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Distribution of bryophytes in south-eastern Brazil: an approach on floristic similarity and environmental filtering

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Abstract – The south-eastern Brazil comprises the Atlantic forest (a region mainly characterized by tropical evergreen forest), subtropical forest, mangroves, and scrub sandbanks. Sandy areas are found at sea level, and high altitude grassland spots and rocky outcrops occur above 2000 m. This region is important because the richness, diversity, and endemism of species, including bryophytes. The similarity of bryophytes occurring on these different areas has not been evaluated yet. This study aimed to analyse the bryofloristic similarity between 12 different areas in south-eastern Brazil, assessing the environmental factors that influence their distribution. Floristic similarity was analysed under cluster and Detrended Correspondence Analysis; multi-response permutation procedures were employed to test the groups' significance. In order to test whether the geographical distance between the areas is a relevant factor to test the similarity of the species, Spearman correlation analysis was performed, and to determine the relationship between the floristic composition and the environmental variables (altitude, temperature, annual rainfall and distance from the ocean), canonical correspondence analysis was applied. A low similarity between the 12 studied areas was observed, but two groups were revealed, the so-called inland areas and coastal areas. The annual precipitation and annual temperature influenced floristic similarity in the coastal areas and, the distance from the ocean and altitude were the variables that most influenced inland areas.

Bryophyte ecology / spatial distribution / liverworts / mosses / multivariate

INTRODUCTION

Bryophytes are more abundant in regions with specific micro-climates with high air humidity levels, and low evapotranspiration, as poikilohydric plants, the hydration state is controlled by the environment (Hallingbäck & Hodgetts, 2000; Gradstein *et al.*, 2001; Glime, 2007), their photosynthetic peak occurs during wet or cloudy period (Tuba, 2011). Most of these plants are perennials and tend to react immediately to favourable intermittent periods (Tuba *et al.*, 1998); thus, it is believed

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that they are, as other plant groups, susceptible to global climate change (Vanderpoorten & Goffinet, 2009). Many authors agree with the idea that the composition and richness of bryophytes are strongly related to the characteristics of a forest, i.e. deterministic distribution (based on ecological niche or environmental filtering); for example, local filters (small scale), as the pH of the substrate, the age of the forest, soil moisture (water availability), the phorophyte's characteristics (Gabriel & Bates, 2005; Strazdiņa, 2010; Patiño & González-Mancebo, 2011; Schmalholz *et al.*, 2011; Baniya *et al.*, 2012; Sekulová *et al.*, 2012; Király *et al.*, 2013). On a regional scale, climate, topography and forest structure have caused an indirect effect on a smaller scale (sample), due to the effects of diversity on a local scale (Medina *et al.*, 2014). Especially in the Neotropics, the diversity of bryophytes is dependent on a heterogeneous habitat related to vegetation zones and topography (regional filters), for example, in forests of the Tropical Andes the bryophytes richness is highest in areas above 2000 m a.s.l. (Churchill, 1991; Frahm & Gradstein, 1991; Churchill *et al.*, 1995; Gradstein, 1995). Environmental heterogeneity suggests that species coexist because they may specialise in different parts of the niche (Mota de Oliveira *et al.*, 2009; Poisot *et al.*, 2011), or share common phenotypic traits conferring abiotic tolerance (Kraft *et al.*, 2015).

The climate has a major role in determining the distribution patterns of different types of plant communities on a large scale, due to its influence on conditions and available resources (Townsend *et al.*, 2010; Medina *et al.*, 2014). However, the lack of uniformity in the composition at the local community scale results from the action of local factors, such as, rainfall, moisture, altitude and others (Townsend *et al.*, 2010). The composition of a local community is determined by ecological processes of selection in favour or against the distribution of species (Mota de Oliveira *et al.*, 2009; Townsend *et al.*, 2010). These processes were described by Keddy (1992) as assembly rules. The selection processes were conceptually classified to "filter" hierarchical working into ever smaller scales, imposing guidelines on the set of communities (Keddy, 1992). The term "ecological assembly" denotes restrictions on the community structure and composition due to any of the ensuing ecological filters: dispersion, which refers to the ability of a species to spread, and the environmental abiotic and biotic interactions, which correspond to the ecological niche which the species occupies (Mota de Oliveira *et al.*, 2009; Götzenberger *et al.*, 2012). Therefore, the establishment of a species can be defined by dispersal limitation, environmental filter, competitive exclusion (Kraft *et al.*, 2015). Some studies of vegetation patterns have been conducted to investigate the relationships of plant communities between areas and which filters influence the processes that regulate these patterns (Condit *et al.*, 2002; Király *et al.*, 2013; Santos *et al.*, 2014; Batke *et al.*, 2015). Although a biome is generally treated as a homogeneous area with vegetation, according to Townsend *et al.* (2010), the biomes do not show homogeneity within their hypothetical borders; every biome has gradients of physical and chemical conditions related to topography and local geology, thus, communities that occur in different parts of the heterogeneous mosaic can be quite different.

In South America, the Atlantic forest extends to the coast in some areas of south-eastern Brazil, eastern Paraguay and Misiones Province of Argentina (Fiaschi & Pirani, 2009). The area is mainly characterised by tropical evergreen forest, and subtropical forests are also usually considered part of the domain. Forest formations, mangroves and scrub sandbanks are common in sandy areas at sea level and high altitude grassland spots and rocky outcrops are generally found above 2000 m a.s.l. along the mountain ranges of Serra do Mar and Serra da Mantiqueira, both located in the region of south-eastern Brazil (Fiaschi & Pirani, 2009; Oliveira-Filho *et al.*, 2013a; Sanchez *et al.*, 2013). These mountain ranges, in addition to being natural barriers to bryophytes, shape climatic factors, such as, orographic rain, which provide different resources for the colonization of them (Santos *et al.*, 2014). Several bryofloristic surveys previously developed in the Atlantic forest area showed high species richness in different areas (Costa & Silva, 2003; Yano, 2005; Yano & Peralta, 2011a, 2011b; Luizi-Ponzo *et al.*, 2013; Yano & Luizi-Ponzo, 2014). This region is of great importance due to its species diversity, the presence of endemic species and the floristic affinities with the Andean flora (Morrone, 2001; Gradstein & Costa, 2003; Oliveira-Filho *et al.*, 2013a).

This study aimed to analyse the bryofloristic similarity among different areas of south-eastern Brazil and to understand the influence of environmental filtering on the bryophyte assemblages. Based on the premise of a deterministic, niche-based, bryophyte distribution, the following hypotheses were developed: (1) areas with similar vegetation type show greater bryofloristic similarity; (2) environmental filters drive the bryophyte assembly in south-eastern Brazil.

MATERIAL AND METHODS

The paper dealt with 24 different areas of the south-eastern region of Brazil, from which bryofloristic data were available.

We used data from our own previous field work (Amorim, 2013), as well as from bryofloristic published papers that complement the studied areas by us. With this aim an extensive bibliographic review was undertaken, followed by a revision of nomenclature.

Afterward, we used the median value of the richness of areas and we excluded those that had value below 77 species. Thus we do not underestimate the analysis, avoiding the misinterpretation of the data. This data collection resulted in 12 areas that were selected to be analyzed (Table 1, Fig. 1).

A similarity qualitative matrix, based on the presence (1) and absence (0) of species in each area, was elaborated. In the matrix, we only included taxa with identification at species level, after checking the synonyms, according to the online Index of Mosses Database (2016). For the assessment of floristic similarity, the following multivariate analyses were applied: (1) cluster analysis, using the *Sørensen* coefficient, which is used for qualitative data and assigns more weight to “common” species in the matrix and unweighted pair group method with arithmetic mean (UPGMA) for representation in the cluster dendrogram (Kent & Coker, 1992; Felfili *et al.*, 2011). The cophenetic correlation coefficient was used for show the degree of deformation of the dendrogram (Palmer, 1993); and (2) Detrended Correspondence Analysis (DCA) to spatial data ordering and representation under a biplot ordination graph. Thus, an indirect gradient analysis was obtained, and sorting of data regarding their species-sampling unit (Kent & Coker, 1992). The analyses were performed using the software Past *v*. 2.17c (Hammer *et al.*, 2001).

We applied the Multi-response Permutation Procedures (MRPP) analysis to test the significances in the groups formed by the cluster using the *Sørensen* index in PCOrd 4.1 software (McCune & Mefford, 1999).

To test whether the geographical distance between the areas is a relevant factor in the similarity of the species, Spearman correlation analysis (Legendre &

Table 1. Areas selected of the south-eastern areas of Brazil for multivariate analysis. **Restinga*: scrub-arboreal and herbaceous vegetation in sandy coastal areas; ***Cabruca*: agroforestry system with dominance of cocoa (*Theobroma cacao* L.)

Analyzed areas	*City(is)/State*	*Main phytophysiognomies (Veloso* et al., *1991)*	*Other phytophysiognomies present*	*Abreviation*	*Number of species*	*Origin of the data*
Jureia-Itatins Ecological Station	Iguape, Miracatu, Itariri and Peruíbe/São Paulo	Tropical submontane and motane rain forest	Tropical lowland rain forests; restinga*; mangrove	EEJI	263	Visnadi (2012)
Ilha da Anchieta State Park	Ubatuba/São Paulo	Tropical montane rain forest	Tropical submontane rain forest; restinga*; mangrove	PEIA	234	Peralta & Yano (2008)
Serra do Mar State Park	Ubatuba/São Paulo	Tropical montane rain forest	Tropical submontane rain forest; restinga*; lowland forests	PESM	204	Visnadi (2009, 2013); Santos *et al.* (2011)
Ilha Grande State Park Praia do Sul State Biological Reserve	Angra dos Reis/Rio de Janeiro	Tropical montane rain forest	Tropical submontane rain forest; lowland forests	IG	203	Oliveira-e-Silva & Yano (2000a, 2000b)
Rio das Pedras Ecological Reserve	Mangaratiba/Rio de Janeiro	Tropical montane rain forest		RRP	133	Oliveira-e-Silva &Yano (2000a, 2000b)
El Nagual Private Natural Heritage Reserve	Magé/Rio de Janeiro	Tropical submontane rain forest	–	REN	131	Santos & Costa (2008)
Serra Negra	Rio Preto/Minas Gerais	Tropical montane rain forest	Tropical upper montane rain forest; semi-deciduous forest; rock outcrops s.l.	SN	92	Amorim (2013)
Ibitipoca State Park	Lima Duarte/Minas Gerais	Tropical montane rain forest	Tropical upper montane rain forest; semi-deciduous forest; rock outcrops s.l.	PEIB	198	Luizi-Ponzo *et al.* (2013); Yano & Luizi-Ponzo (2014)
Juiz de Fora Federal University Botanical Garden	Juiz de Fora/Minas Gerais	Semi-deciduous forest	–	JBUF	83	Paiva *et al.* (2015)
Serra de São José	Tiradentes/Minas Gerais	Semi-deciduous forest	Rock outcrops s.l.	SSJ	113	Yano & Peralta (2011b)
National Park of Serra do Cipó	Jaboticatubas, Santana do Riacho, Morro do Pilar, Itambé do Mato Dentro, Itabira, Nova União/Minas Gerais	Rock outcrops s.l.	Dry forests; semi-deciduous forest	PSC	234	Yano & Peralta (2011a)
Vale do Rio Doce Natural Reserve	Linhares/Espírito Santo	Semi-deciduous forest	Floodplain; cabruca**; restinga*	RNV	149	Costa & Silva (2003); Yano (2005)

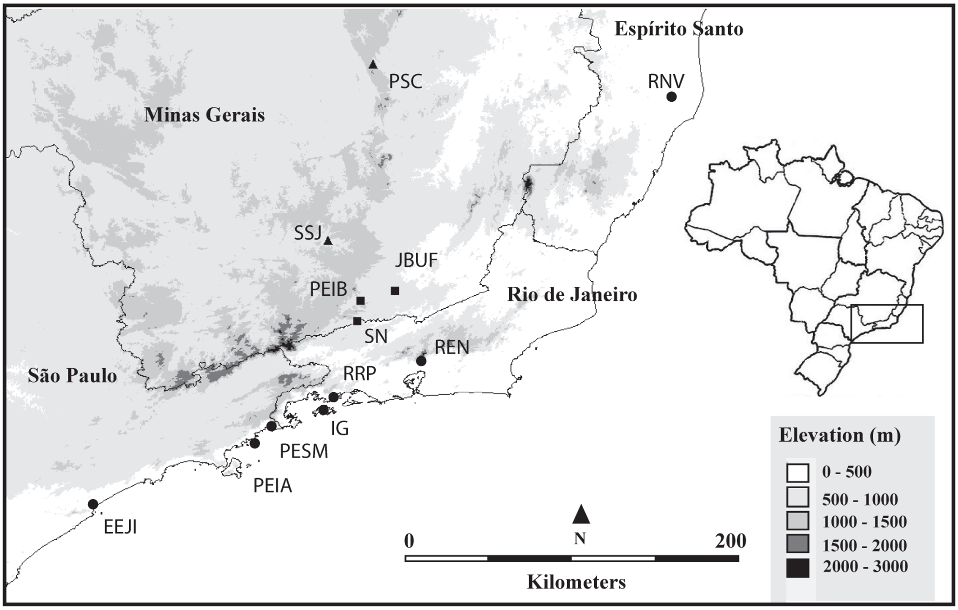

Fig. 1. Map highlighting the location of the selected south-eastern areas of Brazil used for multivariate analysis. **EEJI** – Jureia-Itatins Ecological Station; **PEIA** – Ilha Anchieta State Park; **PESM** – Serra do Mar State Park; **IG** – Ilha Grande State Park and Praia do Sul State Biological Reserve; **RRP** – Rio das Pedras Ecological Reserve; **REN** – El Nagual Private Natural Heritage Reserve; **SN** – Serra Negra; **PEIB** – Ibitipoca State Park; **JBUF** – Juiz de Fora Federal University Botanical Garden; **SSJ** – Serra de São José; **PSC** – National Park of Serra do Cipó; **RNV** – Vale do Rio Doce Natural Reserve. ● Coastal areas; ■ Inland Atlantic forest areas; ▲ Inland areas (the inserted small map on the right shows the situation of the studied areas in Brazil).

Legendre, 1998) was performed. From this, the geographical distance (km) between each area was taken, using the Google Earth program, and later organised in a table of "Distance between areas x similarity". This analysis was also performed using the software Past *v.* 2.17c (Hammer *et al.*, 2001).

In order to determine the relationship between the floristic composition and the environmental variables, Canonical Correspondence Analysis (CCA) was performed; this technique is a direct gradient analysis, ordering the data of species and environmental variables from two different and separate matrices (Palmer, 1993). The analysis was performed using the software Canoco for Windows version 4.5 (ter Braak & Smilauer, 1998).

The environmental variables were extracted from the WorldClim database using current 2.5 arc-minutes resolution. Data analyses were conducted in DIVA-GIS 7.5 software. The variables were chosen taking into account that the water availability, climatic conditions and the altitudinal gradient, are important components for the establishment of bryophytes in a community (Glime, 2007; Santos *et al.*, 2014). We used altitude, annual temperature, minimum temperature, maximum temperature, temperature in the wet season, temperature in the dry season, temperature in hot season, temperature in the cold season, annual precipitation and distance from the ocean. As suggested by ter Braak & Smilauer (1998) and Felfili *et al.* (2011), variables that showed high "variance inflation factor" (VIF > 20) were eliminated gradually during analysis of the matrix in Canoco. The variance inflation factor indicates that the variable is redundant with other variables in the data set. The removal of these variables promotes high collinearity and reduces arc effect (ter Braak & Smilauer, 1998; Felfili, *et al.*, 2011). The permutation of Monte Carlo test was performed to determine the significance of correlations between species and environmental variables with the first axis and the set of all axes of ordination, adopting a significance level of 95% ($p < 0.05$) (Palmer, 1993; ter Braak & Smilauer, 1998).

RESULTS

The similarity dendrogram of species (Fig. 2) shows a low floristic affinity (*Sørensen* coefficient < 0.5) between the majority of groups, except for two groups. One of them includes those species from Rio das Pedras Ecological Reserve (RRP), Ilha Grande State Park (IG), and Ilha da Anchieta State Park (PEIA), and the other one, Serra do Mar State Park (PESM) and Jureia-Itatins Ecological Station (EEJI). The Juiz de Fora Federal University Botanical Garden (JBUF) has no significant

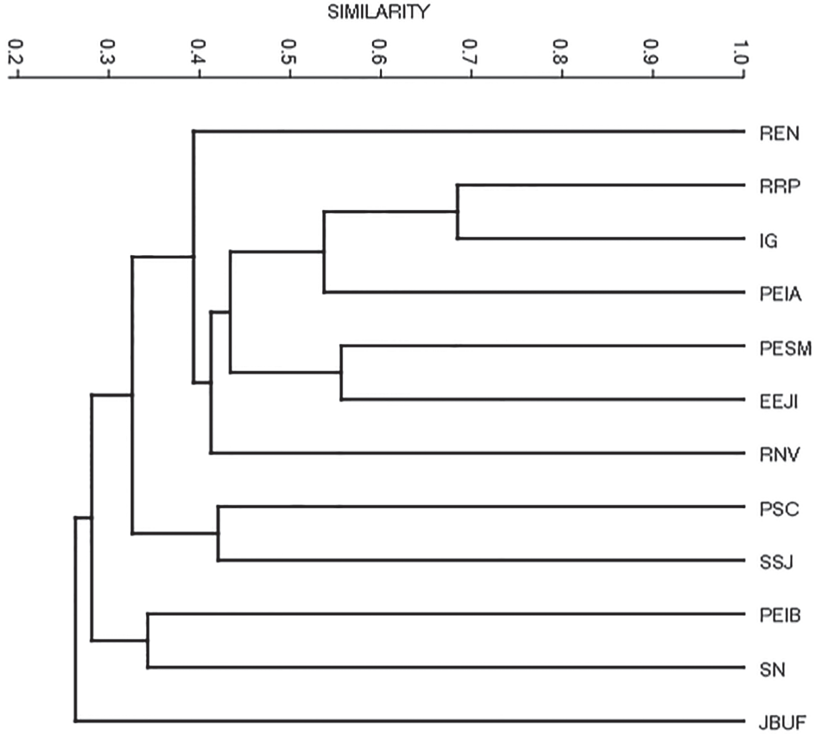

Fig. 2. Similarity dendrogram of species using the *Sørensen* coefficient and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm.

floristic affinities with other areas. The cophenetic correlation coefficient was high (0.87), showing a low degree of deformation of the dendrogram, confirming a good cohesion analysis (Palmer, 1993).

The cluster dendrogram shows a division of tendency among the bryophyte species that composed the coastal Atlantic forests [El Nagual Private Natural Heritage Reserve (REN), RRP, IG, PEIA, PESM,EEJI, and Vale do Rio Doce Natural Reserve (RNV)], the inland areas in south-eastern Brazil [National Park of Serra do Cipó (PSC) and Serra de São José (SSJ)], that are located behind the Serra da Mantiqueira, and the inland Atlantic forests [Ibitipoca State Park (PEIB) and Serra Negra (SN)]. The MRPP test confirms significant differences in values (A = 0.28; p = 0.0005) and indicates that heterogeneity species is greater between the groups and within them. Although, the low values of the index show differences in species composition between areas within the same UPGMA group.

The biplot diagram of DCA (Fig. 3) reiterates the same pattern observed in the cluster analysis, and the existence of groups, even with low floristic affinity. The DCA shows the separation of these groups in coastal areas, represented by IG, RRP, REN, PEIA, RNV, EEIJ, PESM, and inland areas, represented by the SSJ, PSC, SN and PEIB. The JBUF area presents an intersection between the groups. The DCA shows eigenvalues of 0.40 and 0.29 for the first and second axis; those values were considered high for tropical vegetation, according Felfili *et al.* (2011).

The Spearman correlation is not significant (p = 0.96; R = -0.0061) thus, it is understood that geographic distance is not a major factor in the similarity between the studied areas.

The biplot of CCA analysis (Fig. 4) has eigenvalues of 0.42 and 0.30 for the first and second axis, indicating significant relationships between the species and environmental variables, in which the eigenvalue is significant for tropical communities (> 0.3) (Felfili *et al.*, 2011). The correlation of species and the environment for the first and second axes is of 0.99 and 0.98. The percentage of variance explained by environmental variables is 35.42% in the first (cumulative 61.23%); high values are considered significant for the first and second axes. The values of the Monte Carlo significance test are significant (p < 0.01) for all axes (Table 2). The CCA analysis supports the floristic patterns of relationships observed in the cluster analyses and DCA (Fig. 3).

The CCA shows that the floristic similarity among coastal areas (REN, IG, PEIA, RRP, RNV PESM, and EEJI) is affected by

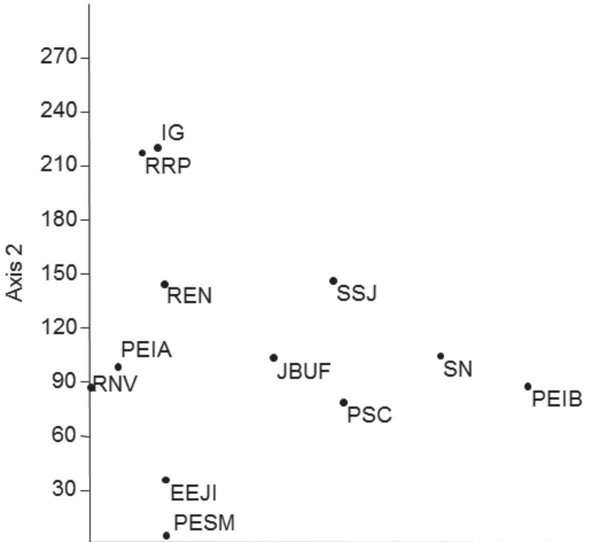

Fig. 3. Ordination diagram obtained by Detrended Correspondence Analysis (DCA).

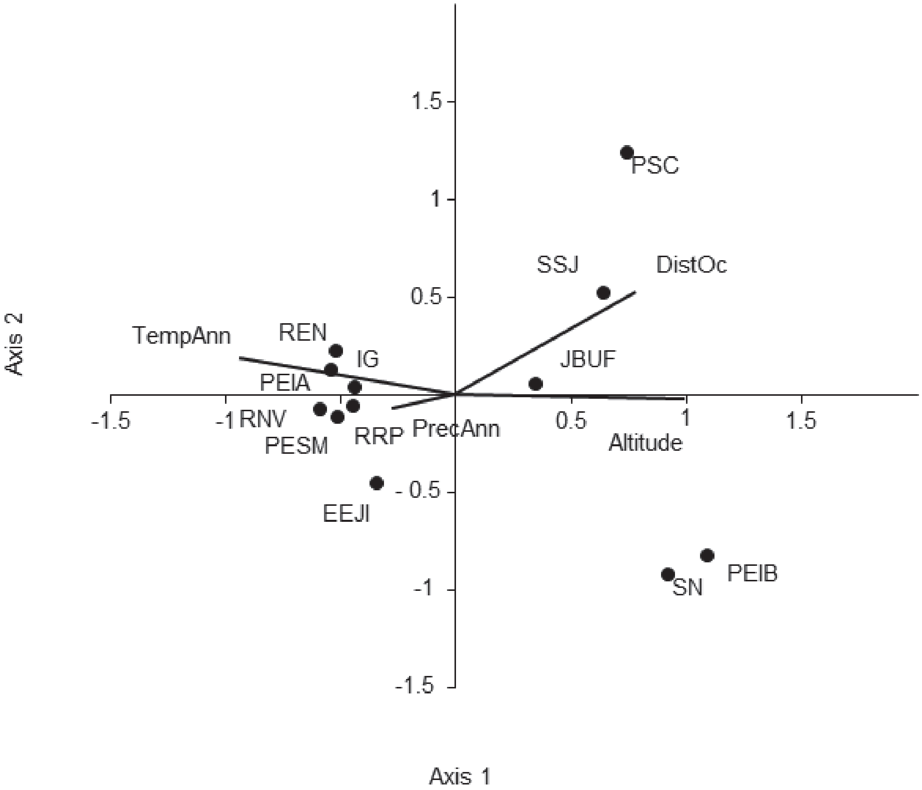

Fig. 4. Diagram ordination biplot resulting from Canonical Correspondence Analysis (CCA), showing the relationships of floristic similarity between environmental variables.

Table 2. Estimators of the first two axis of Canonical Corresponde Analysis (CCA) between species of bryophytes of selected areas with environmental variables (*all canonical axes)

Estimators	*Axis 1*	*Axis 2*
Eigenvalues	0.42	0.30
% cumulative variance of the species	14.30	24.70
% of variance explained by environmental variables	35.42	61.23
Permutation test Monte Carlo	0.004	0.011*

annual temperature and annual precipitation. These areas also are negative correlated with the altitude and distance of the ocean. The inland Atlantic forests SN, PEIB and JBUF and the inland areas as SSJ and PSC are influenced by the distance from the ocean and the altitude. These areas also are negative correlated with the annual temperature and annual precipitation. The altitude and distance from the ocean are the most correlated variables with the first axis, values of 0.88 and 0.52 respectively (Table 3). Thus, the first axis is more strongly associated with environmental variables related to relief.

Table 3. Correlation of environmental variables with the first two axes of Canonical Correspondence Analysis (CCA) (only used variables are shown)

Environmental variables	*Axis 1*	*Axis 2*
Altitude	0.88	0.42
Distance from ocean	0.52	0.80
Maximum temperature	−0.87	−0.28
Annual precipitation	−0.28	−0.05

DISCUSSION

Bryofloristic similarity

The significant indices were found only in those areas with similar altitude and type of vegetation (EIIJ, IG, PEIA, PESM and RRP), corroborating the first hypothesis. The same pattern for bryophyte beta diversity was found by Santos *et al.* (2014) in a study on spatial distribution of liverworts in the Atlantic coastal forest of south-eastern Brazil. They observed higher similarity indices between areas with similar altitudes or areas located in the same unit of conservation near the sea, suggesting a local floristic gradient due a influence of the local filters. The dissimilarity observed, in our study, showed the specific bryofloristc composition on a regional scale. In the present study, the beta diversity of bryophytes was high, also suggesting a strong influence of environmental filtering on the bryophyte assemblage, corroborating the second hypothesis. Differences in soil, river and forest formation were observed on PSC and SSJ areas; ultisol soil type characterizes SSJ (Oliveira-Filho & Machado, 1993; Gonzaga *et al.*, 2008; Alves & Kolbek, 2009), while oxisol and cambisol soil types are found in PSC (Rapini *et al.*, 2008), Rio Grande watershed influences SSJ (Oliveira-Filho & Machado, 1993; Gonzaga *et al.*, 2008; Alves & Kolbek, 2009), whereas São Francisco and Rio Doce watersheds affect PSC (Rapini *et al.*, 2008). These factors influence the phytophysiognomy of the areas, justifying the low floristic affinity between them.

The floristic distance observed in the grouping formed between areas PEIB and SN, can be explained by the influence of different tree compositions between areas observed by Valente *et al.* (2011). Fragments of tropical rain forest within the park, surrounded by rock outcrops *s.l.* formations characterizes PEIB (Oliveira-Filho *et al.*, 2013b), distinguishing it from SN, which presents different tropical rain forest fragments scattered among rock outcrops *s.l.*, pastures region and agricultural activities (Salimena *et al.*, 2013). Such differentiations, plus the fact that PEIB is a protected area, seem to influence the composition of the flora of the areas and allow us to understand the low bryofloristic similarity between them.

The dendrogram showed the floristic distance of the JBUF with the other areas assessed, which is justified because it consists of an urban fragment, which suffered severe local interference. Such interference, related to deforestation and coffee growing, among others (Fonseca & Carvalho, 2012), influence the composition of the local tree structure by degradation of the area. Thus, occurring the colonization of more light-tolerant bryophytes species and reducing the colonization by shade species

(Gradstein *et al*., 2001; Silva & Pôrto, 2009). The area has a lower diversity of trees in relation to more preserved forests, common in urban fragments (Brito & Carvalho, 2014; Fonseca & Carvalho, 2012); this occurs with a smaller supply of substrates for the colonization of bryophytes. This floristic dissimilarity was also obtained by Paiva *et al*. (2015) in a study of the species of mosses in the area, which agrees with the similarity value of the JBUF with the other areas studied. In the areas of the State Park of Serra do Mar, the author cites the predominance of generalist species, because survive best in disturbed areas (Visnadi, 2013). PEIB and SN share a common physiognomy, rocky outcrop fields associated to quartzitic soils, and cloud forests, besides high altitude. These characteristics can contribute to the existence of affinity between areas observed in the analysis. Studies on other plant groups corroborate the floristic affinities found for the bryophytes between PEIB and SN; Abreu *et al*. (2011) studied the Orchidaceae flora of both areas, and showed that 63% of the species co-occur in SN and PEIB; Souza *et al*. (2012) observed 60% of co-occurrence of fern species in both areas. These floristic affinities support the hypothesis 1, that the areas have similar characteristics, in the case of bryophytes, have floristic congruence.

The DCA biplot showed a separation between the coastal areas and the inland areas which is supported by the eigenvalue of the first axis. These areas are set apart by an extensive chain of mountains, formed e.g. by Serra do Mar and Serra da Mantiqueira. Since most dispersion processes are short distances (Heinrichs *et al*., 2009; Vanderpoorten & Goffinet, 2009), such chains act as natural barriers and influence the dispersion of the species as a physical barrier, holding the air mass, causing orographic rainfall, and increasing relative humidity, especially in the eastern face of the Serra do Mar (Scheer & Mocochinski, 2009; Sanchez *et al*., 2013; Santos *et al*., 2014), which justifies the segregation of these areas in the diagram of analysis. Once again, JBUF is apart from the others inland areas, what is explained by the strong anthropogenic influence suffered on the site.

Environmental filtering

The low similarity values corroborate the proposal that bryophytes are regulated by specific local factors, such as the climate. Different authors report that the micro-climate conditions are decisive for the colonization of bryophytes (León-Vargas *et al*. 2006; Batke *et al*., 2015; Dynesius, 2015). Silva & Pôrto (2010) observed, in a study on edge effect, that specific micro-climate conditions (altitudinal differences and the canopy dynamic) of bryophytes communities in Atlantic forest fragments in north-eastern Brazil influenced the richness and diversity of species. Holz *et al*. (2002) demonstrated that the distribution of species and life forms in different micro-habitats were correlated with humidity and light regimes, which presented distinct difference in species found in the tree bases, trunks, branches, and twigs. In a study developed by Costa *et al*. (2015), the authors reported bryophyte peaks endemism and high species richness occurred at high elevations (2100 m) in the upper montane forest in Itatiaia National Park, that demonstrated the high specificity of species of bryophytes to summit climates.

The results of direct gradient analysis (CCA) showed the presence of environmental filtering for bryophytes, as the annual temperature and the annual precipitation were the environmental variables that grouped the coastal areas. The high local rainfall in coastal areas (caused by orographic rains as mentioned) generates high water availability, increasing the local humidity, a factor that tends to be predominant for the establishment of bryophyte species characteristic of rainforests (Santos *et al*., 2014). Such abiotic variables influence the physiological processes of bryophytes (Glime, 2007); thus, areas with similar climatic conditions such as precipitation and temperature tend to share a large number of species of bryophytes. Medina *et al*. (2014) demonstrated how the climate variability influences the richness and abundance of assembly bryophytes epiphytes. According to these authors, the interactions between the availability of water and the temperature have the controlling effect of diversity of the group. Thus, low temperatures constrain the capacity of sites with high precipitations to support more species; on the other hand, the effect of summer drought is more severe in the localities that also have low rainfall during springtime. The CCA showed that the distance of the ocean and the altitude was the main factor that brought together the inland areas, showing a strong correlation with the first canonical axis. The relationship between the distances of the ocean reveals areas with a low influence of coastal elements, such as orographic rainfall and low temperature (negative correlation with temperature annual) values that contribute to the existence of an affinity between these areas. Also, the inland areas PSC and SSJ include a large expanse of rocky fields and are influenced by elements of the *cerrado* (Brazilian Savanna)*,* soil, climate and vegetation type (Giulietti *et al.*, 1987; Oliveira-Filho & Machado, 1993; Alves & Kolbek, 2009), promoting the relationship between areas.

The JBUF area also presented an intermediate position in the biplot diagram of the CCA correlated with the first axis, having an influence on the distance of the ocean and altitude. Moreover, as mentioned, the area is located in an urban centre and suffers extensive human influence, which contributes to its intermediate position in the analyses and their poor floristic affinity with the other assessed areas. Alvarenga & Pôrto (2007) also reported an increase in species with large niches (general) in fragmented habitats affected by anthropic actions in the fragmented Atlantic forest in the northeast of Brazil.

Thus, through the presented study, we realized that the bryophytes are highly sensitive to climatic differences of areas of south-eastern Brazil. Mota de Oliveira *et al.* (2015) demonstrated that the phorophyte vertical gradient is the determining factor for the composition of epiphytic bryophytes in the Amazon. Here, we understand that the climatic differences created by altitude and distance from the ocean (continentality) are responsible for bryofloristic composition in a regional scale in Atlantic forest. Hence, the coexistence or not of bryophyte species are determined by environmental filter caused by the characteristics of those habitats (Kraft *et al*., 2015).

CONCLUSIONS

The study showed both proposed hypotheses were confirmed. Areas sharing similar vegetation type exhibited higher bryoflorist similarity. Most of the evaluated areas have low floristic affinity, suggesting that the distributions of species of bryophytes are highly influenced by local filters, such as the climate. The mountain ranges generate climatic conditions that interfere with the physiognomy of the vegetation and substrate availability in influencing the distribution of bryophytes to the areas considered here. The rainfall, temperature and distance from the ocean were the variables that most influenced the distribution of bryophytes in the areas analysed.

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REFERENCES

ABREU N.L., MENINI-NETO L. & KONNO T.U.P., 2011 — Orchidaceae das Serras Negra e do Funil, Rio Preto, Minas Gerais, e similaridade florística entre formações campestres e florestais do Brasil. *Acta botanica Brasilica* 25(1): 58-70.

ALVARENGA L.D.P. & PÔRTO K.C., 2007 — Patch size and isolation effects on epiphytic and epiphyllous bryophytes in the fragmented Brazilian Atlantic forest. *Biological conservation* 134(3): 415-427.

ALVES R.J.V. & KOLBEK J., 2009 — Summit vascular flora of Serra de São José, Minas Gerais, Brazil. *Check list* 5(1): 35-73.

AMORIM E.T., 2013 — *Estudo florístico e ecológico das briófitas da Serra Negra (Minas Gerais) e sua relação com outras áreas do sudeste do Brasil*. Dissertation, Universidade Federal de Juiz de Fora, Brazil.

BANIYA C.B., SOLHØY T., GAUSLAA Y. & PALMER M.W., 2012 — Richness and composition of vascular plants and cryptogams along a high elevational gradient on Buddha Mountain, Central Tibet. *Folia geobotanica* 47: 135-151.

BATKE S.P., MURPHY B.R., HILL N. & KELLY D.L., 2015 — Can air humidity and temperature regimes within cloud forest canopies be predicted from bryophyte and lichen cover? *Ecological indicators* 56: 1-5.

BRITO P.S.D. & CARVALHO F.A., 2014 —. Tree structure and diversity in a secondary Semideciduous Seasonal Forest in the Juiz de Fora Federal University Botanical Garden. *Rodriguésia* 65(4): 817-830.

CHURCHILL S.P., 1991 — The floristic composition and elevational distribution of Colombian mosses. *The bryologist* 94 (2): 157-167.

CHURCHILL S.P., GRIFFIN III D. & LEWIS M., 1995 — Moss diversity of the Tropical Andes. *In*: Churchill S.P., Balslev H., Forero E. & Luteyn J.L. (eds.), *Biodiversity and Conservation of Neotropical Montane Forest*. New York, The New York Botanical Garden, pp. 335-346.

CONDIT R., PITMAN N. & LEIGH J.E.G., 2002 — Beta-diversity in tropical forest trees. *Science* 295: 666-669.

COSTA D.P. & SILVA A.G., 2003 — Briófitas da Reserva Natural da Vale do Rio Doce, Linhares, Espírito Santo, Brasil. *Boletim do museu de biologia Mello Leitão* 16: 21-38.

COSTA D.P., SANTOS N.D., REZENDE M.A., BUCK W.R. & SCHÄFER-VERWIMP A., 2015 — Bryoflora of the Itatiaia National Park along an elevation gradient: diversity and conservation. *Biodiversity and conservation* 24(9): 2199-2212.

DYNESIUS M., 2015 — Slow recovery of bryophyte assemblages in middle-aged boreal forests regrown after clear-cutting. *Biological conservation* 191: 101-109.

FELFILI J.M., CARVALHO F.A., LIBANO A.M., VENTUROLI F., PEREIRA B.A.S. & MACHADO E.L.M., 2011 — Análise Multivariada: princípios e métodos em estudos de vegetação. *In*: Felfili J.M., Eisenlohr P.V., Melo M.M.R.F., Andrade L.A. & Meira-Neto J.A.A. (eds), *Fitossociologia no Brasil: Métodos e estudos de casos*. Viçosa, Editora da Universidade Federal de Viçosa, pp. 122-155.

FIASCHI P. & PIRANI J.R., 2009 — Review of plant biogeographic studies in Brazil. *Journal of systematics and evolution* 47(5): 477-496.

FONSECA C.R. & CARVALHO F.A., 2012 — Aspectos florísticos e fitossociológicos da comunidade arbórea de um fragmento urbano de Floresta Atlântica (Juiz de Fora, MG, Brasil). *Bioscience journal* 28(5): 820-832.

FRAHM J.-P. & GRADSTEIN S.R., 1991 — An altitudinal zonation of tropical rain forests using byrophytes. *Journal of biogeography* 18(6): 669-678.

GABRIEL R. & BATES J.W., 2005 — Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. *Plant ecology* 177(1): 125-144.

GIULIETTI A.M., MENEZES N.L., PIRANI J.R., MEGURO M. & WANDERLEY M.G.L., 1987 — Vegetação da Serra do Cipó, Minas Gerais 1: Caracterização e lista das espécies. *Boletim de botânica da Universidade de São Paulo* 9: 1-151.

GLIME J.M., 2007 — *Bryophyte Ecology. Volume 1. Physiological Ecology.* Ebook Michigan Technological University and the International Association of Bryologists. Available at http://www.bryoecol.mtu.edu. Accessed November 11, 2014.

GONZAGA A.P.D., OLIVEIRA-FILHO A.T., MACHADO E.L.M., HARGREAVES P. & MACHADO J.N.M., 2008 — Diagnóstico florístico-estrutural do componente arbóreo da floresta da Serra de São José, Tiradentes, MG, Brasil. *Acta botanica Brasilica* 22(2): 505-520.

GÖTZENBERGER L., DE BELLO F., BRATHEN K.A., DAVISON J., DUBUIS A., GUISAN A., LEPŠ J., LINDBORG R., MOORA M., PARTEL M., PELLISSIER L., POTTIER J., VITTOZ P., ZOBEL K. & ZOBEL M., 2012 — Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological reviews* 87: 111-127.

GRADSTEIN S.R., 1995 — Diversity of hepaticae and anthocerotae in montane forest of the Tropical Andes. *In*: Churchill S.P., Balslev H., Forero E. & Luteyn J.L. (eds), *Biodiversity and Conservation of Neotropical Montane Forest*. New York, The New York Botanical Garden, pp. 321-334.

GRADSTEIN S.R., CHURCHILL S.P. & SALAZAR-ALLEN N., 2001 — Guide to the bryophytes of tropical America. *Memoirs of the New York botanical garden* 86: 1-577.

GRADSTEIN S.R. & COSTA D.P., 2003 — The hepaticae and anthocerotae of Brazil. *Memoirs of the New York botanical garden* 87: 1-318.

HALLINGBÄCK T. & HODGETTS N., 2000 — *Mosses, liverworts, and hornworts, status survey and conservation action plan for bryophytes*. Gland, Switzerland and Cambridge, UK, IUCN/SSC Bryophyte Specialist Group. IUCN, 106 p.

HAMMER Ø., HARPER D.A.T. & RYAN P.D., 2001 — *PAST* Paleontological statistics software package for education and data analysis*. Palaeontologia Electronica. Available in http://folk.uio.no/ohammer/past. Accessed March 20, 2012.

HEINRICHS J., HENTSCHEL J., FELDBERG K., BOMBOSCH A. & SCHNEIDER H., 2009 — Phylogenetic biogeography and taxonomy of disjunctly distributed bryophytes. *Journal of systematics and evolution* 47(5): 497-508.

HOLZ I., GRADSTEIN S.R., HEINRICHS J. & KAPPELLE M., 2002 — Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. *The bryologist* 105(3): 334-348.

INDEX OF MOSSES DATABASE (W3MOST), 2016 — *Tropicos.org*. Missouri Botanical Garden. Available in http://www.tropicos.org. Accessed January 22, 2013.

KEDDY P.A., 1992 — Assembly and response rules: two goals for predictive community ecology. *Journal of vegetation science* 3: 157-165.

KENT M. & COKER P., 1992 — *Vegetation description and analysis: A practical approach*. London, Belhaven Press, 319 p.

KIRÁLY I., NASCIMBENE J., TINYA F. & ÓDOR P., 2013 — Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodiversity and conservation* 22(1): 209-223.

KRAFT N.J., ADLER P.B., GODOY O., JAMES E.C., FULLER S. & LEVINE J. M., 2015 — Community assembly, coexistence and the environmental filtering metaphor. *Functional ecology* 29(5): 592-599.

LEGENDRE P. & LEGENDRE L., 1998 — *Numerical Ecology*. Amsterdam, Elsevier Science B, 853 p.

LEÓN-VARGAS Y., ENGWALD S. & PROCTOR M.C., 2006 — Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. *Journal of biogeography* 33(5): 901-913.

LUIZI-PONZO A.P., SIVIERO T.S., AMORIM E.T., HENRIQUES D.K., ROCHA L.M., GOMES H.C., PAIVA L.A., RODRIGUES R.S., SILVA G.D., RIBEIRO G.C., GOMES C.Q. & CAMPEÃO A.S., 2013 — Briófitas do Parque Estadual do Ibitipoca (Minas Gerais, Brasil). *In*: Forzza R.C., Menini-Neto L., Salimena F.R.G. & Zappi D. (eds), *Flora do Parque Estadual do Ibitipoca e seu entorno*. Juiz de Fora, Universidade Federal de Juiz de Fora, pp. 95-122.

McCUNE B. & MEFFORD M.J., 1999 — *PC-ORD: multivariate analysis of ecological data, version 4.10.* Gleneden Beach, Oregon, USA, MjM Sofware Design.

MEDINA N.G., ALBERTOS B., LARA F., MAZIMPAKA V., GARILLETI R., DRAPER D. & HORTAL J., 2014 — Species richness of epiphytic bryophytes: drivers across scales on the edge of the Mediterranean. *Ecography* 37(1): 80-93.

MORRONE J.J., 2001 — Homology, biogeography and areas of endemism. *Diversity and distributions* 7(6): 297-300.

MOTA DE OLIVEIRA S., TER STEEGE H., CORNELISSEN J.H. & GRADSTEIN S.R., 2009 — Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. *Journal of biogeography* 36(11): 2076-2084.

MOTA DE OLIVEIRA S., TER STEEGE H. & ZOTZ G., 2015 — Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *Journal of ecology* 103(2): 441-450.

OLIVEIRA-E-SILVA M.I.M.N., & YANO O., 2000a — Musgos de Mangaratiba e Angra dos Reis, Rio de Janeiro, Brasil. *Boletim do instituto de botânica* 14: 1-137.

OLIVEIRA-E-SILVA M.I.M.N. & YANO O., 2000b — Anthocerotophyta e Hepatophyta de Mangaratiba e Angra dos Reis, Rio de Janeiro. Brasil. *Boletim do instituto de botânica* 13: 1-102.

OLIVEIRA-FILHO A.T. & MACHADO J.N.M., 1993 — Composição florística de uma floresta semidecídua montana, na Serra de São José, Tiradentes, Minas Gerais. *Acta botanica Brasilica* 7(2): 71-88.

OLIVEIRA-FILHO A.T., BUDKE J.C., JARENKOW J.A., EISENLOHR P.V. & NEVES D.R.M., 2013a — Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. *Journal of plant ecology* 2: 1-23.

OLIVEIRA-FILHO A.T., FONTES M.A.L., VIANA P.L., VALENTE A.S.M., SALIMENA F.R.G. & FERREIRA F.M., 2013b — O mosaico de fitofisionomias do Parque Estadual do Ibitipoca. *In*: Forzza R.C., Menini-Neto L., Salimena F.R.G. & Zappi D. (eds), *Flora do Parque Estadual do Ibitipoca e seu entorno*. Juiz de Fora, Universidade Federal de Juiz de Fora, pp. 53-93.

PAIVA L.A., SILVA J.C., PASSARELLA M.A. & LUIZI-PONZO A.P., 2015 — Briófitas de um fragmento florestal urbano de Minas Gerais (Brasil). *Pesquisas, botânica* 67: 181-199.

PALMER M.W., 1993 — Putting things in even better order: The advantages of canonical correspondence analysis. *Ecology* 74(8): 2215-2230.

PATIÑO J. & GONZÁLEZ-MANCEBO J.M., 2011 — Exploring the effect of host tree identity on epiphyte bryophyte communities in different Canarian subtropical cloud forests. *Plant ecology* 212(3): 433-449.

PERALTA D.F. & YANO O., 2008 — Briófitas do Parque Estadual da Ilha Anchieta, Ubatuba, estado de São Paulo, Brasil. *Iheringia série botânica* 63(1): 101-127.

POISOT T., BEVER J.D., NEMRI A., THRALL P.H. & HOCHBERG M. E., 2011 — A conceptual framework for the evolution of ecological specialisation. *Ecology letters* 14(9): 841-851.

RAPINI A., RIBEIRO P.L., LAMBERT S. & PIRANI J.R., 2008 — A flora dos campos rupestres da Cadeia do Espinhaço. *Megadiversidade* 4(12): 16-24.

SALIMENA F.R.G., MATOZINHOS C.N., ABREU N.L., RIBEIRO J.H.C., SOUZA F.S. & MENINI-NETO L., 2013 — Flora fanerogâmica da Serra Negra, Minas Gerais, Brasil. *Rodriguésia* 64(2): 311-320.

SANCHEZ M., PEDRONI F., EISENLOHR P.V. & OLIVEIRA-FILHO A.T., 2013 — Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, south-eastern Brazil, from near sea level to 1000 m of altitude. *Flora* 208: 184-196.

SANTOS N.D. & COSTA D.P, 2008 — A importância de Reservas Particulares do Patrimônio Natural para a conservação da brioflora da Mata Atlântica: um estudo em El Nagual, Magé, RJ, Brasil. *Acta botanica Brasilica* 22(2): 359-372.

SANTOS N.D., COSTA D.P., KINOSHITA L.S. & SHEPHERD G.J., 2011 — Aspectos briofloristicos fitogeográficos de duas formações costeiras de Floresta Atlântica da Serra do Mar, Ubatuba/SP, Brasil. *Biota neotropica* 11(2): 425-438.

SANTOS N.D., DA COSTA D.P., KINOSHITA, L. S. & SHEPHERD, G.J., 2014 — Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? *Ecological indicators* 36: 431-440.

SCHEER M.B. & MOCOCHINSKI A.Y., 2009 — Florística vascular da floresta ombrófila densa altomontana de quatro serras no Paraná. *Biota neotropica* (9)2: 51-69.

SCHMALHOLZ M., HYLANDER K. & FREGO K., 2011 — Bryophyte species richness and composition in young forests regenerated after clear-cut logging versus after wildfire and spruce budworm outbreak. *Biodiversity and conservation* 20(12): 2575-2596.

SEKULOVÁ L., HÁJEK M., HÁJKOVÁ P., MIKULÁŠKOVÁ E., BUTTLER A., SYROVÁTKA V. & FAJMONOVÁ Z., 2012 — Patterns of bryophyte and vascular plant richness in European subalpine springs. *Plant ecology* 213(2): 237-249.

SILVA M.P.P. & PÔRTO K.C., 2009 — Effect of fragmentation on the community structure of epixylic bryophytes in Atlantic Forest remnants in the Northeast of Brazil. *Biodiversity and conservation* 18(2): 317-337.

SILVA M.P.P. & PÔRTO K.C., 2010 — Spatial structure of bryophyte communities along an edge-interior gradient in an Atlantic Forest remnant in Northeast Brazil. *Journal of bryology* 32(2):101-112.

SOUZA F.S., SALINO A., VIANA P.L. & SALIMENA, F.R.G., 2012 — Pteridófitas da Serra Negra, Minas Gerais, Brasil. *Acta botanica Brasilica* 26(2): 378-390.

STRAZDIŅA, L., 2010 — Bryophyte community composition on an island of Lake Cieceres, Latvia: dependence on forest stand and substrate properties. *Environmental and experimental biology* 8: 49-58.

TER BRAAK C.J.F. & SMILAUER P., 1998 — *CANOCO* Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination, version 4*. Ithaca, Microcomputer Power.

TOWNSEND C.R., BEGON M. & HARPER J.L., 2010 — *Fundamentos em ecologia*. São Paulo, Editora Artmed, 576 p.

TUBA Z., CSINTALAN Z., SZENTE K., NAGY Z. & GRACE J., 1998 — Carbon gains by desiccation-tolerant plants at elevated CO2. *Functional ecology* 12(1): 39-44.

TUBA Z., 2011 — Bryophyte Physiological Processes in a Changing Climate: an Overview. *In*: Tuba Z., Slack N. & Stark L.R. (eds), *Bryophyte ecology and climate change*. New York, Cambridge University Press, pp. 13-32.

VALENTE A.S.M., GARCIA P.O., SALIMENA F.R.G. & OLIVEIRA-FILHO A.T., 2011 — Composição, estrutura e similaridade florística da Floresta Atlântica, na Serra Negra, Rio Preto – MG. *Rodriguésia* 62(2): 321-340.

VANDERPOORTEN A. & GOFFINET B., 2009 — *Introduction to Bryophytes*. New York, Cambridge University Press, 303 p.

VELOSO H.P., RANGEL-FILHO A.L.R. & LIMA J.C.A., 1991 — *Classificação da vegetação brasileira, adaptada a um sistema universal*. Rio de Janeiro, Instituto Brasileiro de Geografia e Estatística, 124 p.

VISNADI S.R., 2009 — Briófitas do caxetal, em Ubatuba, São Paulo, Brasil. *Tropical bryology* 30: 8-14.

VISNADI S.R., 2012 — Bryophytes from Jureia-Itatins Ecological Station, São Paulo state, Brazil Briófitas da Estação Ecológica Jureia-Itatins, estado de São Paulo, Brasil. *Tropical bryology* 34: 17-31.

VISNADI S.R., 2013 — Briófitas de áreas antrópicas do Parque Estadual da Serra do Mar, Núcleo Picinguaba, Ubatuba, estado de São Paulo, Brasil. *Boletim do museu Paraense Emílio Goeldi* 8: 49-62.

YANO O., 2005 — Adição às Briófitas da Reserva Natural da Vale do Rio Doce, Linhares, Espírito Santo, Brasil. *Boletim do museu de biologia Mello Leitão* 18: 5-48.

YANO O. & PERALTA D.F., 2011a — Bryophytes from the Serra de São José, Tiradentes, Minas Gerais State, Brazil. *Boletim do instituto de botânica* 21: 141-172.

YANO O. & PERALTA D.F., 2011b — Flora da Serra do Cipó, Minas Gerais: Briófitas (Anthocerotophyta, Bryophyta e Marchantiophyta). *Boletim de botânica da Universidade de São Paulo* 29: 135-299.

YANO O. & LUIZI-PONZO A.P., 2014 — Adições à Brioflora do Parque Estadual do Ibitipoca, Minas Gerais, Brasil. *Revista de biologia neotropical* 11(2): 71-96.