



Can regional and local filters explain epiphytic bryophyte distributions in the Atlantic Forest of southeastern Brazil?

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ABSTRACT

Environmental conditions in distinct tropical rainforest phytophysiognomies can act as regional filters in determining the distribution of montane bryoflora likewise, local filters inherent to phorophyte species can have modulating influences. We analyzed the bryophyte communities in three phytophysiognomies of Atlantic Forest, in order to examine the influences of local (phorophyte species) and regional (forest phytophysiognomies) filters on their distributions. The study was undertaken in the Serra do Mar State Park, Ubatuba, SP, Brazil, using 1 ha plots in three forest phytophysiognomies along an elevational gradient. Four phorophyte species were selected, with three to seven replicates each. The line-intercept method was used on each phorophyte for collecting botanical material. Multivariate analyses were used to correlate species distributions with environmental filters. A total of 71 taxa were identified. Mean bryophyte coverage did not vary among the different phytophysiognomies, and although their species compositions were markedly distinct, no cohesive or isolated groups were found. Among the local filters examined, phorophyte DBH was found to be correlated with bryophyte coverage; the pH of the bark of *Euterpe edulis* and the high rugosity of the trunk of the Cyatheaceae influenced species compositions. Other filters not evaluated here may also be relevant for determining species distributions.

Keywords: environmental filtering, liverworts, mosses, phorophytes, spatial distribution, tropical rainforests

Introduction

The variety and structural complexities of habitats encountered in tropical rainforests favor the establishment of rich bryofloras, which are estimated to comprise between 3000 and 4000 species (Pócs 1982; Frahm 2001). The bryophytes encountered in these ecosystems primarily develop as epiphytes that occupy a number of different micro-environments (such as the bases of tree trunks, the trunks of shrubs, decomposing trunks, and on leaves) (Gradstein & Pócs 1989); with taxa exclusive to certain height zones in host trees (*i.e.*, phorophytes) (Cornelissen

& Steege 1989; Oliveira *et al.* 2009; Oliveira & Steege 2015) or evidencing preferences for some phorophyte species (Gabriel & Bates 2005).

Epiphytic bryophytes are structural components characteristic of tropical rainforests (Gradstein & Pócs 1989) and have important ecological roles in ecosystem functioning – aiding in maintaining the forest water balance by capturing and maintaining atmospheric humidity; recycling nutrients (*e.g.*, carbon and nitrogen); and fostering ecological interactions by providing habitats for other organisms (Richards 1984; Hallingbäck & Hodgetts 2000; Turetsky 2003).

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Tropical mountains can demonstrate elevational gradients reflected in different forest phytophysiognomies (Joly *et al.* 2012). According to Körner (2007), altitude itself is not technically a variable, but rather a surrogate that can be used to represent the environmental variations that occur along that gradient, such as temperature, luminosity, and humidity. Studies undertaken in the Atlantic Forests of southeastern Brazil have identified indicator species in the different phytophysiognomies found there, as well as evidence for the influence of regional environmental filters on bryophyte communities (related to temperature and water resource availability) (Santos & Costa 2010; Santos *et al.* 2014).

Studies focusing on the specificities of bryophyte species and their phorophytes have been undertaken in both tropical and temperate forests (*e.g.*, Cornelissen & Steege 1989; Schmitt & Slack 1990; Wolf 1994; Mancebo *et al.* 2003). Among the determining factors of epiphytic bryophyte colonization discussed in the literature are local abiotic filters (including attributes of the phorophyte such as height and diameter; physical-chemical characteristics of the bark, such as rugosity, thickness, porosity, pH, and water retention capacity) and regional abiotic filters (such as environmental conditions of temperature, luminosity, and humidity) (Smith 1982; Frahm 1990; Bates 1992).

Very few studies undertaken in Brazil have examined local filters acting on epiphytic bryophyte communities to determine the specificity of the relationships between those bryophytes and their phorophyte hosts (Lisboa 1976; Gottsberger & Morawetz 1993; Campelo & Pôrto 2007) – and even then, most of those studies have not identified any significant relationships between bryophytes and host trees. Lisboa (1976), for example, analyzed the bryoflora in an Amazonian meadow, and reported that most of the species were indifferent to the physical-chemical properties of the host bark and very few had their distributions correlated with its pH. Gottsberger & Morawetz (1993) found that bryophytes are more abundant on older trees while lichens dominate in young trees in Amazonia savanna. Campelo & Pôrto (2007), in their study of the epiphytic and epiphyllous bryoflora of an Atlantic Forest fragment (Seasonal Semi-Deciduous Forest) in northeastern Brazil reported that bryoflora compositions did not significantly vary according to the phorophyte species, with luminosity (a regional filter) being the principal factor influencing bryophyte distributions. No studies of this type have yet been undertaken in the Atlantic Forest (Dense Ombrophilous Forest) of southeastern Brazil, which differs from the Atlantic Forest in the northeastern region by climatic regime, latitude, floristic composition and by still having relatively large areas with continuous and well-preserved remnant forest formations.

As such, the present work examined the spatial distribution of bryophyte communities and the morphofunctional groups (life forms) occurring on arboreal phorophytes in three Atlantic Forest phytophysiognomies in

southeastern Brazil and the influence of local and regional environmental filters on those communities.

Materials and methods

Study area and sampling methodology

The present study was undertaken in an area of Atlantic Forest (Dense Ombrophilous Forest) in the *Núcleo Picinguaba* of the Serra do Mar State Park, along the northern coast of São Paulo State, Brazil. The *Núcleo Picinguaba* (23°31'–23°34'S, 45°02'–45°05'W), situated in the municipality of Ubatuba, covers 47,500 ha, with altitudes varying from 0–1,340 m a.s.l., with a tropical humid climate without a dry season, and a mean annual rainfall rate greater than 2200 mm (Joly *et al.* 2012). Collections were undertaken in 1 ha permanent plots that had been established during the Funcional Gradient Thematic Project of the Programa Biota/FAPESP (Joly *et al.* 2012); plots A – Restinga Forest (RF - 10 m), B – Lowland Forest (LF - 50 m) and J – Submontane Forest (SF - 350 m), which included three Atlantic Forest phytophysiognomies distributed along an elevational gradient. All of the collections were made between February and November/2009. The vegetation classification adopted follows Veloso *et al.* (1991), with modifications proposed by the Funcional Gradient Thematic Project Biota/FAPESP: where Restinga Forest (RF) has an essentially level topography, with a maximum altitude of 10 m; Lowland Forests (LF) occur at 50–100 m; and Submontane Forests (SF) occur at 100–500 m. Maps and detailed descriptions of the structures of these phytophysiognomies can be found Alves *et al.* (2010), Assis *et al.* (2011), Joly *et al.* (2012) and Rochelle *et al.* (2011).

Sampling

Phorophyte specificity

The following phorophyte trees were selected: *Euterpe edulis* Mart., *Guapira opposita* (Vell.) Reitz, *Sloania guianensis* (Aubl.) Benth., and two species of the family Cyatheaceae, with three to seven replicates in each elevational band, totaling 28 trees sampled in the LF, 27 in SF, and 20 in RF (as this phytophysiognomy did not have any individuals of Cyatheaceae).

Community structures

Contiguous 1x10 cm plots were established in each phorophyte to sample the epiphyte communities, totaling 100 cm (at heights of 60 cm to 160 cm in each tree), each running in the cardinal North direction. The line-intercept method was used in each of the plots to estimate bryophyte coverage.



Collecting environmental data

Local filters - the following physical-chemical characteristics of the phorophytes were evaluated: diameter at breast height (DBH), trunk pH and rugosity (Tab. 1). Rugosity was quantified using the following classes: 0 = smooth, 1 = slightly rough, 2 = rough, 3 = very rough, and 4 = sloughing; the pH of the trunks were measured using pH measuring strips (mixing 1 ml of distilled water with 1 cm² of triturated bark material).

Regional filters: we considered the different Atlantic Forest phytophysiognomies as a proxy of the regional filters, since these areas differ in forest structure (biomass, canopy opening, topography and elevation - see Alves *et al.* 2010 and Joly *et al.* 2012).

Identification of botanical material

The specimens collected were identified based on the specialized literature. The botanical classification adopted follows Goffinet & Shaw (2008). The methodologies of preparing and preserving the collected material followed Yano (1984). All of the collections were deposited in the bryophyte collection of the UFP herbarium.

Data analyses

The classifications adopted for the life forms (morphofunctional groups) follow Mägdefrau (1982), with modifications according to Richards (1984), where turf = gametophytes with vertical stems with limited branching; mat = gametophytes creeping over the substratum, closely attached by rhizoids; weft = gametophytes layers creeping over the substratum often with rather few rhizoidal attachments; fan = gametophytes with leaves arranged in two lateral ranks, arising from vertical substrates, forming flattened photosynthetic surfaces; pendant = gametophyte with long main stem with short side branches; dendroid = gametophyte erect with main stem with tuft of branches at top; thallose = mat of thallose liverwort gametophytes.

Analyses of local filters

Generalized Linear Models (GLM) with Poisson error distribution, log link function and ANCOVA model were used to evaluate the influences of local filters (rugosity, pH, and DBH) on bryophyte coverage using R 3.1.2 software (R Development Core Team 2014). To evaluate the influences of these filters on species compositions, direct gradient analyses (Canonical Correspondence Analysis - CCA) were performed using Fitopac 2.1 software (Shepherd 2010). The phorophyte data used in these analyses was transformed (*ranging*). The Monte Carlo test using 1000 permutations was used to evaluate the significance of the first two ordination axes.

Floristic similarity

The floristic affinities of the bryophyte species among the different phorophytes and phytophysiognomies studied were calculated using the Bray-Curtis dissimilarity index, employing the unweighted pair group method with averaging (UPGMA), using Fitopac 2.1 software (Shepherd 2010). The species compositions of the groups analyzed (phorophytes and phytophysiognomies) were tested using "Multi-Response Permutation Procedures" (MRPP), with 1000 permutations, using PCOrd 4.1 software (McCune & Mefford 1999). MRPP is a nonparametric method that examines the null hypothesis that two or more predefined groups are equal in composition. The A index describes the homogeneity within the groups and can vary between zero and one, with A = 0 indicating that the heterogeneities within and between the groups are equal, while A = 1 signifies that all the members of each group are identical among themselves but different from the members of other groups (McCune & Grace 2002).

Results

Species richness and distributions

Seventy-one taxa (Tab. 2) were identified, including liverworts (39) and mosses (32), which were distributed among 23 families; Lejeuneaceae (23 spp.), Calymperaceae (six spp.), Plagiochilaceae (five spp.), and Neckeraceae (four spp.) were the most represented. In relation to species richness in the different phytophysiognomies, 26 species were encountered in RF (six exclusive to it), including 17 liverworts and nine mosses; 39 species were encountered in the LF (nine exclusive to it), including 20 liverworts and 19 mosses; and 48 in SF (21 exclusive to it), including 25 liverworts and 23 mosses. Six species were shared between RF and LF, four between RF and SF, and 14 between LF and SF; only 10 species occurred in all three phytophysiognomies. It was quite notable that RF shared few species with the other areas. In relation to the occurrences of the bryophyte species on the phorophytes, 43 epiphyte species were encountered on *E. edulis* (14 exclusive to that tree species), 40 spp. on *G. opposita* (eight exclusive), 27 spp. on Cyatheaceae (seven), and 14 spp. on *S. guianensis* (four). Of the shared species, only four taxa (*Lejeunea laetevirens*, *Brachythecium plumosum*, *Lepidopilum caudicaule*, and *Microlejeunea bullata*) occurred on all of the phorophyte species. *E. edulis* and *G. opposita* shared 10 species, notably *P. patula*, which colonized those phorophytes in RF, LF and SF. *E. edulis*, *G. opposita* and Cyatheaceae likewise shared 10 taxa. The following phorophytes shared epiphyte species: *G. opposita*, *S. guianensis* and Cyatheaceae (two species in common); *E. edulis*, *S. guianensis* and *G. opposita* (1); *E. edulis* and *S. guianensis* (1); *E. edulis* and Cyatheaceae (1); *S. guianensis* and Cyatheaceae (1); *S. guianensis* and *G. opposita* (1); and *G. opposita* and Cyatheaceae (1).



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Table 1. Physical-chemical characteristics of the phorophytes (local filters). DBH = diameter at breast height; Tree Code = tree code in the permanent plot.

| Phytophysiognomies | Phorophyte | Tree Code | Rugosity | pH | DBH |
|---------------------------|------------|-----------|----------|----|------|
| <i>Euterpe edulis</i> | | | | | |
| Restinga Forest | EUTRF1 | A611 | 1 | 7 | 9.5 |
| Restinga Forest | EUTRF2 | A906 | 1 | 7 | 8.3 |
| Restinga Forest | EUTRF3 | A952 | 1 | 7 | 9.7 |
| Restinga Forest | EUTRF4 | A1320 | 1 | 7 | 8 |
| Restinga Forest | EUTRF5 | A1347 | 1 | 7 | 9.9 |
| Restinga Forest | EUTRF6 | A1078 | 1 | 7 | 10.3 |
| Restinga Forest | EUTRF7 | A1644 | 1 | 7 | 10.2 |
| Lowland Forest | EUTLF1 | B0045 | 1 | 7 | 10.8 |
| Lowland Forest | EUTLF2 | B0700 | 2 | 7 | 12.1 |
| Lowland Forest | EUTLF3 | B0983 | 2 | 7 | 12.5 |
| Lowland Forest | EUTLF4 | B0614 | 2 | 6 | 11.4 |
| Lowland Forest | EUTLF5 | B314 | 1 | 7 | 12.2 |
| Lowland Forest | EUTLF6 | B123 | 1 | 7 | 10.3 |
| Lowland Forest | EUTLF7 | B574 | 1 | 7 | 9.8 |
| Submontane Forest | EUTSF1 | J112 | 1 | 6 | 11.9 |
| Submontane Forest | EUTSF2 | J154 | 1 | 7 | 11.5 |
| Submontane Forest | EUTSF3 | J337 | 1 | 7 | 11.6 |
| Submontane Forest | EUTSF4 | J945 | 1 | 7 | 10.7 |
| Submontane Forest | EUTSF5 | J1336 | 1 | 7 | 10.3 |
| Submontane Forest | EUTSF6 | J1651 | 1 | 7 | 9.4 |
| <i>Guapira opposita</i> | | | | | |
| Restinga Forest | GUARF1 | A1594 | 1 | 5 | 16.2 |
| Restinga Forest | GUARF2 | A1022 | 2 | 6 | 16.2 |
| Restinga Forest | GUARF3 | A1077 | 1 | 5 | 22.9 |
| Restinga Forest | GUARF4 | A871 | 2 | 5 | 17.8 |
| Restinga Forest | GUARF5 | A0001 | 2 | 6 | 14 |
| Restinga Forest | GUARF6 | A972 | 2 | 5 | 16.2 |
| Restinga Forest | GUARF7 | A457 | 2 | 5 | 16.8 |
| Lowland Forest | GUALF1 | B1180 | 2 | 5 | 28.9 |
| Lowland Forest | GUALF2 | B858 | 1 | 5 | 34.9 |
| Lowland Forest | GUALF3 | B298 | 2 | 5 | 22.9 |
| Lowland Forest | GUALF4 | B262 | 1 | 5 | 10 |
| Lowland Forest | GUALF5 | B991 | 2 | 5 | 28.7 |
| Lowland Forest | GUALF6 | B636 | 2 | 5 | 25 |
| Lowland Forest | GUALF7 | B292 | 2 | 5 | 10 |
| Submontane Forest | GUASF1 | J281 | 3 | 5 | 17 |
| Submontane Forest | GUASF2 | J572 | 1 | 7 | 9 |
| Submontane Forest | GUASF3 | J736 | 2 | 5 | 14.5 |
| Submontane Forest | GUASF4 | J1371 | 4 | 5 | 27.2 |
| Submontane Forest | GUASF5 | J1459 | 2 | 5 | 20.9 |
| Submontane Forest | GUASF6 | J1832 | 1 | 7 | 18.9 |
| Submontane Forest | GUASF7 | J969 | 1 | 7 | 21.3 |
| <i>Sloania guianensis</i> | | | | | |
| Restinga Forest | SLORF1 | A1686 | 1 | 5 | 17.3 |
| Restinga Forest | SLORF2 | A855 | 1 | 6 | 9.9 |
| Restinga Forest | SLORF3 | A850 | 1 | 6 | 7.2 |
| Restinga Forest | SLORF4 | A829 | 1 | 6 | 20.1 |
| Restinga Forest | SLORF5 | A662 | 1 | 5 | 6.4 |
| Restinga Forest | SLORF6 | A495 | 1 | 6 | 7 |
| Lowland Forest | SLOLF1 | B209 | 1 | 5 | 11.8 |
| Lowland Forest | SLOLF2 | B102 | 1 | 5 | 19.1 |
| Lowland Forest | SLOLF3 | B171 | 1 | 6 | 7 |
| Lowland Forest | SLOLF4 | B374 | 1 | 5 | 19.7 |
| Lowland Forest | SLOLF5 | B132 | 2 | 5 | 24.5 |



Table 1. Cont.

| Phytophysiognomies | Phorophyte | Tree Code | Rugosity | pH | DBH |
|--------------------|------------|-----------|----------|----|------|
| Lowland Forest | SLOLF6 | B310 | 2 | 5 | 18.7 |
| Lowland Forest | SLOLF7 | B407 | 1 | 5 | 13.2 |
| Submontane Forest | SLOSF1 | J56 | 2 | 5 | 18.8 |
| Submontane Forest | SLOSF2 | J135 | 1 | 5 | 12.3 |
| Submontane Forest | SLOSF3 | J995 | 2 | 5 | 13.4 |
| Submontane Forest | SLOSF4 | J1182 | 2 | 4 | 19.8 |
| Submontane Forest | SLOSF5 | J1218 | 1 | 5 | 23.9 |
| Submontane Forest | SLOSF6 | J1264 | 2 | 5 | 16.7 |
| Submontane Forest | SLOSF7 | J159 | 3 | 3 | 28.5 |
| Cyatheaceae | | | | | |
| Lowland Forest | CYALF1 | B117 | 4 | 5 | 10 |
| Lowland Forest | CYALF2 | B339 | 3 | 5 | 11.6 |
| Lowland Forest | CYALF3 | B834 | 3 | 5 | 10.6 |
| Lowland Forest | CYALF4 | B1079 | 3 | 5 | 10.7 |
| Lowland Forest | CYALF5 | B563 | 3 | 5 | 10.3 |
| Lowland Forest | CYALF6 | B750 | 3 | 6 | 11 |
| Lowland Forest | CYALF7 | B745 | 3 | 5 | 15.1 |
| Submontane Forest | CYASF1 | J61 | 3 | 5 | 5 |
| Submontane Forest | CYASF2 | J140 | 2 | 5 | 5.3 |
| Submontane Forest | CYASF3 | J387 | 3 | 5 | 10.5 |
| Submontane Forest | CYASF4 | - | 3 | 5 | 10.5 |
| Submontane Forest | CYASF5 | J596 | 3 | 5 | 4.9 |
| Submontane Forest | CYASF6 | J1786 | 4 | 5 | 5.6 |
| Submontane Forest | CYASF7 | - | 3 | 5 | 10.9 |

Table 2. Incidence of bryophyte species on phorophyte species in the different forest phytophysiognomies and their respective life forms.

| Species | Life form | Restinga Forest | | | Lowland Forest | | | | Submontane Forest | | | |
|---|-----------|-----------------|-----|-----|----------------|-----|-----|-----|-------------------|-----|-----|-----|
| | | Eut | Slo | Gua | Eut | Slo | Gua | Cya | Eut | Slo | Gua | Cya |
| MARCHANTIOPHYTA | | | | | | | | | | | | |
| <i>Acanthocoleus aberrans</i> (Lindenb. & Gottsche) Kruijt | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Aphanolejeunea kunertiana</i> Steph. | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Archilejeunea parviflora</i> (Nees) Stephani | Mat | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 4 | 3 |
| <i>Bazzania heterostipa</i> (Steph) Fulford | Mat | 0 | 0 | 0 | 0 | 7 | 6 | 1 | 0 | 0 | 0 | 0 |
| <i>Bryopteris filicina</i> (Sw.) Nees | Weft | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| <i>Ceratolejeunea cubensis</i> (Mont.) Schiffn. | Mat | 37 | 1 | 6 | 3 | 0 | 11 | 0 | 0 | 0 | 1 | 0 |
| <i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn. | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 24 | 0 |
| <i>Cheilolejeunea adnata</i> (Kunze ex Lehm.) Grolle | Mat | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cheilolejeunea rigidula</i> (Mont.) R.M. Schust. | Mat | 7 | 5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cheilolejeunea trifaria</i> (Reinw., Blume & Nees) Mizut. | Mat | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Chiloscyphus martianus</i> (Nees) J.J. Engel & R.M. Schust. | Mat | 0 | 0 | 0 | 0 | 0 | 7 | 16 | 3 | 0 | 0 | 0 |
| <i>Chyloscyphus muricatus</i> (Lehm.) J.J. Engel & R.M. Schust. | Weft | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| <i>Cylindrocolea rhizantha</i> (Mont.) R.M. Schust. | Weft | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 |
| <i>Harpalejeunea oxyphylla</i> (Nees & Mont.) Steph. | Mat | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Harpalejeunea stricta</i> (Lindenb. & Gottsche) Steph. | Mat | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Kurzia capillaris</i> Grolle | Weft | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Lejeunea controversa</i> Gottsche | Mat | 17 | 0 | 0 | 3 | 0 | 5 | 4 | 4 | 0 | 0 | 0 |
| <i>Lejeunea flava</i> (Sw.) Nees | Mat | 1 | 0 | 12 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Lejeunea filipes</i> Spruce | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| <i>Lejeunea huctumalcensis</i> Lindenb. & Gottsche | Mat | 0 | 0 | 0 | 0 | 31 | 0 | 11 | 0 | 19 | 0 | 0 |
| <i>Lejeunea immersa</i> Spruce | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Lejeunea laetevirens</i> Nees & Mont. | Mat | 19 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 2 | 0 | 1 |
| <i>Lejeunea sp.</i> | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 |
| <i>Lopholejeunea nigricans</i> (Lindenb.) Stephani | Mat | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 |



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Table 2. Cont.

| Species | Life form | Restinga Forest | | | Lowland Forest | | | | Submontane Forest | | | |
|--|-----------|-----------------|-----|-----|----------------|-----|-----|-----|-------------------|-----|-----|-----|
| | | Eut | Slo | Gua | Eut | Slo | Gua | Cya | Eut | Slo | Gua | Cya |
| <i>Metalejeunea cucullata</i> (Reinw., Blume & Nees) Grolle | Mat | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 |
| <i>Microlejeunea bullata</i> (Tayl.) Steph. | Mat | 1 | 10 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 |
| <i>Microlejeunea globosa</i> Spruce Steph. | Mat | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Metzgeria brasiliensis</i> Schiffl. | Thallose | 0 | 0 | 0 | 0 | 0 | 42 | 0 | 1 | 0 | 25 | 8 |
| <i>Metzgeria ciliata</i> Raddi | Thallose | 13 | 0 | 0 | 0 | 0 | 0 | 7 | 26 | 0 | 18 | 0 |
| <i>Plagiochila disticha</i> (Lehm. & Lindenb.) Lindenb. | Fan | 3 | 0 | 6 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| <i>Plagiochila martiana</i> (Nees) Lindenb. | Fan | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Plagiochila patentissima</i> Lindenb. | Fan | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Plagiochila patula</i> (Sw) Lindenb. | Fan | 26 | 0 | 10 | 7 | 0 | 7 | 0 | 16 | 0 | 11 | 0 |
| <i>Plagiochila rutilans</i> Lindenb. | Fan | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 0 |
| <i>Radula ligula</i> Steph. | Mat | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 15 | 0 |
| <i>Radula recubans</i> J. Taylor | Weft | 0 | 0 | 0 | 4 | 0 | 1 | 4 | 0 | 0 | 1 | 4 |
| <i>Symbiezidium barbiflorum</i> (Lindenb. & Gottsche) A. Evans | Mat | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| <i>Stictolejeunea squamata</i> (Willd. Ex Weber) Schiffl. | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 14 | 0 |
| <i>Telaranea diacantha</i> (Mont.) Engel & Merr. | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| BRYOPHYTA | | | | | | | | | | | | |
| <i>Brachythecium plumosum</i> (Hedw.) Schimp. | Mat | 6 | 1 | 8 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Calymperes</i> sp. | Turf | 1 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Calymperaceae</i> sp. 2 | Turf | 0 | 5 | 5 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 |
| <i>Calymperaceae</i> sp. 3 | Turf | 0 | 0 | 0 | 0 | 19 | 0 | 0 | 0 | 7 | 0 | 0 |
| <i>Calymperaceae</i> sp. 4 | Turf | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Fissidens</i> sp.1 | Fan | 0 | 0 | 0 | 1 | 0 | 6 | 2 | 10 | 0 | 23 | 0 |
| <i>Fissidens</i> sp.2 | Fan | 0 | 0 | 0 | 0 | 0 | 4 | 6 | 0 | 0 | 2 | 4 |
| <i>Helicodontium capillare</i> (Hedw.) A. Jaeger | Weft | 4 | 0 | 9 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 |
| <i>Isodrepanium lentulum</i> (Wilson) E. Britton | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| <i>Isopterygium tenerum</i> (Sw.) Mitt. | Mat | 5 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 |
| <i>Dicranaceae</i> sp. | Turf | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Jaegerina scariosa</i> (Lorentz) Arzeni | Fan | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Leskeodon aristatus</i> (Geh. & Hampe) Broth. | Fan | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>Lepidopilidium brevisetum</i> (Hampe) Broth. | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 0 | 28 | 10 |
| <i>Lepidopilum caudicaule</i> (Müll. Hal.) Broth. | Mat | 6 | 0 | 0 | 17 | 1 | 19 | 0 | 0 | 0 | 8 | 2 |
| <i>Leucophanes molleri</i> Müll. Hal. | Turf | 4 | 0 | 1 | 6 | 0 | 11 | 12 | 2 | 0 | 0 | 0 |
| <i>Leucoloma serrulatum</i> Brid. | Turf | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Meteoridium remotifolium</i> (Müll. Hal.) Manuel | Pendant | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Neckeropsis disticha</i> (Hedw.) Kindb. | Fan | 6 | 0 | 0 | 1 | 0 | 5 | 1 | 2 | 0 | 2 | 1 |
| <i>Neckeropsis undulata</i> (Hedw.) Kindb. ex J. A. Allen | Fan | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 5 | 0 |
| <i>Octoblepharum albidum</i> Hedw. | Turf | 0 | 27 | 0 | 0 | 3 | 3 | 15 | 0 | 0 | 0 | 0 |
| <i>Pilotrichella flexilis</i> (Hedw.) Ångstr. | Pendant | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Porotrichum longirostre</i> (Hook.) Mitt. | Dendroid | 0 | 0 | 0 | 0 | 0 | 2 | 7 | 18 | 0 | 0 | 0 |
| <i>Porotrichum piniforme</i> (Brid.) Mitt. | Dendroid | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Phyllogonium viride</i> Brid. | Pendant | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Racopilum tomentosum</i> (Hedw.) Brid. | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 3 | 0 | 0 | 0 |
| <i>Rhynchostegium serrulatum</i> (Hedw.) A. Jaeger | Mat | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Tortula</i> sp. | Turf | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| <i>Taxithelium planum</i> (Brid.) Mitt. | Mat | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Syrrhoptodon gardneri</i> (Hook.) Schwägr. | Turf | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Vesicularia vesicularis</i> (Schwägr.) Broth. | Mat | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 3 | 0 | 0 | 0 |

Morphofunctional groups

Seven bryophyte life forms were encountered: mat (36 species), fan (12), turf (10), weft (six), pendant (three), dendroid (two) and thallose (two). The principal life form encountered was mat, represented by 36 taxa (RF = 15, LF

= 16, SF = 26). The life forms varied among the different phytophysionomies and phorophytes (Fig. 1). No taxa with pendant or dendroid life forms occurred in RF. LF likewise did not have any pendant species. In relation to the phorophytes, Cyatheaceae stood out for the lack of any pendant epiphytes, while the *S. guianensis* phorophytes bore only turf and mat species.



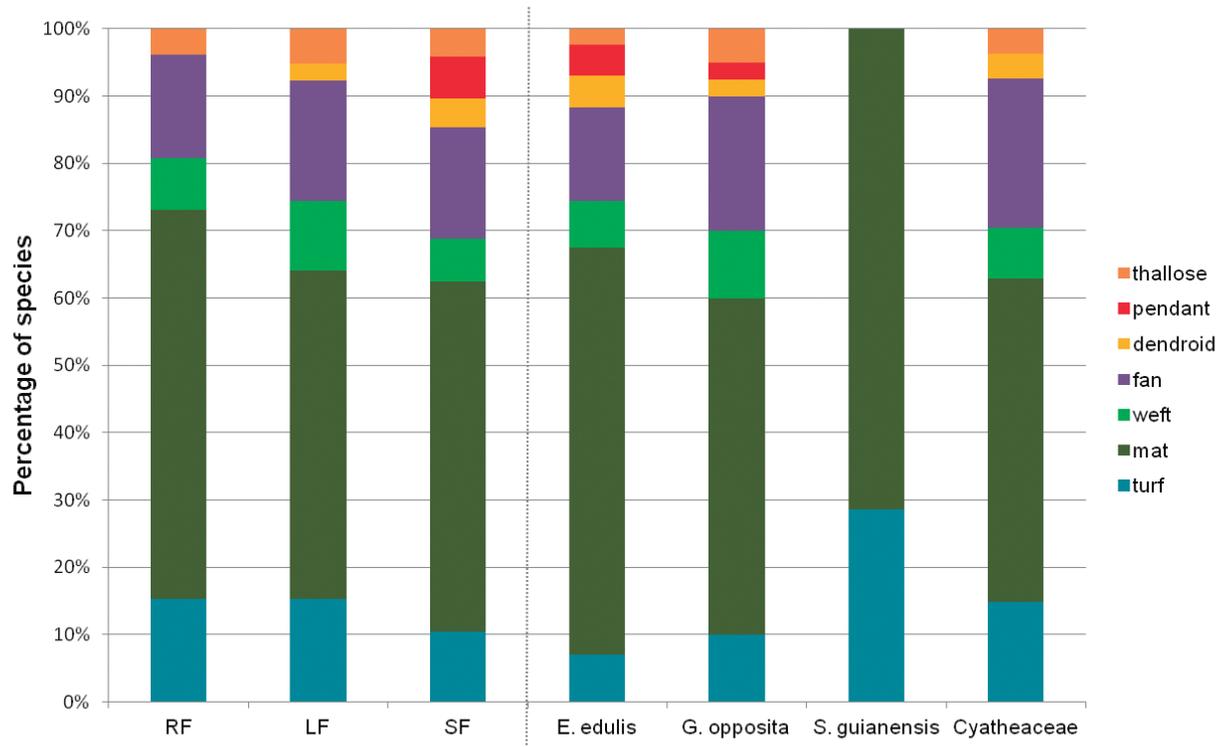


Figure 1. Percentages of the bryophyte life forms in the forest phytophysionomies and on the phorophytes in Serra do Mar State Park. RF = Restinga Forest; LF = Lowland Forest; SF = Submontane Forest. Please see the PDF version for color reference.

Floristic similarity

Similarities between the phorophytes as well as between the phytophysionomies analyzed in terms of their bryophyte floras were relatively low. In terms of the phorophytes, the greatest similarity indices were observed between the trees of *S. guianensis* (SLO). The phorophyte SLO3 in the LF phytophysionomy demonstrated the same composition as species SLO4 in the SF. Other phorophytes that demonstrated high similarity indices (low Bray-Curtis dissimilarity) were: SLO3 in the LF and SLO7 in the SF (0.14); SLO4 in the LF and SLO4 in the SF (0.20); SLO4 in the LF and SLO7 in the SF (0.23). The grouping analyses using UPGMA, without considering rare species (cophenetic correlation: 0.789), demonstrated grouping among the *S. guianensis* phorophytes in the LF and SF (Fig. 2). The MRPP for the bryophyte species compositions on the phorophytes indicated that, while significant (different from that expected by chance), no cohesive groups were formed among phorophytes of the same species ($A = 0.076$; $T = -12.6$; $p < 0.001$), corroborating the results of the grouping analyses. In relation to the bryophyte compositions in the different phytophysionomies, SF differed slightly from RF and LF, probably due to its larger number of exclusive species (approximately 52% of the taxa were not shared). The forest phytophysionomies demonstrated bryophyte compositions different from those expected solely by chance,

and likewise did not form either cohesive or isolated groups ($A = 0.063$; $T = -13.005$; $p < 0.001$).

The influence of environmental filters on bryophyte coverage and composition

The parameters of the bryophyte communities analyzed in the present study (coverage and species compositions) responded in distinct manners to the quantified environmental variables. Mean bryophyte coverage did not differ among the different forest phytophysionomies. Among the local filters, only DBH was correlated with bryophyte coverage ($\text{Chisq} = 48.027$; $\text{d.f.} = 1$; $p = 0.02$).

In terms of the influences of the local filters on species compositions, the CCA (Fig. 3) demonstrated low accumulated variance on the first two axes (Axis 1 = 4.0% of the total variation; eigenvalue = 0.36 and Axis 2 = 2.6%; eigenvalue = 0.24). The Monte Carlo test was significant for those axes ($p = 0.005$ and $p = 0.01$ respectively) and the residuals of the analyses (non-canonic part) did not demonstrate pattern, which demonstrated that the pattern was captured in the canonic portion of the analysis. The bark pH was the variable most correlated with axis 1 (-0.89), especially among the phorophytes on *E. edulis* (higher pH values - ranging between 6 and 7), while high rugosity was associated with axis 2 (-0.9), where the phorophytes on *Cyatheaceae* were grouped.

Can regional and local filters explain epiphytic bryophyte distributions in the Atlantic Forest of southeastern Brazil?

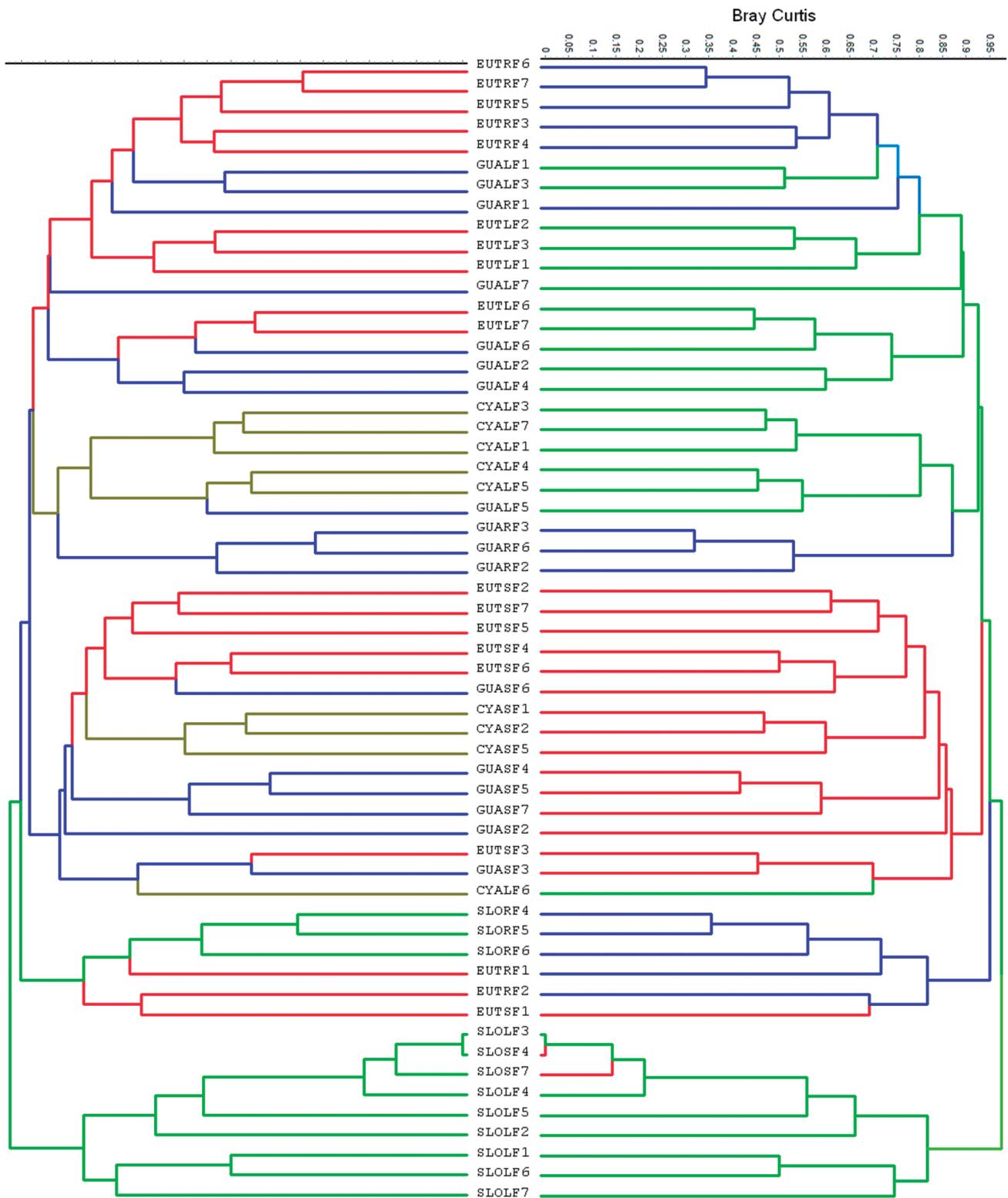


Figure 2. Combined similarity dendrogram (UPGMA) without considering rare species. Colors denote the forest phytophysioonomies (to the right) and the phorophyte species (to the left). CYA = Cyatheaceae; EUT = *Euterpe edulis*; GUA = *Guapira opposita*; SLO = *Sloanea guianensis*; RF = Restinga Forest; LF = Lowland Forest; SF = Submontane Forest. Please see the PDF version for color reference.



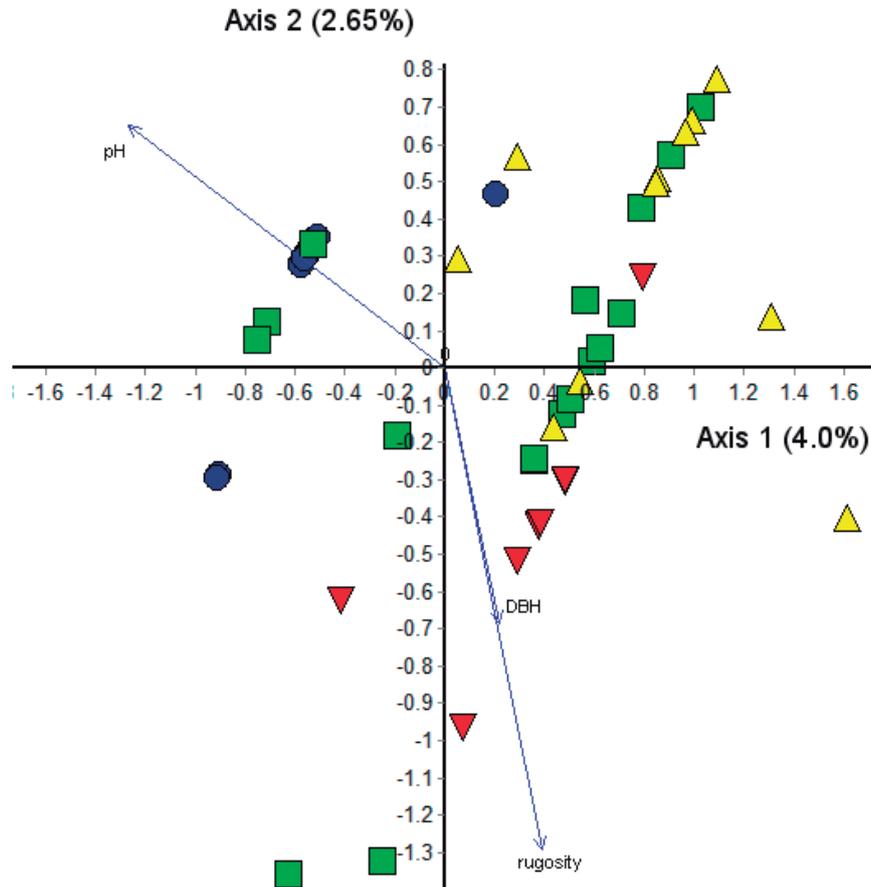


Figure 3. Ordination diagram of the Canonical Correspondence Analysis (CCA) between species composition and local filters (diameter at breast height [DBH], pH and rugosity) of phorophytes. Blue circles = *Euterpe edulis*; Red inverted triangles = Cyatheaceae; Yellow triangles = *Sloania guianensis*; Green squares = *Guapira opposita*. Please see the PDF version for color reference.

Discussion

Distributions of the bryophyte species

Expressive bryophyte richness were found on the phorophytes analyzed, with a predominance of liverwort species. According to Santos *et al.* (unpubl. res.), liverwort richness was generally greater than moss richness along an elevational gradient in the Atlantic Forest in the Serra do Mar mountains in the study area. The most abundant species in the present study was *Plagiochila patula*, with 76 occurrences. This species is typical of shaded environments and is found distributed throughout the neotropical region and occurs widely in Brazil (reported from the states of Acre, Bahia, Minas Gerais, Rio de Janeiro and São Paulo) (Costa 2016). Among the dominant bryophyte species in the three forest phytophysionomies examined, *Ceratolejeunea cubensis* stood out in RF (44 occurrences). According to Dauphin (2003), this species is distributed throughout the tropical regions of the Americas, from the United States through southeastern Brazil. It has a generalist spectrum

of habitat preferences, occurring in both primary and secondary vegetation and in humid and seasonal forests. Altitude is an important factor in the distribution of the genera, with *C. cubensis* being commonly found in lowland areas (0-500 m). *Metzgeria brasiliensis* and *Lejeunea huctumalcensis* where frequently encountered in the LF (42 occurrences). *M. brasiliensis* is endemic to Brazil and occurs in the Atlantic Forest domain (Costa 2008), while the geographic distribution of *L. huctumalcensis* includes North, Central, and South America, with expressive occurrences in lowland ombrophilous forests (Bastos & Yano 2009). *Metzgeria ciliata* was very frequent in SF (44 occurrences), and shows ample distribution throughout tropical and subtropical regions of the southern hemisphere (Costa 2008).

Influence of local filters on bryophyte communities

Due to their poikilohydric nature, bryophytes cannot easily control water losses, and therefore have generally restricted ecological amplitudes controlled by environmental determinants and occur only in very

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specific micro-environments (Gradstein *et al.* 1996). In addition to causing alterations in community compositions, environmental filters related to humidity and luminosity can influence the morphofunctional habits of bryophytes (*i.e.* their life forms), selecting life forms that maximize primary production in specific microenvironments while also reducing evapotranspiration (Bates 1998). Among the phorophytes, Cyatheaceae stands out in terms of its lack of pendant species, while individuals of *S. guianensis* harbor only turf and mat life forms. The expressive number of turf bryophytes encountered on *S. guianensis* and the absence of any other life forms may reflect the bark characteristics of that phorophyte, with low rugosity that suggests a low water retention capacity and the turf life form tends to maximize water retention (Glime 2007).

Approximately 72% of the epiphyte species encountered on *S. guianensis* were shared with the other phorophyte species analyzed, and this tree demonstrated the lowest richness of them all – indicating that few bryophytes could colonize its trunk. The high similarity between the six individuals of *S. guianensis* may likewise reflect the existence of local environmental filters that restrict bryophyte establishment. This high similarity was only noted, however, among individuals growing on mountain slopes (LF and SF sites), which have similar forest structures (regional filters) in comparison with the RF site (Joly *et al.* 2012) – reflecting the fact that regional filters can act in additive manners to influence bryophyte distributions.

The influence of local filters on bryophyte coverage and composition demonstrated relationships with distinct variables such as DBH, bark rugosity, and pH. DBH reflects the general age of a phorophyte, so that its bryophyte coverage could reflect more ample time periods available for substrate colonization (Mezaka *et al.* 2008). Simultaneously, the larger the DBH the lower will be total sunlight exposure on phorophyte surfaces, increasing the water retention properties of the bark and establishing a more favorable microclimate for bryophyte development.

Phorophytes with rough bark will retain more humidity (Mezaka & Znotina 2006), thus providing better conditions for epiphyte establishment. As such, the high pH of the bark of *E. edulis*, as well as the elevated rugosity of the trunks of Cyatheaceae may help explain their bryophyte species compositions. This influence, however, must be relatively small, in light of the low explanation level obtained along the first two ordination axes in the direct analyses of the gradients (CCA). It is also important to remember that other filters not considered here may be relevant to structuring epiphytic bryophyte communities.

Influence of regional filters on bryophyte communities

The RF demonstrated greater canopy openness than LF in the study area (Santos *et al.* 2011), so that the bryophyte

species in RF must have greater tolerances to solar radiation as compared to those present on mountain slopes (LF and SF), which have more amenable temperature and luminosity conditions.

Some morphofunctional groups were restricted to mountain slope sites (LF and SF). The gametophytes of pendant life forms (exclusive to SF) are generally exposed directly to the air and capture more light and more water from rainfall or mists, thus being typical of humid tropical forests (Richards 1984; Bates 1998; Glime 2007). These adaptive traits reflect the influences of environmental filters in those sites.

The RF had the largest percentage of species with mat life forms, and the marked occurrence of turf species, together with the absence of pendant and dendroid forms, reflected the greater degree of luminosity encountered in that phytophysiognomy (Glime 2007; Santos *et al.* 2011) – as life forms respond to environmental conditions (Gimingham & Birse 1957). As a consequence of these traits, bryophytes can be used as bioindicators of environmental and microclimatic conditions, and have shown themselves to be efficient indicators of phytophysiognomies and/or elevational belts in humid tropical forests (*e.g.*, Frahm & Gradstein 1991; Gradstein *et al.* 2001; Costa & Lima 2005; Santos & Costa 2010; Santos *et al.* 2014).

Conclusions

Analyses of the coverage, life forms and floristic composition of bryophytes can provide important information about the spatial distributions of those organisms. We were able to establish that environmental determinism (local and/or regional abiotic filters) influences, at least in part, the distributions of epiphytic bryophytes in the Atlantic Forest, although the variables examined were relatively inefficient in explaining those effects. In spite of the fact that the species compositions significantly differed among the forest phytophysiognomies and phorophyte species examined, no cohesive and isolated groups were identified. The DBH of the phorophyte constituted a filter for bryophyte coverage, while bark pH and rugosity were the most important filters in terms of bryophyte composition.

Better understanding the responses of these organisms to local and regional filters is important, as bryophytes have important roles in ecosystem functioning and can act as bioindicators to detect and monitor changes in biodiversity driven by anthropogenic impacts or natural factors.

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