guianas, species turnover along the vertical gradient has been shown to be consistent accross local as well as regional scales, with data from three different localities following the same pattern (Cornelissen & Steege 1989; Oliveira *et al.* 2009).

Studies dealing with vertical zonation of bryophytes in the Atlantic Forest have found little differentiation between understory and canopy, since a significant turnover in bryophyte species composition was not present, which can

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be a consequence of the altered microclimatic conditions in fragmented forests (Germano 2003; Campelo & Pôrto 2007; Silva & Pôrto 2013). The closed canopy of undisturbed forests is more favorable to vertical species turnover of epiphytes, because microenvironmental conditions are clearly distinct (Werneck & Espírito-Santo 2002).

Epiphytic bryophytes with different life forms and with different water conduction and retention structures could be indicators of the height zone where they occurr due to their potential strict reliance on a particular level of water supply, gas exchange and light availability (Proctor 1990). The strong correlation of life forms with moisture and light conditions has been extensively discussed (Thiers 1988; Sporn *et al*. 2010), however, there have been few studies of these patterns in the Atlantic Forest. According to Gimingham & Birse (1957), cushions, mats and turf can be roughly considered as xeric life forms with increasing drought-tolerance, whereas dendroids, fans, pendants, and wefts are life forms characteristic of wet environments.

In this work, we investigated the epiphytic bryophyte communities of four fragments of Atlantic Forest that belong to the same forest matrix, with the aim of assessing their vertical zonation and the relationship between canopy and understory. We also evaluated species richness and composition among the studied fragments.

Materials and methods

Study area

The study was carried out in the Ecological Reserve Michelin, property of *Plantações Michelin da Bahia LTDA*, in the municipalities of Igrapiúna and Ituberá (13°48'08''S, 39°10'03''W) in Bahia State, Brazil (Fig. 1). The total area of the reserve is 3,096 ha and includes a range of environments that are part of the Atlantic Forest biome, such as restinga, mangrove and estuary, besides the main tropical rainforest matrix. The region has a humid tropical climate (Af) with an average annual precipitation of 2,051 mm, which is distributed throughout the year. The average temperature varies between 18 °C and 30 °C (CEI/CONDER 1993). The forest is classified as a Lowland Tropical Rainforest and its altitude varies from sea level to 327 m (Veloso *et al*. 1991).

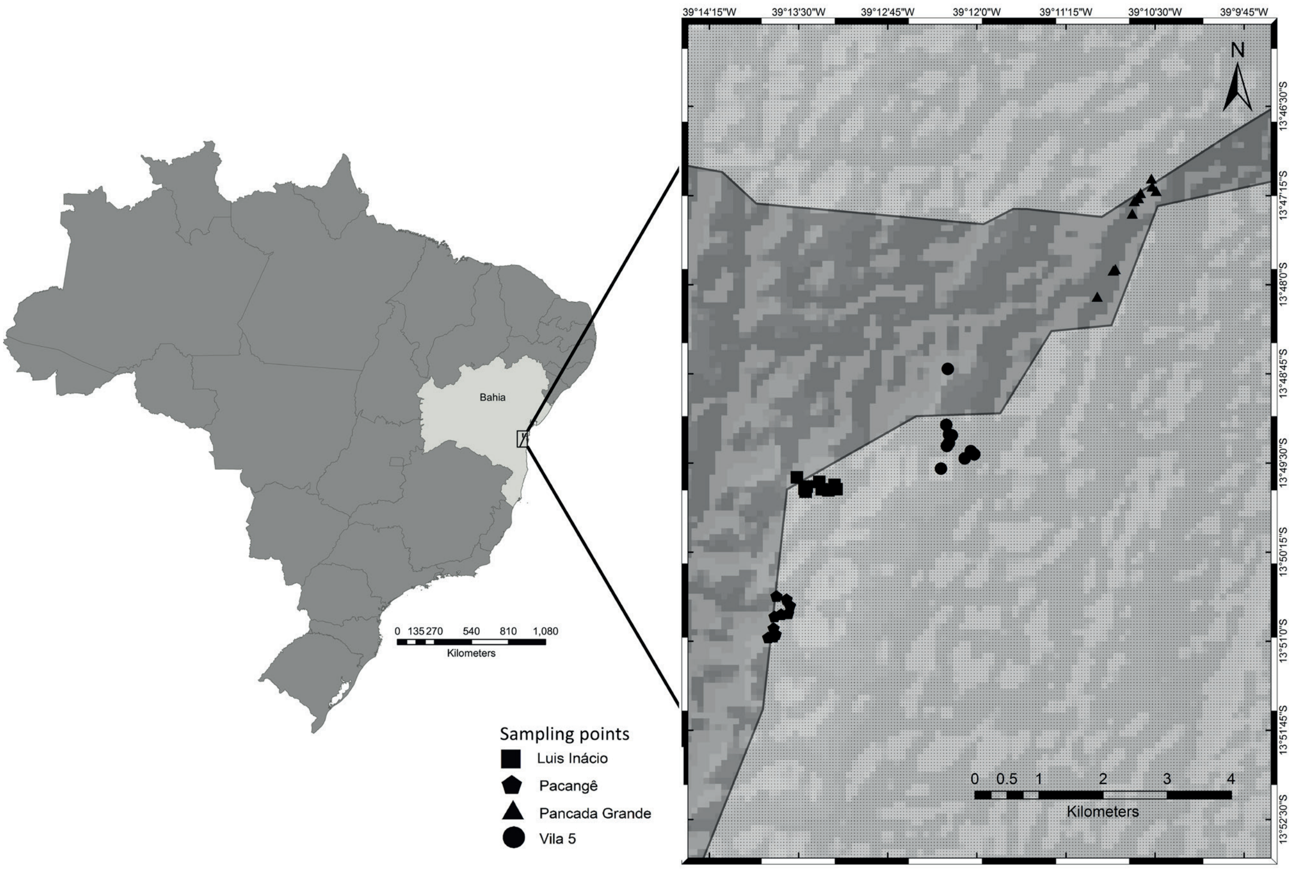


Figure 1. Location of the Michelin Ecological Reserve in the state of Bahia, Brazil, with the sampling points indicated.

Sampling design

Bryophyte sampling took place in four forest fragments within this complex: Mata de Pacangê (PAC) – 550 ha; Mata da Vila Cinco (MV) – 180 ha; Mata de Pancada Grande (PG) – 172 ha; and Mata do Luis Inácio (LI) – 140 ha, with a total forest cover of 1,042 ha. In each of the four fragments, five canopy trees were selected, considering size for climbing and bryophyte cover, that were separated from each other by at least 100 m, for a total of 20 trees. Four height zones were established to standardize sampling of vertical zonation, following Pócs (1982). Samples were collected in each height zone of all selected trees, which ammounted to 80 sample units (20 trees x 4 zones). Additionally, 10 plots of 100 m^2 were established in each forest fragment, where understory bryophytes were sampled from the stems of five young trees of CAP >0.30<1.0 m, up to a maximum of 2 m high, and from leaves of shrubs or young trees (Gradstein *et al.* 1996).

Plant Material

Samples were identified to species level using identification keys, illustrations and descriptions from specialized literature (Florschütz 1964; Fulford 1963, 1966, 1968, 1976; Sharp *et al.* 1994; Buck 1998; Dauphin 2003; Gradstein & Costa 2003). The classification system used was Crandall-Stotler *et al.* (2009) for liverworts and Goffinet *et al.* (2009) for mosses. After observation and identification, the samples were deposited in the Herbarium ALCB of the Federal University of Bahia.

To verify changes in life forms and water conduction and retention structures, six life forms were recorded following the classification of Frahm (2003): cushion, dendroid, mat, pendent, turf and weft. Presence/absence of seven morphological adaptations related to water conduction/retention (Glime 2007) were also recorded: long acuminate or piliferous apex, lobules, concave leaves, hyalocysts, tomentose gametophyte, allar cells and papillae.

Data analysis

Species accumulation curves were built using bulk samples of all height zones of each tree, with host tree as surrogate unit of area. We used Analysis of Variance (ANOVA) to test for differences in species richness between height zones in the data subset from the canopy trees (N=80), as well as to test for differences in species richness between fragments in the complete data set (N=120). Furthermore, we performed a Kolmogorov–Smirnov Analysis of Similarities (ANOSIM) with all sample pairs of the complete dataset to detect significant differences in species composition between fragments.

In order to identify intrinsic gradients in community composition, we carried out Detrended Correspondence Analysis (DCA), an indirect ordination method (solely based on species composition of communities) which assumes that species show an unimodal response along the gradient (McCune & Grace 2002). The ordination was carried out for the dataset obtained from canopy host trees, first with all fragments and then by fragment. After visual inspection including sample labels, such as height zone, elevation and spatial location (fragment), correlation between the axis and height zone was tested for significance through permutation procedure, since grouping of samples were only detected for height zone. All analyses were performed in R 2.14.1 (R Core Team 2012).

Indicator Species Analysis (ISA, McCune & Grace 2002) was carried out to explore species preference for a specific height zone on host trees and for a given fragment. Indicator species of zones 1 and 2 were classified as understory specialists; indicators species of zones 3 and 4 were classified as canopy specialists. In order to score the occurrence of the life forms and morphological features per height zone, the percentage of occurrence per zone relative to the percentage of incidence of the life form/morphological feature in the species list was used.

Results

A total of 114 bryophyte species were found on the 20 sampled phorophytes, of which 76 belonged to Marchantiophyta (liverworts), distributed among six families and 24 genera, and 38 to Bryophyta (mosses), distributed among 11 families and 21 genera. Including samples from small trees of the understory, the total number of species recorded increases to 165, with 62 moss species belong to 16 families and 32 genera and 103 liverwort species belong to eight families and 30 genera (Tab. S1 in supplementary material). Among the liverworts, Lejeuneaceae was the most represented family with 71 species, while Aneuraceae was the least represented with only one species. Among the mosses, Calymperaceae was the most represented family with 16 especies, while Bryaceae, Fissidentaceae, Hypnaceae and Stereophyllaceae had only one species each. Species accumulation curves (species – host tree) show that a sample of ten trees is sufficient to capture 75% of the number of species that are captured when the number of sampled trees is doubled (i.e., the total of 20 trees; Fig. 2).

Species richness did not vary significantly either among fragments, with 89 species on average, or among height zones ($P > 0.05$). Average number of species per host tree was also similar among fragments (Fig. 3). The greatest similarities in species composition among height zones were found between adjacent zones, and decreased with increasing distance between zones (Tab. 1).

The DCA analysis of the 114 bryophyte species produced three primary axes with eigenvalues of 0.73, 0.63 and 0.44. Axis I explained 41% of the variation and axis II 14.38%

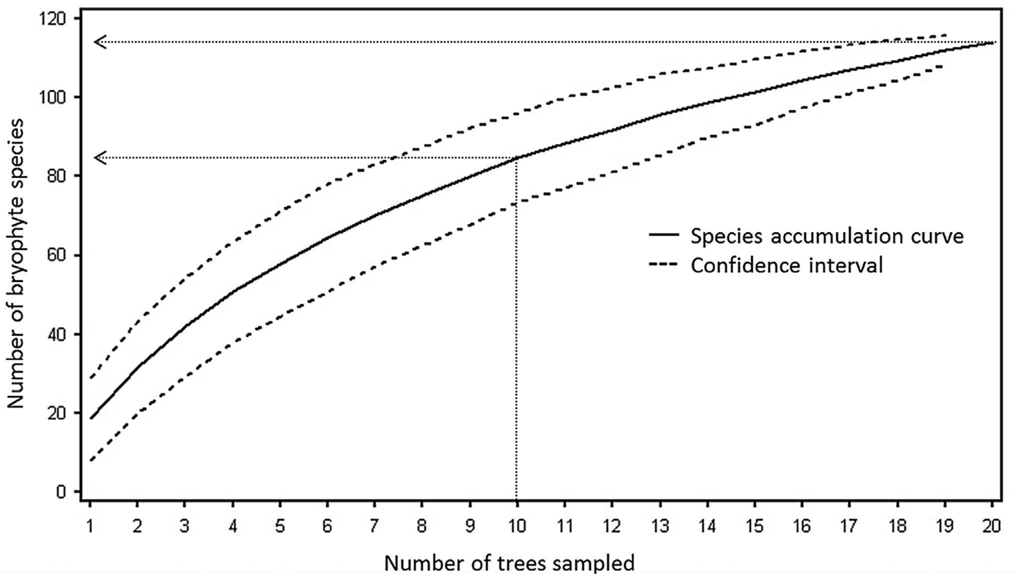


Figure 2. Randomized species phorophyte curve for the 114 species found in 20 trees sampled, showing that only half of the effort is needed to sample 75% of the species found in 20 trees.

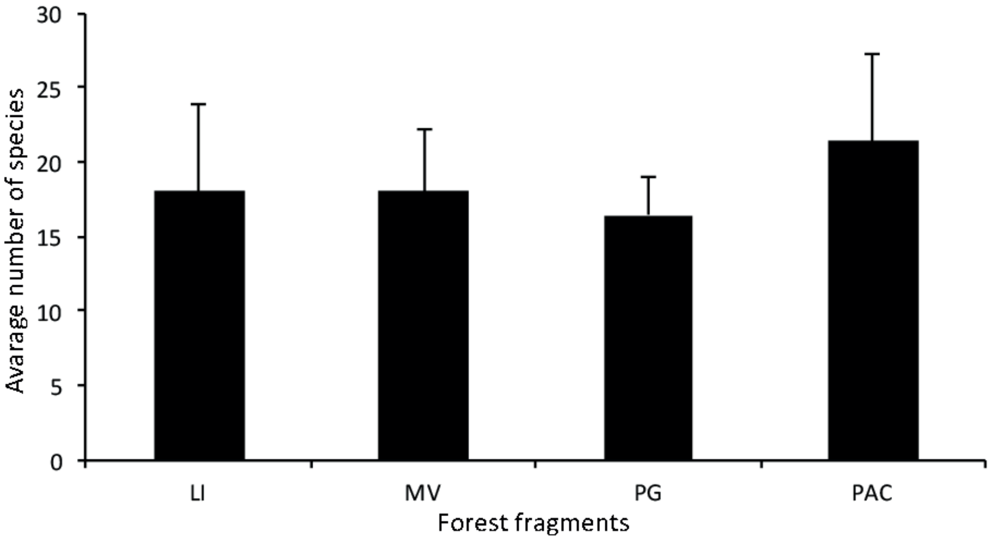


Figure 3. Average number and standard deviation of epiphytic bryophyte species per host tree in each of the four forest fragments.

Table 1. Sørensen index and number of species shared for each pair of height zones, including samples from the base of understory trees (UN).

	UN	Z1	Z2	Z3	Z4
		Number of species shared			
UN	–	53	38	41	37
Z1	0.55	–	33	29	25
Z2	0.33	0.45	–	34	28
Z3	0.29	0.42	0.63	–	36
Z4	0.26	0.33	0.52	0.61	–
	Sørensen index				

(Fig. 4). On the first axis, sample units from heigh zones 1 and 4 were clearly separated, while zones 2 and 3 exhibited overlap. Pearson correlation of the scores of the first axis for the DCA and height zone was significant ($P < 0.001$) after permutation test. None of the explanatory variables we measured could be correlated with axis II or III. When the same analysis was applied for fragments separetely, only Pacangê showed a slightly, yet significant, correlation ($P < 0.01$) between axis I scores and height zones, where axis I had an eigenvalue of 0.56 and explained 91% of the variation (Fig. 5).

Among the 114 species recorded, 10 showed significative preferences for a given height zone ($P < 0.05$), according to the Indicator Species Analysis (ISA). Most of these species, here classified as specialists, were found at the extremes of the gradient: *Calymperes lonchophyllum*, *Plagiochila aerea*, *Prionolejeunea scaberula* and *Taxithelium planum* were indicator species of zone 1 and *Cheilolejeunea trifaria, Cheilolejeunea xanthocarpa, Frullania caulisequa* and *Groutiella apiculata* were indicator species of zone 4. *Ceratolejeunea rubiginosa* and *Ceratolejeunea fallax* were indicators of zones 2 and 3, respectively (Fig. 6).

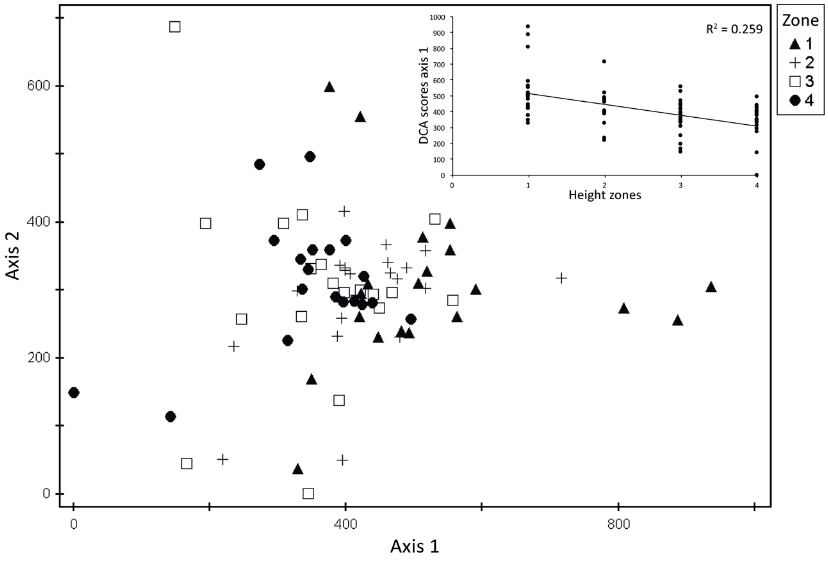


Figure 4. Scatterplot showing first and second axes of DCA of 114 species of epiphytic bryophytes in different height zones in the studied fragments. Height zone to which the plot belongs are as follows: triangles = zone 1; plus sign = zone 2; squares = zone 3; circles = zone 4. Eigenvalues were 0.73 (Axis 1), 0.63 (Axis 2). Top right corner: correlation between height zones and DCA values (Axis 1; P = 0.0000008).

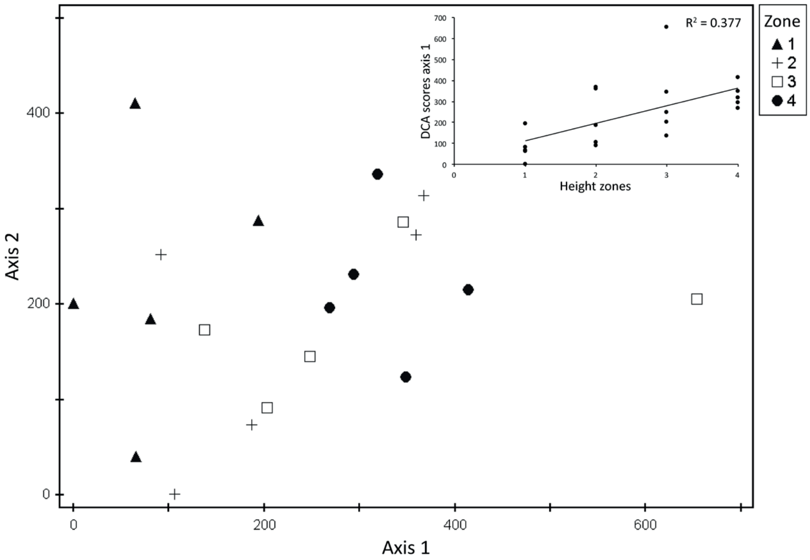
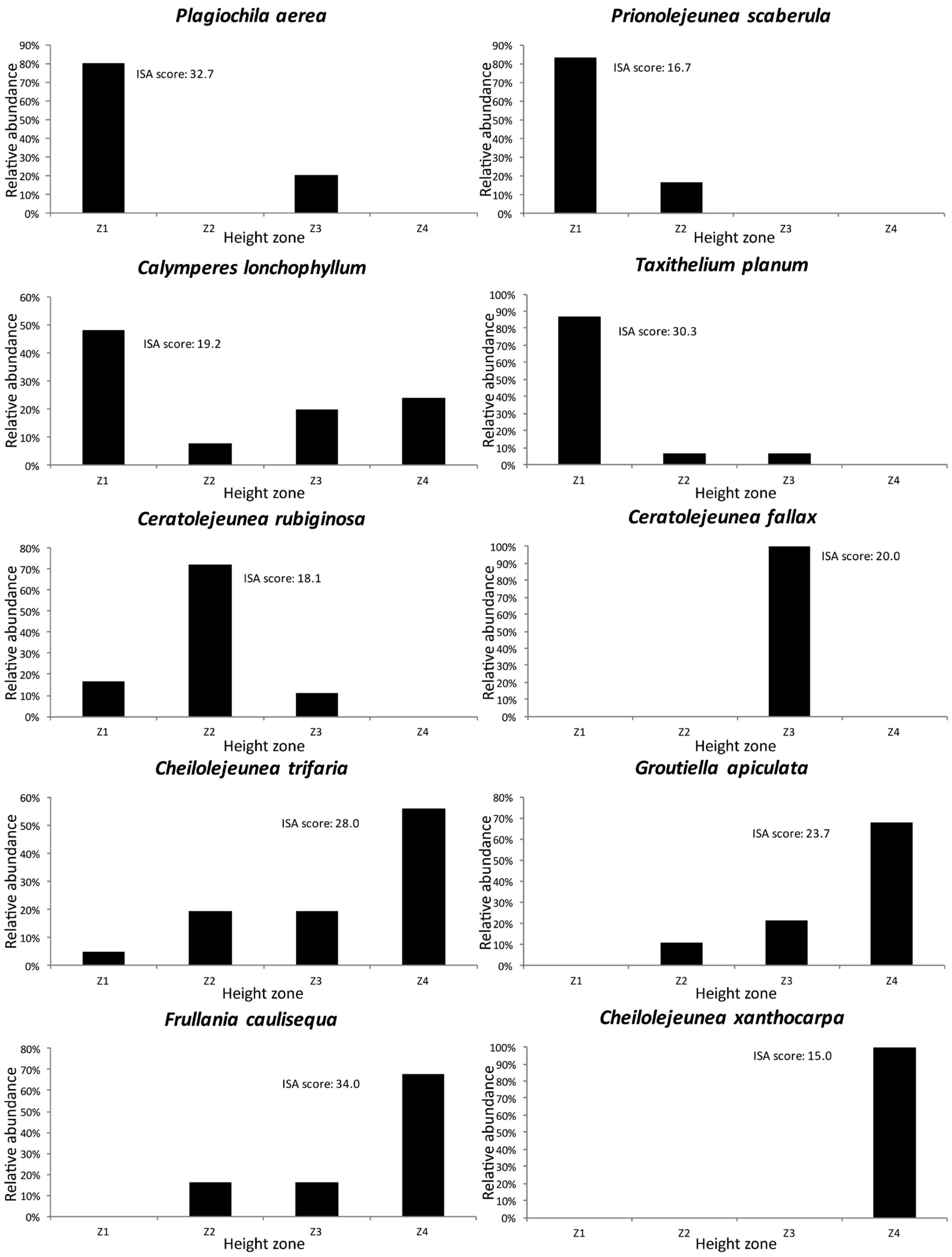


Figure 5. Scatterplot showing first and second axes of DCA of 54 species of epiphytic bryophytes in different height zones in Pacangê fragment. Height zone to which the plot belongs are as follows: triangles = zone 1; plus sign = zone 2; squares = zone 3; circles = zone 4. Eigenvalues were 0.74 (Axis 1) and 0.47 (Axis 2). Top right corner: correlation between height zones and the DCA values (Axis 1) in Pacangê fragment (P = 0.003).



Plagiochila aerea

Prionolejeunea scaberula

Calymperes lonchophyllum

Taxithelium planum

Ceratolejeunea rubiginosa

Ceratolejeunea fallax

Cheilolejeunea trifaria

Groutiella apiculata

Frullania caulisequa

Cheilolejeunea xanthocarpa

Figure 6. The relative abundance of individuals of each of the specialist species per height zone in Michelin Ecological Reserve.

About 70% of the bryophyte species grew as mats (Fig. 7). Species with this life form occurred on all trees and in all height zones. Each of the other life forms represented less than 10% of the species. The number of dendrois, pendents and crusts did not vary significantly among zones, while cushions were restricted to zones 2 and 3, and wefts were significantly more abundant in zone 1.

Among the morphological features that can be related to water retention and/or water conduction, lobules and papillae did not vary significatively among height zone. Long acuminate leaf apex, concave leaf shape and well developed alar cells were present more in zone 1, while hyalocysts and tomentose were present more on the higher strata– zones 3 and 4 (Fig. 8).

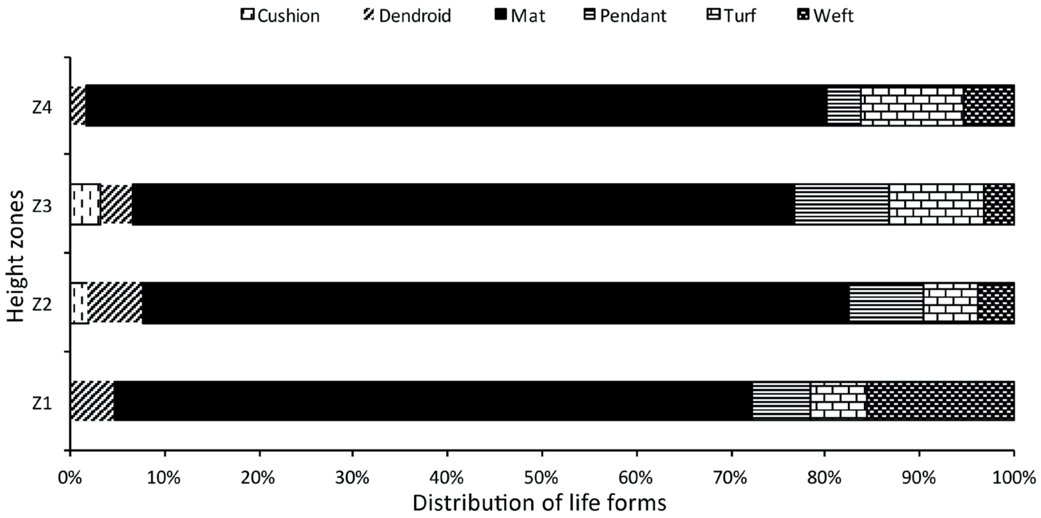


Figure 7. Distribution of life forms along the vertical gradient.

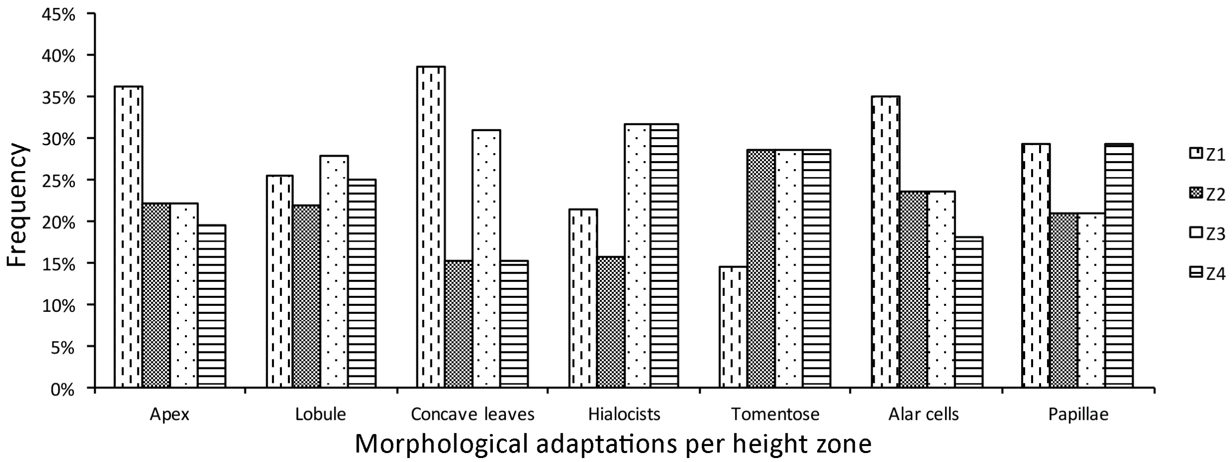


Figure 8. Distribution of morphological adaptations for water retention and/or conduction along the vertical gradient.

Discussion

The distribution of bryophytes among height zones and understory exhibited a well-known pattern for tropical rain forests; liverworts were more frequent than mosses in all height zones, both in number of species and in abundance, and mosses were mainly concentrated in the understory (Gradstein & Culmsee 2010). The dominance of liverworts was due to the high number of species of Lejeuneaceae, which represented 44% of the total number of species. Lejeuneaceae can represent up to 70% of the bryoflora of a tropical rainforest (Cornelissen & Gradstein 1990; Gradstein *et al.* 1990), and, together with Plagiochillaceae, comprise the most important pantropical families of liverworts in terms of number of species (Gradstein *et al.* 2001; Holz *et al.* 2002).

The samples from the understory included 77% of all species of bryophytes sampled. This result is in agreement with other studies carried out in the Atlantic Forest, where the turnover of species along the vertical gradient is absent or not pronounced (Germano 2003; Campelo & Pôrto 2007; Alvarenga *et al.* 2009). Although species zonation along the vertical gradient was not very clear, the changes observed from zone 1 to zone 4 were statistically significant. This differs from what has been found in other studies in the Atlantic Forest in the Northeast Region of Brazil, where no significant differences in species composition along the vertical gradient were found. Generally, the lack of zonation in tropical forests is thought to be related to homogeinization of environmental conditions due to forest fragmentation, fragment isolation and forest exploitation, which changes forest structure by creating openings and therefore decreasing moisture and shade (Alvarenga *et al.* 2009). Such alteration allows canopy species to colonize lower strata of the forest and hampers the occurrence of several understory species. The mechanisms that influence species establishment in specific microhabitats are, mostly, physiological (Glime 2007). Shade especialists are innibited by long periods of exposure to light and are frequently limited to the understory of a forest, sheltered by the canopy cover of individual trees. Therefore, shade specialists tend experience a drastic reduction in abundance with forest fragmentation (Alvarenga & Pôrto 2007) or disapear altogether after deforestation (Costa 1999; Acebey *et al.* 2003). Indeed, species classified as shade specialists in this study (zones 1 and 2 indicators) are commonly found in the undersory of other tropical forests and hardly ever in the canopy (Montfoort & Ek 1990; Acebey *et al.* 2003; Campelo & Pôrto 2007). On the other hand, some species require high levels of solar radiation, such as some highly pigmented species in the families Frullaniaceae and Orthotrichaceae (Glime 2007). Species of *Frullania* are particularly tolerant to dissecation (Romero *et al.* 2006) and are comonly found in the higher zones of trees, and especially in the outer canopy, as we have found in our study with *Frullania caulisequa* and *Groutiella apiculata*, being among the few species classified as zone 4 indicators (sun specialists).

The percentage of species classified as specialists according to ISA (8%, 10 spp.) is much lower than what was found in a similar study of epiphytic bryophytes in the Guianas, where 96 species, corresponding to 66% of the species found, were classified as specialists (Oliveira *et al.* 2009). The low percentage of specialists in the present study might be indicative of a high degree of disturbance to the reserve. Because bryophytes are sensitive to changes in the microclimate, habitat fragmentation can negatively affect species richness and composition and increase the representation of generalist species and diminish both sun and shade specialists (Alvarenga & Pôrto 2007). According to Werneck & Espírito-Santo (2002), the closed canopy of undisturbed forests is more favorable for the establishment of a vertical species turnover of epiphytes, because microenvironmental conditions are more distinct.

The predominant life form found in our study (mats), is in agreement with what has been documented in other tropical forests (Cornelissen & Steege 1989; Montfoort & Ek 1990; Costa 1999; Pardow *et al.* 2012). It is widely accepted that life forms reflect habitat characteristics, and are closely related to moisture availability (Pócs 1982; Thiers 1988; Proctor 1990). Life forms such as mats or wefts have a high capacity for water retention, and grow strongly appressed to the surface of the substrate (Glime 2007). They are abundant growing along trunks in tropical secondary forests, which have high levels of humidity and light (Sillet *et al.* 1995), as was recorded in the present study.

Life form classifications are based on morphological characters, and so those structures that seem to be adaptations to water conduction and retention can be used as indicators of environmental conditions (Frahm 2003). The higher frequency of occurrence of some of these morphological adaptations in certain height zones at Michelin ecological reserve reflects the microenvironmental gradient along tree trunks. The predominance of leaves with a long acuminate apex in lower zones, as well as concave leaves and well developed allar cells, was expected since these are typical of understory families like Calymperaceae, Pylaisiadelphaceae and Sematophyllaceae. Among the other morphological characteristics investigated, lobules are present in almost all Lejeuneaceae, which were distributed throughout the entire height gradient with no tendency for preference to a specific height zone. Likewise, papillae were abundant in all zones and revealed no pattern of altitudinal distribution, as was also found in a study of altitudinal zonation in Borneo (Frey *et al.* 1990). Until now, lobules and papillae had been successfully used as indicators of environmental conditions in altitudinal zonation, such as in a study in Central Africa (Kürschner & Seifert 1995). Adaptation to water retention and conduction along the vertical gradient in tropical forests needs further study.

We verified that there is substitution of species of epiphytic bryophytes along the height zones of host trees, however, this zonation is relatively weak in comparison with the results usually found in tropical forest environments. The morphological adaptations for water conduction or retention, as well as life forms, are strongly associated with microhabitat. A better understanding of the spatial distribution of these organisms in Atlantic Forest fragments is essential, since bryophytes have important roles in the proper functioning of ecosystems and can serve as bioindicators for monitoring changes in biodiversity, be they natural or caused by human actions.

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