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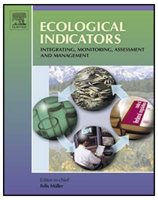

Original Articles

# Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest?

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## ABSTRACT

Liverworts are non-vascular cryptogamic plants with wide geographic distributions due to their capacity to disperse their spores over long distances, although they have no epidermal cuticle, sensitive to external environmental conditions, found only in very specific microenvironments – and are therefore widely used as bioindicators. We evaluated the floristic composition of liverworts in localities located in different Atlantic Forest vegetation types in southeastern Brazil to address the following questions: Is the liverwort flora distributed uniformly or randomly, or does it demonstrate environmental niche restrictions at regional scales? If the distribution of liverworts is deterministic, do geoclimatic variables act as environmental filters for this flora? Can liverwort species be considered bioindicators of the different Atlantic Forest vegetation types? We undertook floristic surveys in 26 localities to evaluate the beta diversity of the liverwort flora and its correlation with environmental gradients (geoclimatic variables) using multivariate analyses and the Mantel Test. Ordination and classification methods indicated elevated beta diversity in a deterministic distribution of the liverwort flora along the Atlantic coast of southeastern Brazil. Altitude was significantly associated with the first axis of the CCA, demonstrating a floristic gradient between Lowland Forests and High Montane Forests and "Campos de Altitude". Five floristic groups were identified and 34 species could be considered bioindicators. The principal geoclimatic variables that explained the floristic groupings of liverwort species were altitude, temperature, and precipitation. The prediction that liverwort plants demonstrated environmentally determined distributions was confirmed by the Mantel Test (rM 0.557; $p < 0.0001$). Our results support the idea that the liverwort flora of the coastal Atlantic Forest in southeastern Brazil comprises part of a regional pool of species whose establishment and survival are determined by abiotic filters acting in those habitats. The low similarities between localities and the high numbers of indicator species suggest that the liverwort vegetation has a deterministic distribution at the regional level – which corroborates their use as bioindicators of vegetation types and of environmental conditions. Although species distributions are principally determined by environmental niches, geographical distances (dispersal limitation) are important in regions such as oceanic islands and coastal mountains.

## 1. Introduction

Understanding the patterns of floristic compositional variations between different regions (beta diversity) is one of the central aims of ecology (Chave, 2008; de Bello et al., 2010; Legendre et al., 2005). In the context of current theories, the distributions of plant species can be explained by three principal hypotheses: (1) Oligarchical Dominance, where a region is dominated by a group of superior competitors and demonstrates compositional uniformity of species over large areas (Pitman et al., 1999, 2001); (2) Neutral Assembly, where species distributions are apparently random but spatially autocorrelated due to dispersal limitations (Hubbell, 2001); or (3) Niche Assembly, with species distributions being unequal and environmentally determined (Tuomisto et al., 2003). As such, the manners in which organisms are dispersed (e.g., by wind or animal vectors – Cain et al., 2000; Nekola and White, 1999; Tuomisto et al., 2003) and environmental filters (e.g., edaphic factors – Condit et al., 2002; Honorio Coronado et al., 2009) strongly influence floristic configurations in different regions. Vegetation

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*Abbreviations:* NP, National Park; SP, State Park.

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scientists need to examine the floristic affinities between different regions in order to understand the processes that drive existing vegetation patterns (Condit et al., 2002; Tuomisto et al., 2003) and these studies are usually based on the hypothesis that floristic similarities can be predicted by examining environmental variables and/or the geographical distances between the regions in question (Chase and Myers, 2011; Chave, 2008).

Liverworts (Marchantiophyta) represent a phylum of terrestrial plants that, together with mosses (Bryophyta) and hornworts (Anthocerothophyta), form a paraphyletic group commonly known as "bryophytes" – the oldest lineage among the Embryophyta (Goffinet et al., 2009; Magallón and Hilu, 2009). The liverworts are represented by 5000 species throughout the world, with 1350 in the Neotropics and approximately 700 in Brazil, of which 463 occur in the Atlantic Forest (Costa, 2009; Gradstein et al., 2001; Gradstein and Costa, 2003). The spores of these plants can be dispersed over very long distances by wind, resulting in wide phytogeographical distributions as compared to angiosperms (Heinrichs et al., 2009; Schofield, 1992; van Zanten and Pócs, 1981). On the other hand, these plants do not have epidermal cuticles, are especially sensitive to adverse environmental conditions and only occur in very specific microenvironments – and are therefore frequently utilized as bioindicators of local climatic, environmental, and ecological conditions (Vanderpoorten and Goffinet, 2009).

Bryophytes can be used as bioindicators of altitudinal gradients in neotropical regions (Frahm and Gradstein, 1991; Gradstein et al., 2001) and have been identified as indicators of different vegetation types in the Atlantic Forest, with different species of mosses and liverworts being characteristic of different altitudinal belts (Costa and Lima, 2005; Santos and Costa, 2010). No studies have yet been undertaken, however, that evaluated the patterns of beta diversity of the bryophyte flora across areas with different vegetation types of Atlantic Forest at a regional scale.

Southeastern Brazil is an important region within the continuum of remnant coastal Atlantic Forest areas, and a center of diversity and endemism for many animal and plant taxa because it holds large stretches of continuous and relatively well-preserved forests (Guedes-Bruni and Lima, 1997; Laurence, 2009; Stehmann et al., 2009). The Brazilian states of Rio de Janeiro and São Paulo are known to be very species-rich and have been well studied in terms of their liverwort flora (Gradstein and Costa, 2003; Santos and Costa, 2010). Additionally, these states demonstrate wide altitudinal variations, with different Atlantic Forest vegetation types being found over relatively short distances – presenting an excellent opportunity for evaluating the importance of deterministic or stochastic processes (Niche Assembly vs Neutral Assembly) on the configuration of liverwort species distributions at a regional scale.

According to the first law of geography (Tobler, 1970), the similarities between two regions would be expected to diminish as the distance between them increased (Nekola and White, 1999); and regions that are geographically closer would also be expected to have more similar floras due to the greater possibility of their diaspores reaching those sites. Considering, however, that deterministic process, such as environmental filtering (based on ecological niches) may act more strongly on the liverwort flora than do processes related to their airborne dispersal, we hypothesize that will there will be high similarities between liverwort communities in localities with the same Atlantic Forest vegetation types, as they will provide similar environmental conditions.

We here examine the beta diversity of the liverwort floras of areas with distinct Atlantic Forest vegetation types in order to evaluate the sensitivity of the species to environmental variables related to altitude by addressing the following questions: (1) Are geoclimatic conditions good predictors of the vegetation types of the Atlantic Forest sites investigated? (2) Is the liverwort flora distributed uniformly or randomly, or does it demonstrate environmental niche-restrictions along the Atlantic coast of southeastern Brazil? If the distribution of the liverwort flora is in fact deterministic, two additional questions arise: (3) Are there liverwort species that can be considered indicators of the different vegetation types of the Atlantic Forest? (4) Do any of the geoclimatic variables analyzed act as filters to the liverwort flora?

## 2. Methods

### 2.1. Study area

The study region was located on the Atlantic coastal plain of southeastern Brazil (21°88′–23°24′S and 45°10′–41°92′W) with four altitudinal units: Baixada, Serra do Mar, Vale do Paraíba, and Serra da Mantiqueira (Domingues, 1976). The regional topography is quite irregular and is composed of mountain chains (the scarps of coastal plains) of crystalline rocks (Domingues, 1976). The highest points there are the Pico das Agulhas Negras (2791 m) located in the Planalto da Serra da Mantiqueira in the municipality of Itatiaia, Rio de Janeiro State; the Pedra dos Três Picos (2310 m) in the municipality of Nova Friburgo; and the Pedra do Sino (2263 m) in Teresópolis (the latter two being located in the Serra do Mar Range in Rio de Janeiro State) (Guedes-Bruni and Lima, 1997). The regional climate is quite variable due to altitudinal factors as well as the orientations of the mountain slopes. Proximity to the ocean results in higher regional humidity and rainfall, which tends to diminish in more inland area (Domingues, 1976). The predominant climate in Baixada and in Vale do Paraíba is hot and humid, and defines two seasons – a rainy season (in the Austral summer) and a dry season (Austral winter). The average annual temperature varies between 24 and 26 °C; the average annual precipitation is approximately 1000 mm in Baixada and 1500 mm in Vale do Paraíba. In the highest regions of the Serra do Mar and Mantiqueira ranges the climate is mesothermic super-humid, without a dry season, with average annual temperatures between 18 and 19 °C; the average annual rainfall is between 2000 and 2500 mm (Domingues, 1976; Nimer, 1989).

The concept of Atlantic Forest (*sensu lato*) adopted in the present work corresponds to that described by Oliveira-Filho and Fontes (2000) and includes both ombrophilous and semideciduous forests. The vegetation classification adopted here corresponds to that of Veloso et al. (1991), and includes the vegetation types of Lowland Forest = 5–50 m a.m.s.l., Submontane Forest = 50–500 m, Montane Forest = 500–1500 m, and High Montane Forest => 1500 m. Three additional vegetation types were included in the study: Restinga Forest – a forest formation that occurs on sandy coastal sites at altitudes between 0 and 50 m whose genesis, composition, and structure are distinct from Dense Ombrophilous Forest (César and Monteiro, 1995; Assis et al., 2011); Mountain-Top Forest – a Cloud Forest type that occurs on the tops of tall peaks in the Serra do Mar Range on thin, rapidly draining soils (Bertoncello, 2009; Mantovani et al., 1990; Neto, 2007); and "Campos de Altitude" – open, humid formations dominated by grasses, which generally occur above 2000 m as well as on the tops of some peaks in southeastern Brazil (Martinelli and Bandeira, 1989; Safford, 1999; Vasconcelos, 2011).

### 2.2. Data organization

Twenty-six localities were selected (Fig. 1) in 10 separate federal, state, and private Protected Areas in the states of Rio de Janeiro and São Paulo in southeastern Brazil. We utilized data from published floristic inventories, from the databank of the bryophyte flora of Rio de Janeiro (Costa et al., 2007), and from field studies undertaken between 2009 and 2011 in ten 10 m × 10 m plots in each locality (Table 1). These plots had been established in areas with

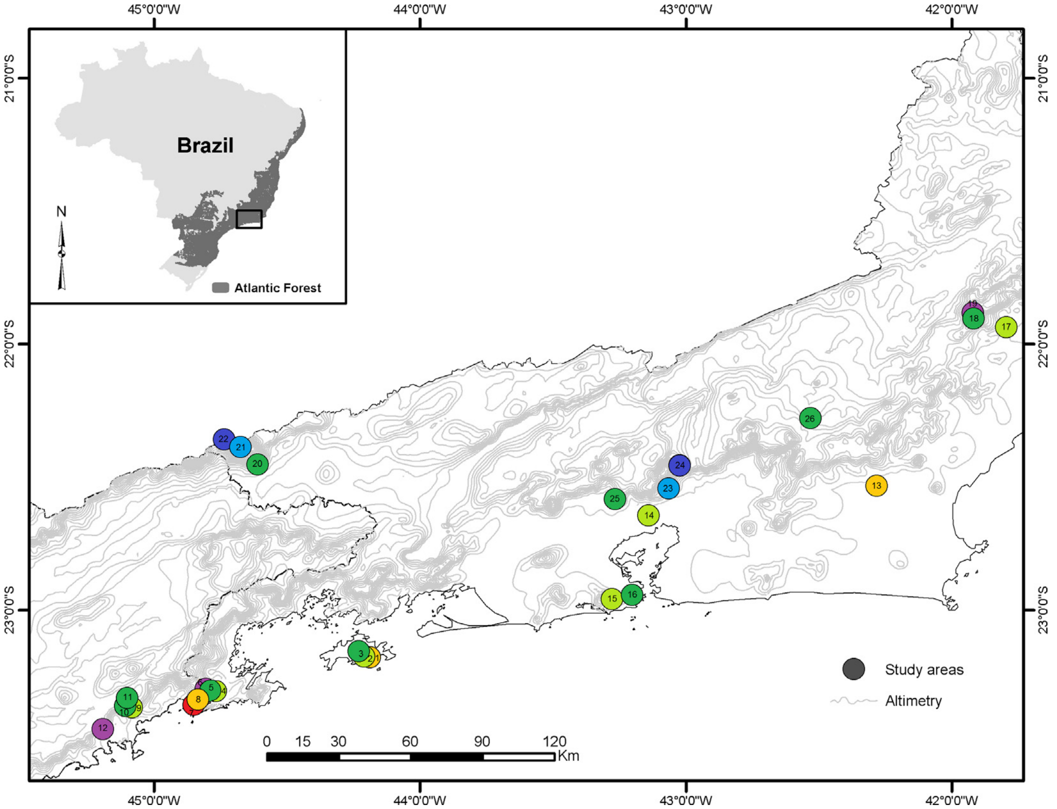

**Fig. 1.** Locations and distribution of the 26 sites sampled in seven vegetation types of Atlantic Forest in southeastern, Brazil. Site numbers Figs. [1,2 and 4] will appear in black and white in print and in color on the web. Based on this, the respective figure captions have been updated. Please check, and correct if necessaryaccording to Table 1. Colors denote vegetation types: red = Restinga Forest, orange = Lowland Forest, green light = Submontane Forest, green = Montane Forest, light blue = High Montane Forest, blue = "Campos de Altitude", purple = Mountain-Top Forest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

different vegetation types during the Biota Gradiente Funcional project funded by FAPESP (Joly et al., 2012) in the Serra do Mar State Park (SP). The floristic data used here is derived from published papers and databanks from general floristic surveys undertaken mostly by the project team employing random sampling along trails and in the forest. In order to minimize possible erroneous interpretations originating from problems of plant identifications all synonyms were checked, and any doubtful species were excluded

**Table 1**
List of protected areas of Atlantic forest included in the analysis of liverwort beta diversity in southeastern Brazil.

| Number (locality) | Acronym | Protected area | Vegetation type (locality) | Species richness | Floristic group | Reference |
|---|---|---|---|---|---|---|
| 1 | peig tb | Ilha Grande State Park | Lowland | 25 | 1 | Oliveira-e-Silva and Yano (2000) |
| 2 | peig sm | Ilha Grande State Park | Submontane | 58 | 1 | Oliveira-e-Silva and Yano (2000) |
| 3 | peig m | Ilha Grande State Park | Montane | 38 | 1 | Oliveira-e-Silva and Yano (2000) |
| 4 | pesm vsm | Serra do Mar State Park | Submontane | 44 | 2 | Visnadi (1998) |
| 5 | pesm vm | Serra do Mar State Park | Montane | 61 | 2 | Visnadi (1998) |
| 6 | pesm vcus | Serra do Mar State Park | Mountain-top | 22 | 5 | Visnadi (1998) |
| 7 | pesm FR | Serra do Mar State Park | "Restinga" | 59 | 2 | This study |
| 8 | pesm TB | Serra do Mar State Park | Lowland | 66 | 2 | This study |
| 9 | pesm SM | Serra do Mar State Park | Submontane | 66 | 2 | This study |
| 10 | pesm M800 | Serra do Mar State Park | Montane | 59 | 2 | This study |
| 11 | pesm M950 | Serra do Mar State Park | Montane | 66 | 2 | This study |
| 12 | pesm COR | Serra do Mar State Park | Mountain-top | 51 | 5 | This study |
| 13 | rebiopa tb | Poço das Antas Reserve | Lowland | 31 | 1 | Costa (1999) |
| 14 | rppnen sm | El Nagual Private Reserve | Submontane | 70 | 3 | Santos and Costa (2008) |
| 15 | pnt sm | Tijuca National Park | Submontane | 56 | 3 | Costa et al. (2007) |
| 16 | pnt m | Tijuca National Park | Montane | 59 | 4 | Costa et al. (2007) |
| 17 | ped sm | Desengano State Park | Submontane | 31 | 3 | Costa et al. (2007) |
| 18 | ped m | Desengano State Park | Montane | 102 | 4 | Costa et al. (2007) |
| 19 | ped des | Desengano State Park | Mountain-top | 14 | 5 | Costa et al. (2007) |
| 20 | pni m | Itatiaia National Park | Montane | 150 | 4 | Costa et al. (2007) |
| 21 | pni am | Itatiaia National Park | High montane | 102 | 5 | Costa et al. (2007) |
| 22 | pni ca | Itatiaia National Park | "Campo de altitude" | 87 | 5 | Costa et al. (2007) |
| 23 | pnso am | Serra dos Órgãos National Park | High montane | 60 | 5 | Costa et al. (2007) |
| 24 | pnso ca | Serra dos Órgãos National Park | "Campo de altitude" | 70 | 5 | Costa et al. (2007) |
| 25 | ap m | Petrópolis Environmental Protection Area | Montane | 36 | 4 | Costa et al. (2007) |
| 26 | frib m | Três Picos State Park | Montane | 97 | 4 | Costa et al. (2007) |

(Gradstein and Costa, 2003). Three matrices were prepared: floristic, geographic, and environmental.

In the floristic matrix, the samples consisted of the localities – Protected areas separated by vegetation types – and the liverwort species were assigned binary presence/absence values (Appendix A). To improve the analyses, rare species were eliminated (only a single occurrence). As such, the floristic matrix consisted of the occurrence data of 272 liverwort species (descriptors) from 26 localities (samples); the geographic matrix recorded the geographic coordinates (in decimal degrees) of each of the 26 localities; and the environmental matrix was composed of data expressing the altitudes, distance from the sea (in a straight line), the annual temperature amplitudes, temperature seasonality, annual precipitation, precipitation seasonality, and dry season precipitation for each locality. All of the climatic variables were obtained from the DIVA-GIS 5.2 software program (Hijmans et al., 2005a) using the current (2.5 arc-minute resolution) WorldClim database (Hijmans et al., 2005b).

### 2.3. *Statistical analyses*

In order to determine if the geoclimatic variables were reliable predictors for the Protected Areas or for the vegetation types studied, the matrix data was standardized (ranging) and Principal Component Analysis – PCA was performed using a covariance matrix. This matrix was subsequently used in Canonic Correspondence Analyses – CCA and in Mantel Tests.

To clarify the distribution patterns of the liverwort flora in southeastern Brazil, the floristic matrix was submitted to outlier analyses with a 2.0 cutoff level using the PCOrd 4.1 software program (McCune and Mefford, 1999) and Detrended Correspondence Analysis – DCA (Hill and Gauch, 1980). Parallel to this, Two-Way Indicator Species Analysis – TWINSPAN (Hill, 1979) as well as similarity analyses (Jaccard index) using the Weighted Pair Method with Averaging – WPGMA were was employed to define the floristic groups. This linking method assigns equal weights to the groups without considering their sizes, and is most robust when groups of significantly different sizes are compared (Shepherd, 1995). As the multivariate methods of ordination and classification revealed the same patterns, we only present here the TWINSPAN results.

We compared the groups formed by the different multivariate methods (DCA, TWINSPAN, and WPGMA) and evaluated whether these groupings comprised liverwort floras that were more similar than expected by chance, using Multi-Response Permutation Procedures – MRPP (Mielke and Berry, 2007) provided by the PCOrd 4.1 software program (McCune and Mefford, 1999). MRPP represents a robust, nonparametric method that utilizes Sørensen similarity indices to test the null hypothesis that two or more predefined groups have equal compositions. The $A$ index of the MRPP describes the homogeneity within these groups (and varies from 0 to 1), where $A = 0$ signifies that the heterogeneities within and between the groups are equal, while $A = 1$ signifies that all of the members of each group are identical among themselves and different from members of the other groups (McCune and Grace, 2002).

Indicator Species Analysis – ISA (Dufrêne and Legendre, 1997) was used to define the indicator values (IndVal) of the species characteristics of each grouping that was formed, using the PCOrd 4.1 program (McCune and Mefford, 1999). In this method (and different from TWINSPAN), the indicator value of a given species is independent of the relative abundances of the other species, and it is not necessary to use pseudo-species. The significance of each species indicator value was evaluated using Monte Carlo tests with 1000 permutations to test the null hypothesis that the species did not have any indicator value. We considered species to be indicators when they showed $p \leq 0.05$ and an indicator value (IndVal) $\geq$ 25% (Dufrêne and Legendre, 1997).

In order to better understand the influence of the environment on the liverwort flora we evaluated the correlations between floristic and environmental gradients using Canonical Correspondence Analysis – CCA. CCA is a canonic ordination technique based on Correspondence Analysis that restricts the ordination of a species matrix through multiple linear regressions performed on the variables within an environmental matrix (McCune and Grace, 2002) – with the CCA allowing the ordination axes to express linear combinations of the environmental variables (Manly, 1994). Environmental variables that demonstrated correlation indices > 0.8 were removed from the analyses. Monte Carlo tests (ter Braak and Prentice, 1988) with 1000 permutations were used to confirm the significance of the first ordination axis. All of the grouping, classification, and ordination analyses were undertaken using the Fitopac 2.1 software (Shepherd, 2010).

We also examined the correlations between the floristic dissimilarity and geographic and environmental distances using simple and partial Mantel Tests – rM (Legendre and Legendre, 1998), with the Mantel statistic being tested by 10,000 permutations, using the Passage 2 software program (Rosenberg and Anderson, 2011). These tests consider the null hypotheses to be the absence of linear correlations between the two distance matrices (Legendre and Legendre, 1998). To that end, we calculated the Euclidean distances between the sampling pairs of the floristic, geographic, and environmental matrices. According to our working hypothesis, liverworts demonstrate distributions that are environmentally determined, thus generating the following expectations: (1) the existence of a positive correlation between the floristic and environmental matrices; and, (2) the absence of a correlation between the floristic and geographic matrices.

## 3. Results

The 26 localities analyzed comprised a total richness of 344 liverwort species (Appendix). The Montane Forest was the richest vegetation type (252 taxa), followed by Submontane Forest (165), High Montane Forest (134), "Campos de Altitude" (122), Lowland Forest (88), Mountain-Top Forest (69), and Restinga Forest (59).

The PCA of geoclimatic matrix showed a homogeneous diagram (Fig. 2). The percentage of accumulated variance in the first two axes was 72%, being greater than that expected by the broken stick model (55%). The first axis was most strongly correlated with precipitation seasonality (0.91), the average annual temperature (−0.88), distance from the sea (0.85), and altitude (0.79); the second axis was most strongly correlated with annual precipitation (0.92), precipitation during the dry season (0.63), and the amplitude of annual temperatures (0.57).

The analyses of the outliers of the floristic matrix separated one sample with a standard error > 2.0, the Cuscuzeiro Mountain-Top Forest (pesm vcu – 2.08); as this value was close to the cutoff level (2.0), this sample was not removed from the analyses. TWINSPAN resulted in a hierarchical classification into two principal groups (Fig. 3), one including the Mountain-Top, High Montane Forest, and "Campos de Altitude" localities, and another comprising forests located below 1500 m. In this analysis, as was seen with the DCA (data not shown), the localities of the Ilha Grande SP and the Serra do Mar SP grouped among themselves; however, the montane and submontane areas of Rio de Janeiro State formed a single group.

We undertook comparisons between the groups suggested by the multivariate analyses and the a priori vegetation classification (Veloso et al., 1991) and designated five groupings to define the indicator species (Table 1). Before undertaking the Indicator Species Analysis (ISA), we tested the groupings adopted by the MRPP. The hypothesis that there were no significant differences between the

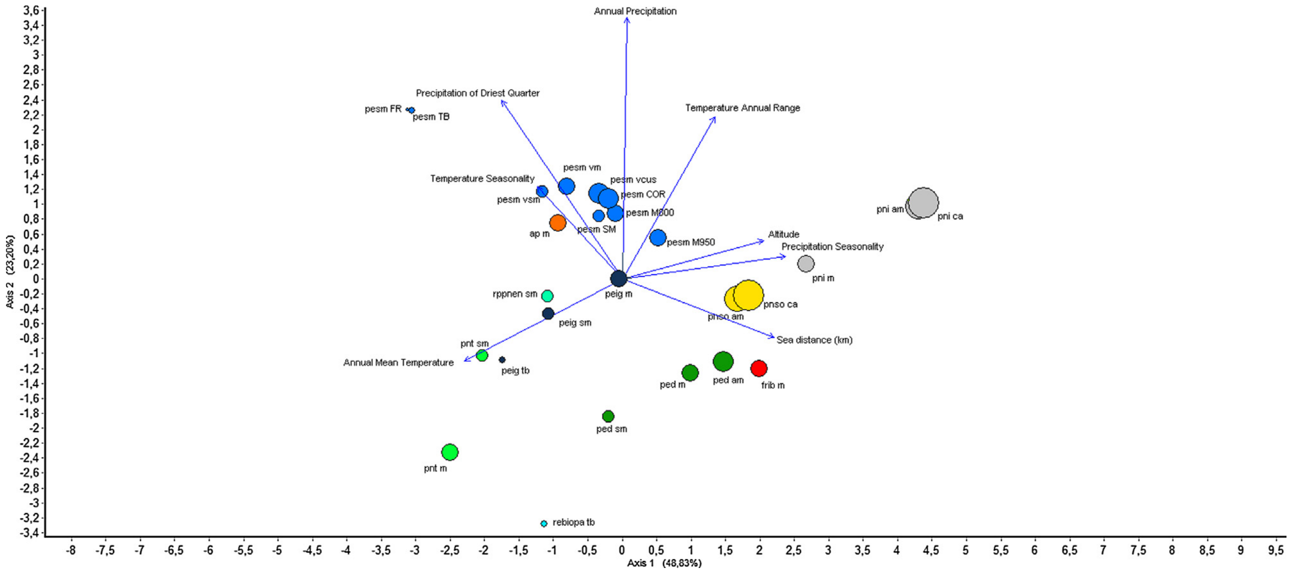

**Fig. 2.** Plot of two first axis of a Principal Component Analysis (PCA) of environmental matrix. Colors denote locality and size vegetation type. Acronym according to Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

groups was refuted, as the MRPP indicated that heterogeneity was greater between the groups and within them ($A = 0.43$; $p < 0.001$), that is, the compositions of the samples within the groupings were different from those that would be expected by chance. We identified 34 indicator species (IndVal ≥ 25%; $p \leq 0.05$) for the groupings tested (Table 2).

The CCA ordination diagram indicated the existence of a gradient from Lowland Forests to High Montane Forests and “Campos de Altitude” related to altitude on the first axis (Fig. 4). The environmental variables that strongly correlated with the first environmental axis (LC scores) were altitude (0.95), average annual temperature (−0.88), temperature seasonality (−0.76), and distance from the sea (0.72). The second axis was associated with precipitation levels, and indicated the existence of three groups: one composed of the areas in the Ilha Grande SP, the Poço das Antas Reserve, and the Submontane vegetation of the Desengano SP (with low annual precipitation levels); a second group comprising continental areas of Rio de Janeiro State and the areas sampled by Visnadi (1998) in the Serra do Mar SP; and a third group composed of areas of the Serra do Mar SP and the Serra dos Órgãos National Park (NP), with high precipitation rates during the dry season in the case of the first Protected Area, and high annual precipitation in the second. The correlations of these environmental variables with the second axis were 0.4 (dry season precipitation) and 0.39 (annual precipitation). The canonical eigenvalues (CE) obtained for the first three axes of the analysis were 0.47, 0.22, and 0.21; being responsible for 13.7%, 20.1%, and 26.1% of the total cumulative variance of the data respectively. The percentages of accumulated variance in the first three axes were smaller than those expected by the broken stick model (expected CE1 29.5%, CE2 43.4%, and CE3 56.3%); as such, the results partially explained the observed variance. In spite of this fact, we did not encounter pattern in the non-canonic part, which demonstrated that the pattern was captured in the canonic portion of the analysis. The results of the Monte Carlo tests were significant for the first three ordination axes (eigenvalue 1 $p = 0.001$; eigenvalue 2 $p = 0.003$; eigenvalue 3 $p = 0.001$).

The prediction that liverworts would demonstrate environmentally determined distributions, as evaluated by the Mantel Test, was confirmed (Table 3). A positive correlation was observed between the floristic and environmental matrices (rM 0.557; $p < 0.0001$)

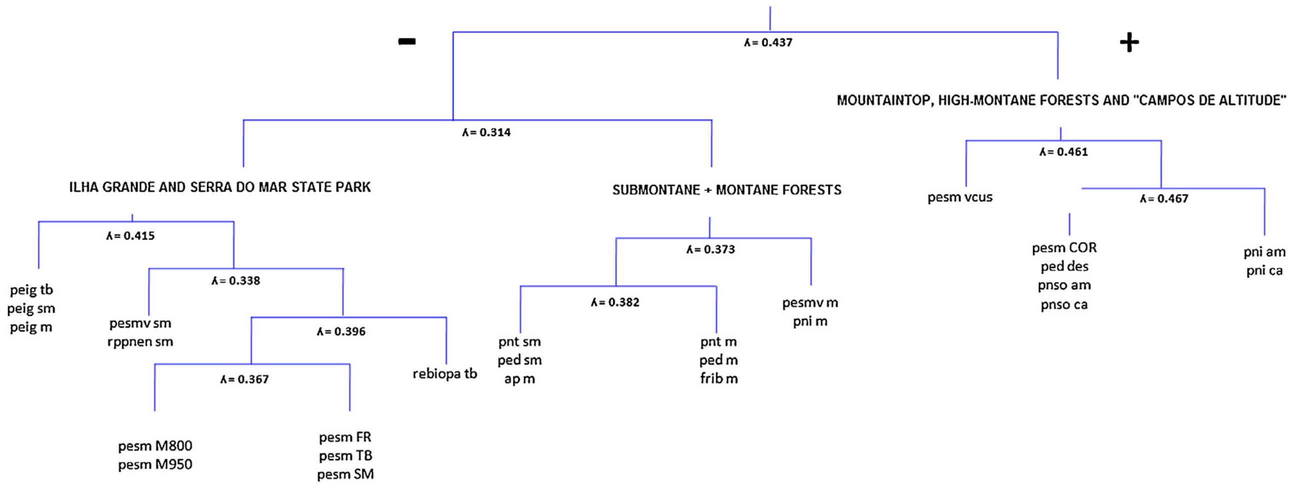

**Fig. 3.** Floristic groups generated by the Two-Way Indicator Species Analysis (TWINSPAN) to the liverwort in southeastern Brazil, with emphasis on the eigenvalues (λ). Acronym according to Table 1.

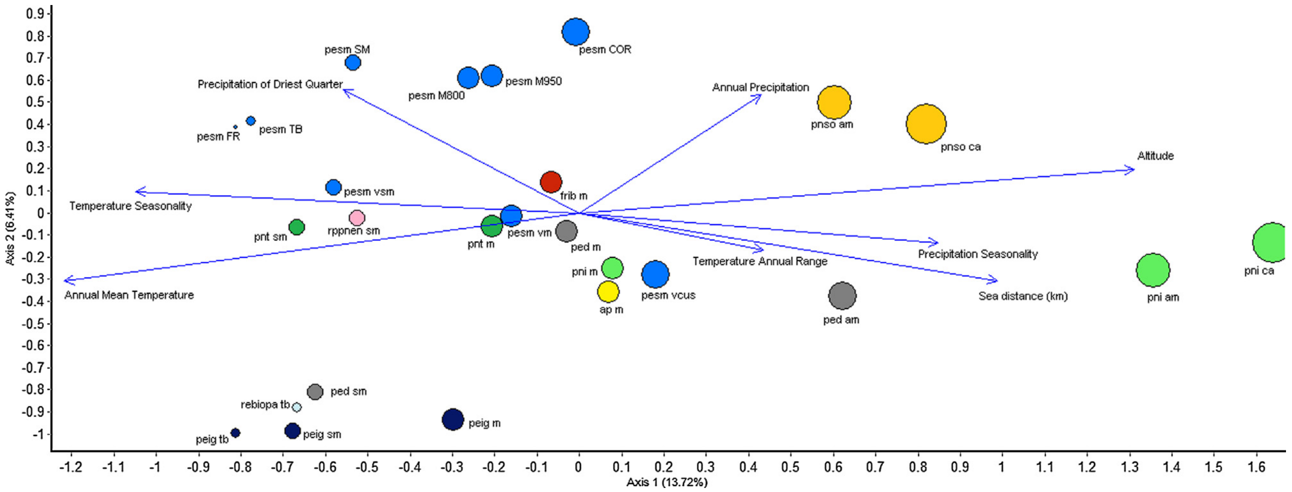

**Fig. 4.** Plot of two first axis of a Canonical Correspondence Analysis (CCA) of floristic and environmental matrices. Colors denote locality and size vegetation type. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

even when the effects of the geographic matrix were removed (rM 0.56; $p < 0.0002$). Additionally, the relationships between the floristic and geographic matrices were not significant.

**Table 2**
Liverwort species indicators of the five groupings of Atlantic forest, southeastern Brazil (IndVal ≥25).

| Indicator species | Indicator value | *p* |
|---|---|---|
| 1 – Ilha Grande State Park + Poço das Antas Biological Reserve (peig tb, peig sm, peig m, rebiopa tb) | | |
| *Acrolejeunea emergens* | 50 | 0.029 |
| *Frullania montagnei* | 50 | 0.024 |
| *Frullania supradecomposita* | 50 | 0.029 |
| *Lopholejeunea subfusca* | 50 | 0.027 |
| 2 – Serra do Mar State Park (except Mountain-Top Forests) (pesm FR, pesm TB, pesm SM, pesm M800, pesm M950, pesm vsm, pesm vm) | | |
| *Haplolejeunea cucullata* | 83.3 | 0.001* |
| *Cyclolejeunea luteola* | 67.2 | 0.003 |
| *Metzgeria brasiliensis* | 66.7 | 0.002 |
| *Bazzania heterostipa* | 64.8 | 0.001* |
| *Prionolejeunea aemula* | 64.8 | 0.001* |
| *Pycnolejeunea contigua* | 50 | 0.04 |
| *Rectolejeunea berteorana* | 50 | 0.04 |
| *Radula ligula* | 44.4 | 0.024 |
| 3 – Submontane Atlantic Forest (ped sm, rppn sm, pnt sm) | | |
| *Riccardia emarginata* | 51.5 | 0.03 |
| *Lejeunea laeta* | 51.3 | 0.026 |
| 4 – Montane Atlantic Forest (ap m, ped m, pnt m, pni m, frib m) | | |
| *Noteroclada confluens* | 70 | 0.001* |
| *Lejeunea grossitexta* | 60 | 0.007 |
| *Plagiochila corrugata* | 60 | 0.003 |
| *Lepidozia cupressina* | 58.9 | 0.01 |
| *Taxilejeunea pterigonia* | 51.1 | 0.023 |
| *Taxilejeunea isocalycina* | 47 | 0.023 |
| *Isotachis aubertii* | 41.9 | 0.035 |
| *Lejeunea raddiana* | 40.6 | 0.038 |
| 5 – Mountain Top + High Montane Atlantic Forests (pesm COR, pesm vcus, pni am, pni ca, pnso am, pnso ca) | | |
| *Radula tenera* | 85.7 | 0.001* |
| ***Jamesoniela rubricaulis*** | 71.8 | 0.002 |
| ***Syzygiella liberata*** | 71.4 | 0.008 |
| *Cephaloziella granatensis* | 57.1 | 0.017 |
| *Colura calyptrifolia* | 57.1 | 0.017 |
| *Frullania ecklonii* | 57.1 | 0.02 |
| ***Brachiolejeunea laxifolia*** | 45.8 | 0.035 |
| *Leptoscyphus amphibolius* | 45.8 | 0.035 |
| *Frullania atrata* | 45.2 | 0.028 |
| *Jensenia spinosa* | 42.3 | 0.044* |
| ***Scapania portoriscensis*** | 42.3 | 0.048* |
| *Kurzia capillacea* | 36.8 | 0.013* |

Bold = species also identified as indicator by Santos and Costa (2010). $^{*}p < 0.001$.

## 4. Discussion

### 4.1. Environmental variables × vegetation types of the Atlantic Forest

Our initial premise that localities with the same Atlantic Forest vegetation types would demonstrate similar environmental conditions was partially refuted, as the geoclimatic variables utilized did not generally result in the localities grouping according to their vegetation types. Apparently there are strong local effects of the environmental variables utilized. The areas of the Serra dos Órgãos NP and the Serra do Mar SP, for example, stand out from the others in terms of their elevated levels of annual precipitation and dry season precipitation respectively. Distance from the sea and precipitation seasonality, on the other hand, represent correlated variables (correlation coefficient = 0.74) and important environmental filters in the Itatiaia NP, Três Picos SP, and the Desengano SP.

It is important to note that the geoclimatic variables utilized may not be the principal predictors of Atlantic Forest vegetation types, as non-quantified variables such as soil type, topography, biomass, illumination, and vertical forest structure are important in distinguishing the different vegetation types (Alves et al., 2010; Assis et al., 2011). Another problem with the climatic variables extracted from the WorldClim database is that they were generated at a macro (global) scale by interpolation from separate data points (Hijmans et al., 2005b). As such, the fine-scale used in the present study (with large variations in altitude over small

**Table 3**
Results of Mantel Test performed with the floristic, geographic and environmental matrices of the 26 study sites in southeastern Brazil.

| Distance | Partial Mantel (rM) | *p* |
|---|---|---|
| Floristic × environmental | 0.557 | 0.0001 |
| Floristic × geographic | 0.0489 | 0.2711 |
| Environmental × geographic | 0.2668 | 0.005 |
| Floristic × environmental (holding the effect of space) | 0.56506 | 0.0002 |
| Floristic × geographic (holding the effect of environment) | −0.12453 | 0.91930 |

geographic distances) may have been problematic, although in the study of altitudinal gradients undertaken by Kluge et al. (2006), the average annual precipitation values detected at individual meteorological stations were compatible with the modeled data used in WorldClim. Additionally, WorldClim data has been widely and successfully utilized in macroecological studies (Kessler et al., 2011; Kreft et al., 2008) and has been cited by Chave (2008) as an important technological advancement for studying the processes that act upon beta diversity. This database has been used for modeling species distributions in the neotropical forests (Carnaval and Moritz, 2008; Mateo et al., 2012; Meireles, 2009; Murray-Smith et al., 2009), although the accuracy of the model appeared to be flawed in some tropical areas in Bolivia (Killeen et al., 2007; Soria-Auza et al., 2010). The geoclimatic patterns encountered here were consistent with those expected for the areas analyzed, as for example, the precipitation gradient from coastal areas to the continental interior (Domingues, 1976). The high precipitation experienced in coastal areas, even during the dry season (winter), is principally due to orographic rainfall (e.g., the Serra do Mar and Serra dos Órgãos areas). As such, although the environmental variables used were not good predictors of Atlantic Forest vegetation types, they were good indicators for the Protected Areas analyzed, and probably acted as filters to the distribution of the liverwort flora.

### 4.2. Liverwort flora beta diversity in the Atlantic Forest

In confirmation of our working hypothesis, we were able to verify that liverworts demonstrated deterministic distributions along the Atlantic coast of Southeastern Brazil, even though geographic distances were important in some areas, such as islands (Ilha Grande SP) or coastal mountains (Serra do Mar SP). The deterministic theory (based on filtering environmental) postulates that species are not randomly distributed, but show spatial patterns that are driven by environmental constraints and competitive displacement (Chave, 2008). Multivariate analyses indicated the existence of a floristic gradient along an altitudinal gradient, with some cohesive groupings being common to the different methodologies (e.g., Mountain-Tops + High Montane Forests + "Campos de Altitude"; localities in Ilha Grande SP; and localities in the Serra do Mar SP). Similarly, Oliveira et al. (2009) evaluated the beta diversity patterns of bryophytes at a regional level along a vertical gradient on their host phorophytes in three lowland forests in the Guianas, and found that the communities there were structured based on niches and that community compositions could principally be explained by the heights above the ground at which the bryophytes were growing, even at distances greater than 600 km, indicating that those communities were influenced by microclimatic conditions acting on regional pools of species.

Altitude represents one of the principal factors determining liverwort species distributions in the Atlantic Forest in southeastern Brazil, as demonstrated by direct analyses of the gradients (CCA), where altitude demonstrated a correlation coefficient of 0.95 with the first ordination axis. Elevated beta diversity was observed, with large numbers of species that were not shared between the altitudinal gradient extremes – thus refuting the hypothesis of uniformity (Pitman et al., 1999, 2001). Similar results have been reported for bryophytes in other parts of the world, showing that elevation is an important environmental filter for bryophyte communities. In their search for factors that influenced bryophyte distributions on a mountain in China, Sun et al. (2013) found that litter depth, air temperature, relative humidity and precipitation were the main factors correlated with bryophyte composition. These factors, as well as temperature and precipitation were variables related to elevational changes. In their study of bryophytes along an altitudinal gradient on a lava flow surface of the Piton de la Fournaise volcano in La Réunion Island, Ah-Peng et al. (2007) demonstrated that their diversity and distributions were affected by altitude and by the host substrate (mineral *x* vegetation). In a study of bryophyte composition and associated invertebrate assemblages along altitudinal gradients in Australia and New Zealand, Andrew et al. (2003) identified an altitudinal effect on bryophyte distribution, but no consistent changes in their diversity or composition throughout the mountains. Different species richness patterns have been found along altitudinal gradients, with Tusiime et al. (2007) reporting that bryophyte richness was negatively correlated with altitude in Tropical Africa, while Wolf (1993) found epiphytic enrichment of bryophytes at middle elevations (ca. 3200 m) in the Northern Andes; Santos and Costa (2010) likewise showed that Montane Forests (500–1500 m) in the Brazilian Atlantic Forest had high species richnesses and endemism rates and Ah-Peng et al. (2007) reported increased species richnesses along an altitudinal gradient at La Réunion.

In spite of the fact that we encountered evidence of altitudinal gradients in the data at the regional level, the vegetation types of the Atlantic Forest did not group well, as the local effects in the Protected Areas were often more important. When the similarity indices between localities were evaluated, for example, it could seem that the greatest indices were encountered among samples located in the same Protected Area and at neighboring altitudes (pesm FR and pesm TB = 0.49; pesm SM and pesm M800 = 0.49; pni am and pni ca = 0.49; pesm M800 and pesm M950 = 0.48 – see Table 2 for acronyms). These results suggest a local floristic gradient where localities at adjacent altitudes have more similar floras. It is possible that, in addition to the regional environmental filters acting in the Atlantic Forest vegetation types, there are local filters that influence the spatial distribution of the liverworts. The sampling method used (within plots) may have affected the patterns of floristic similarity in the survey areas in the Serra do Mar State Park.

In relation to the grouping of the Mountain-Top Forest, High Montane Forest, and the "Campos de Altitude" vegetation types observed in all of the analyses, controversial results have been reported in studies of the vascular flora of the Atlantic Forest in southeastern Brazil. Bertoncello et al. (2011) detected the presence of Cloud Forests at altitudes above 1120 m on Cuscuzeiro Peak and in the Serra do Mar SP that demonstrated greater floristic affinities with High Montane Forests than with the other Atlantic forest types in southeastern and southern Brazil. On the other hand, a regional study of Montane and High Montane forests in southeastern and southern Brazil undertaken by Meireles (2009) reported that the High Montane Forests of the Serra do Mar SP in São Paulo State were more similar to the Atlantic and interior Montane forests of Minas Gerais State than two the group formed by other High Montane Forests. The altitudinal locations of cloud forests are in fact quite variable, and can located within the High Montane, Montane, or even Submontane vegetation types (Doumenge et al., 1995; Bertoncello et al., 2011; Meireles, 2009).

### 4.3. Indicator species

A number of species demonstrate preferences for certain environmental niches and can therefore be used as ecological indicators of community types, habitat conditions, and/or environmental changes (Heink and Kowarick, 2010; Niemi and McDonald, 2004). As liverwort do not have cuticles on their leaves, they will be directly exposed to unfavorable environmental conditions and will thus react in predictable and measurable manners to environmental changes – and can therefore been used as bioindicators (Hallingbäck and Hodgetts, 2000; Vanderpoorten and Goffinet, 2009). Indicator Species Analyses (ISA) identified 34 liverwort species (10% of the total) as indicators of the groups formed by the Protected Areas or by the Atlantic Forest vegetation types analyzed, with high numbers of species typical of High Montane forests (including the Mountain-Top Forest and "Campos de Altitude" areas – 12 taxa) and Montane forests (eight taxa).

Four species identified by Santos and Costa (2010) as indicators of Atlantic Forest vegetation types from High Montane Forest areas (see Table 2), were identified as indicator species by the ISA (IndVal $\geq$ 25%; $p \leq 0.05$). This was due to the fact that the weight of rare species (those that only occurred in one locality among all of the sampling sites) is minimized by the ISA method, and species with elevated fidelity and specificity are considered more important (Dufrêne and Legendre, 1997). High fidelity signifies occurring in all of the localities of the group, while high specificity signifies occurring exclusively within a given group. An efficient indicator species is therefore one that has individuals occurring in all of the samples of a specific group. It is important to note that the analyses undertaken by Santos and Costa (2010) based on the occurrence (presence/absence) of taxa in altitudinal belts identified species typical of each Atlantic Forest vegetation type based on published papers – while the objective of the present study was to determine if some liverwort species are indicators of groups formed by localities with different Atlantic Forest vegetation types.

### 4.4. *Environmental filters for the liverwort flora*

As was seen in the Mantel Test, the liverwort flora demonstrated environmentally determined species distributions in the Atlantic Forest in southeastern Brazil. The geoclimatic variables explained more than 50% of the species distributions, while geographical distance had no explicative power. The Niche Assembly theory predicts that two types of mechanisms will act upon species distributions – physiological filters and biotic filters (Chave, 2008). Environmental variables that can impede species establishment constitute physiological filters (e.g., edaphic factors, illumination, water availability); biotic filters operate through interspecific competition for resources (Chave, 2008; Tilman, 1980, 1982). The present work focused on correlations between species distributions and environmental factors (physiological filters, referred to in the text as environmental filters) through direct analyses of their gradients (CCA).

CCA is a good ordination method for reflecting correlations between the biotic communities and environmental gradients (Lepš and Šmilauer, 2003). The results of the CCA allowed us to determine which geoclimatic variables were associated with the groups formed among the localities analyzed. The diagram obtained from the first axes of the CCA allowed us to visualize the patterns of variation of the liverwort floristic composition along gradients generated by environmental variables – in spite of the fact that the first three axes accounted for only about 26% of the total variance of the data. The remaining unexplained variance could be associated with environmental variables that were not quantified, such as illumination, humidity, and topography. The principal geoclimatic variables that explained the groupings formed by the liverwort flora were altitude, temperature, and precipitation.

Altitude was highly correlated on the first axes of the CCA ordination (correlation coefficient of 0.95), although it is important to note that altitude in itself is not a variable, but rather a surrogate for a set of different environmental factors affecting the biology of the organisms (such as temperature, humidity, and solar radiation – Körner, 2007). The Fig. 4, for example, indicates that altitude and average annual temperatures are negatively correlated. In addition to altitude, the principal environmental filters acting on the liverwort flora were temperature and precipitation, although many localities assumed intermediate positions along the first two CCA axes (Fig. 4). High precipitation, even during the winter (orographic rains), was the principal variable associated with the localities sampled in the present study in the Serra do Mar SP. Annual precipitation was also important in areas of the Serra dos Órgãos NP (high rainfall levels) and in the group formed by the Ilha Grande SP, the Lowlands of the Poço das Antas Reserve, and Submontane Forest in the Desengano SP (low rainfall levels).

Our results corroborated reports in the literature that indicated that the principal abiotic filters of bryophyte development are water availability, light, temperature, and substrate types – with water availability being the single most important factor controlling their species distributions (Vanderpoorten and Goffinet, 2009). As with most bryophytes, liverworts generally occupy well-defined microenvironments (Gradstein and Pócs, 1989); as such, microclimatic variables (such as illumination and humidity) can be important in determining species distributions in localities occupying intermediate positions in the CCA. Even though they were located in the same Protected Area (Serra do Mar SP), for example, the localities sampled by Visnadi (1998) that were situated close to trails (where light is generally more available and humidity more reduced) did not group with the sites surveyed in the present work in forest interior sites (permanent plots established during the Biota Gradiente Funcional project coordinated by FAPESP, Joly et al., 2012). In a study of the spatial structures of bryophyte communities in the Atlantic Forest of northeastern Brazil, Silva and Pôrto (2010) reported that specific microclimatic conditions (altitude, canopy opening, and diffuse lighting) were important environmental filters for bryophytes, even though these authors did not encounter significant differences along border-interior gradients.

The results reported here support our hypothesis that the liverwort species of the coastal Atlantic Forest in southeastern Brazil comprise part of a regional pool of species whose establishment and survival are determined by abiotic filters in their habitats, in spite of the fact that there do not appear to be strong limitations on their dispersal (which is dependent only on the wind). Although species distributions are determined principally by environmental niches, geographical distances (and Neutral Assembly) can be important in some regions, such as oceanic islands or coastal mountains. We have presented evidence here that geoclimatic conditions are important in the configuration of liverwort beta diversity at the regional level, and that altitude is the principal factor affecting species distributions, with temperature and precipitation also acting as important environmental filters for their establishment and growth. Microclimatic variables that were not quantified here (e.g., illumination and humidity) are probably also very important in terms of determining species distributions at local levels, and the relative importance of regional geoclimatic factors and local microclimatic variations will need to be addressed in future studies.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2013.08.020.

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