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Variations in bryophyte communities in a short elevational gradient in Atlantic Forest of southeastern Brazil

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Abstract – In order to better understand the influence of short elevational gradient on the attributes of bryophyte communities, we examined the bryophyte flora within six elevational belts (10, 50, 400, 800, 950, and 1170 m a.s.l.) on a mountain in the Atlantic Forest in southeastern Brazil. Ten subplots (10 × 10 m) distributed randomly in 1 ha forest plot of forest at each elevation were surveyed. A total of 253 species were encountered and the richness did not vary depending significantly on elevation. The floristic similarities of the elevational belts were high > 50%, with the exception of the Mountaintop forest (< 35%), and the classification analyses indicated groups defined by Atlantic Forest vegetation types. Endemism demonstrated a positive correlation with elevation, while the amplitudes of the phytogeographical patterns of the species diminished with increasing elevation. The dioicous condition predominated in all of the elevational belts, and the dioicous/monoicous ratio showed an inverted-parabolic pattern along the gradient. Data concerning bryophyte species richness and distributions will be useful in future projects monitoring the effects of climate change on tropical forests.

Endemism / phytogeographic pattern / sexual system / tropical forest

INTRODUCTION

One of the most striking characteristics of tropical forests is their high species richness (Whitmore, 1990), although with distinct patterns of variation along elevational gradients (Givnish, 1999). During the last 25 years, research into spatial ecology has focused on studying changes in plant communities at different elevational belts on tropical mountains (*e.g.* Vázquez & Givnish, 1998; Kessler, 2000a, 2000b; Hemp, 2006) and on understanding how and why species richness vary geographically (Sanders & Rahbek, 2012). Different explanatory mechanisms have been proposed,

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such as climate and productivity (Rahbek, 1995), climate and area (Stevens, 1992), evolutionary history (Machac *et al.*, 2011), and geometric constraints (Colwell & Less, 2000), but there is a consensus that no single process is responsible for all elevational diversity gradients observed (Sanders & Rahbek, 2012).

Diverse gradients, such as temperature, solar radiation and atmospheric pressure, can be encountered along mountain slopes that vary significantly with changing elevation (Körner, 2007). It is worthwhile noting that elevation itself is not a variable, but rather a surrogate used to represent these vertical environmental changes. The environmental gradients observed with increasing elevation (hereafter referred to as “elevational gradient”) can act upon many attributes of plant communities, including species richness (Kessler, 2000a; Kluge *et al.*, 2006), floristic composition (Frahm & Gradstein, 1991; Santos *et al.*, 2014), biomass (Wolf, 1993; Alves *et al.*, 2010), the proportions of endemic species (Kessler, 2002a, 2002b; Kluge & Kessler, 2006), their phytogeographical patterns (Gradstein *et al.*, 1989; Costa & Lima, 2005; Santos & Costa, 2010a), physiology (Wagner *et al.*, 2012; Bader *et al.*, 2013), and sexual systems (Jacquemyn *et al.*, 2005; Vamosi & Queenboroug, 2010).

The structural complexities and varieties of microhabitats in tropical rain forests favor the development of a rich bryophyte flora, estimated at 3000 to 4000 species (Pócs, 1982; Frahm, 2001). Bryophytes (liverworts, mosses and hornworts) have important ecological roles in the dynamics of these forests as they aid in maintaining the local water balance and atmospheric humidity, in recycling nutrients, as well as providing habitat for many other organisms (Richards, 1984; Turestsky, 2003). Bryophytes generally demonstrate strict ecological amplitudes and occur only in very specific micro-environments. Due to their poikilohydric nature, bryophytes are very sensitive to environmental changes and can be used as bioindicators of environmental and microclimatic conditions (Vanderpooten & Goffinet, 2009), including the elevational gradient (Frahm & Gradstein, 1991).

The present work assumes that elevation (through its associated variables) acts as an environmental filter on bryophyte communities. We therefore undertook an analysis of the alpha and beta diversities of different elevational belts on a small tropical mountain (1170 m high) to determine how elevation influences the bryophyte communities and hypothesized: 1) the existence of a unimodal curve of species richness, with a peak halfway through the elevational gradient, as has been observed for cryptogamic plants in tropical forests (Wolf, 1993; Kessler *et al.*, 2011); 2) a peak of endemism above the peak of species richness in relation to the elevational gradient (Kessler, 2010); 3) the existence of high beta diversity, with taxa exclusive to certain elevational belts (Frahm & Gradstein, 1991; Costa & Lima, 2005; Santos & Costa, 2010b; Santos *et al.*, 2014); 4) wider phytogeographical patterns at lower altitudes (Santos & Costa, 2010a; Santos *et al.*, 2011); and 5) an increase in the proportions of dioicous species with elevation, as montane forests generally show higher humidity indices than lowland forests, which would facilitate sexual reproduction (Glime, 2007).

MATERIALS AND METHODS

Study area

The study region included the Picinguaba (23°31’-23°34’ S and 45°02’-45°05’ W) and Santa Virgínia (23°17’-23°24’ S and 45°03’-45°11’ W) nucleus of the

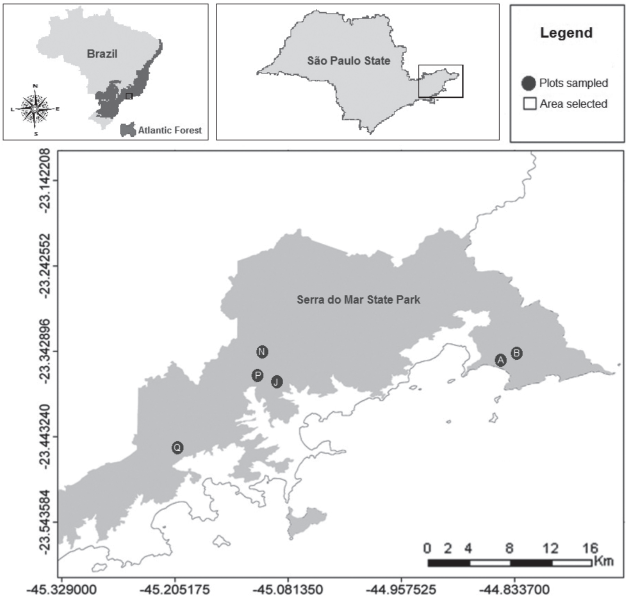

Fig. 1. Study area with indication of plots sampled in the Serra do Mar State Park, São Paulo, southeastern Brazil.

Serra do Mar State Park, situated along the northern coast of São Paulo State, Brazil (Fig. 1). We evaluated the bryophyte communities in 1 ha plots established along six elevational belts between sea level and 1170 m a.s.l. To that end, five permanent plots that had been established during the Functional Gradient Thematic Biota Project and located within continuous and well-preserved remnants of Atlantic Forest were selected: plots A (10 m), B (50 m), J (400 m), P (800 m), and N (950 m). We maintained the same identifications of the plots and subplots established in the Functional Gradient Project (Joly *et al.*, 2012). A sixth plot was established, Q (1170 m), on Corcovado Peak in the municipality of Ubatuba (Table 1). The regional climate is Equatorial fully humid (Af) according to the Köeppen-Geiger system (Kottek *et al.*, 2006), with higher rainfall during the summer (Morellato *et al.*, 2000). The mean annual precipitation is 2500 mm, and mean monthly temperatures range from 19.1 to 25.5ºC (Sentelhas *et al.*, 1999). There are clear decreases of both mean annual precipitation and temperature along the slope (Alves *et al.*, 2012). Detailed descriptions of the study area are available in Assis *et al.* (2011), Padgurshi *et al.* (2011), Rochelle *et al.* (2011), Alves *et al.* (2012), Joly *et al.* (2012) and Eisenlohr *et al.* (2013).

The vegetation classification system of Veloso *et al.* (1991) was used as a reference for the definition of the different vegetation types of the Atlantic Forest: Dense ombrophilous lowland forest = 5-50 m; Dense submontane ombrophilous forest = 50-500 m; Dense ombrophilous montane forest = 500-1500 m. We included two additional vegetation types in the present study: Restinga forest, a forest formation growing on coastal sandy strands at elevations between 0-50 m, whose genesis, floristic composition, and structures are distinct from other Dense ombrophilous forests (César & Monteiro, 1995; Assis *et al.*, 2011); and Mountaintop forest, a type of cloud forest that occurs near the peaks of steep scarps in the Serra do Mar Range with shallow and rapidly draining soils (Micheletti Neto, 2007; Bertoncello, 2009).

Sampling and examination of collected materials

Samples of bryophyte were collected in 10 subplots (10 × 10 m) randomly distributed within each 1 ha forest plot, during the period between January/2009 and March/2011. Collections were undertaken in each subplot from all of the substrates colonized by bryophytes; 20 × 20 cm collection samples were taken from all available substrates (217 samples on tree trunks, 24 on leaves, 11 in soil, 0 on rocks and 37 on dead trunks in plot A; 173, 23, 5, 38 and 21 in plot B; 171, 6, 16, 30 and 30 in plot J; 188, 8, 7, 25, 25 in plot P; 148, 6, 6, 1 and 47 in plot N; and 95, 1, 60, 8 and 2 in plot Q respectively). The samples on the phorophytes were positioned from the tree base up to 2 m. All tree species were sampled. The collection, preparation, and preservation of the plant material followed Yano (1984). Identifications were based principally on the following literature: Heinrichs *et al.* (1988), Buck (1998), Reiner-Drehwald & Goda (2000), Gradstein *et al.* (2001), Gradstein & Costa (2003) and Vaz-Imbassahy *et al.* (2008).

The classification adopted follows that proposed by Crandall-Stotler *et al.* (2009) for the dDivision Marchantiophyta, by Goffinet *et al.* (2009) for the Division Bryophyta, and by Renzaglia *et al.* (2009) for the Division Anthocerotophyta. All the collected specimens were deposited in the Universidade Estadual de Campinas herbarium (UEC).

Data analyses

The characterizations of endemic species were based on data from the literature (Gradstein & Costa, 2003; Costa *et al.*, 2009a, 2009b; Costa & Peralta, 2015), considering as endemic those species that only occur in the Atlantic Forest. The endemism ratio was calculated by dividing the number of endemic species by the total species richness of a particular elevational belt. The Spearman coefficient was used to evaluate the correlations between endemism ratios and elevation, using the BioEstat 5.0 program (Ayres *et al.*, 2007). Mountaintop plots (characterized as outliers) were not considered in these analyses.

We evaluated the elevational distributions of the families by ordering the species richness of each family by elevational belt, using the Comunidata 1.5 program (Dias, 2006). In order to determine bryophyte beta diversity along the elevational gradient, a floristic matrix was prepared using the incidence data (presence/absence) of the species in the 60 subplots. Rare species (those that occurred in only a single sample) were eliminated (42 species) from the classification and ordination analyses to increase their efficiency. The final matrix therefore consisted of the data from the 60 subplots (samples) and the 211 bryophyte species (descriptors). Sørensen's index (Sørensen, 1948) was used to calculate floristic similarities. Classification analyses were subsequently performed using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) method run on Fitopac 2.1 software (Shepherd, 2010). The floristic matrix was submitted to Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980) using PCOrd 4.1 software (McCune & Mefford, 1999). The significance of the groups formed by UPGMA and DCA (data not shown) was tested using Multi-Response Permutation Procedures – MRPP (Mielke & Berry, 2007) in PCOrd 4.1 software (McCune & Mefford, 1999). MRPP is a robust, nonparametric method that uses the Sørensen similarity index to examine the null hypothesis that two or more predefined groups are of equal composition. The A index of the MRPP describes the homogeneity within the groups and can vary between zero and one, with A = 0 indicating that the heterogeneities within and between the groups are equal, while A = 1 signifies that all the members of each group are identical among themselves but different from the members of other groups (McCune & Grace, 2002).

To evaluate the influence of substrate availability on species composition, direct gradient analysis (Canonical Correspondence Analysis, CCA) was performed using Fitopac 2.1 software (Shepherd, 2010). Monte Carlo testing using 1000 permutations was used to evaluate the significance of the first two ordination axes. For that purpose, all of the substrates collected in the different subplots inventoried were considered. This substrate matrix was correlated with the matrix of species utilized in the classification and ordination analyses.

Indicator Species Analysis (ISA, Dufrêne & Legendre, 1997) was used to identify indicator species by assigning an indicator value (IndVal) to the species in each of the Atlantic Forest vegetation types. This method calculates an indicator value for each species according to a combination of their frequencies and relative abundances in each of the groups analyzed. The significance of the indicator value of each species was evaluated using Monte Carlo simulations with 1000 permutations to examine the null hypothesis that it does not have an indicator value. Indicator species were considered to be those that showed $p \leq 0.05$ and had indicator values (IndVal) ≥ 50. This analysis was performed in the PCOrd 4.1 software (McCune & Mefford, 1999).

The phytogeographical patterns of the taxa were characterized based on their global distributions, according to information available in the literature (Cabrera & Willink, 1980; Gradstein & Costa, 2003; Costa *et al.*, 2011). In the present study, "Cosmopolitan" phytogeographical distributions refer to taxa that occur on more than three continents, including extra-tropical sites.

Published data (*e.g.*, taxonomic revisions, floras, etc.) were used to identify the sexual systems: monoicous, dioicous, monoicous/dioicous and pseudo-autoicous (with male dwarf plants epiphytes in female plants, Luizi-Ponzo *et al.*, 2006) of the species encountered. The dioicous/monoicous ratios per elevational belt were calculated using linear regressions to correlate the types of sexual systems with altitude. The regressions were performed with and without the Mountaintop site samples (outliers), using the BioEstat 5.0 program (Ayres *et al.*, 2007).

RESULTS

Species richness

A total of 253 bryophyte species (150 liverworts, 102 mosses, and one hornwort) belonging to 138 genera and 50 families were encountered in the plots studied in the Serra do Mar State Park (Table 6 in Supplementary Material, doi/10.7872/cryb/v38.iss2.2017.Suppl.Mat.2). Species richness did not vary in relation to elevation and was lower in the Mountaintop forest (77 species) (Table 1). The species richness of liverworts was greater than that of mosses in all of the elevational belts, and greatest at elevations of 50 m, 400 m, and 950 m (66 taxa). Moss richness was highest in the Montane forests at 950 m (58 species) and 800 m (52) (Table 1). The rarefaction curves of the six elevational belts showed no apparent asymptotes, but did tend toward stabilization (Fig. 2). The rarefaction curves greatly overlap the belts located between 10 m and 800 m, indicating similar richness. A distinct curve was found for the Mountaintop belt (1170 m). The evenness of

Table 1. Elevational belts studied in Serra do Mar State Park, São Paulo, southeastern Brazil, with data of elevation, vegetation type, species richness and endemism

Plot	*A*	*B*	*J*	*P*	*N*	*Q*
Altitude (m)	10	50	400	800	950	1170
Vegetation type	Restinga forest	Lowland forest	Submontane forest	Montane forest	Montane forest	Mountaintop forest
Bryophyte species richness	109	112	113	112	124	77
Liverwort species richness	60	66	66	60	66	50
Moss species richness	49	46	47	52	58	27
Endemic bryophyte species	2	6	8	8	11	1
Percentage of endemic species	2	5	7	7	9	1

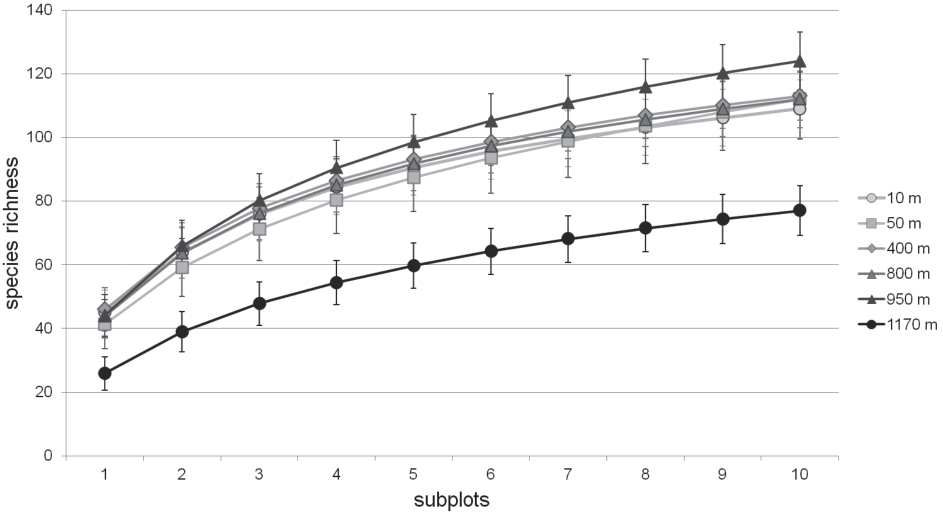

Fig. 2. Sample-based rarefaction curves for the elevational belts examined in the Serra do Mar State Park. The bars represent 95% confidence intervals.

bryophyte communities was similar within the elevational gradient (Fig. 3). The proportion of rare species (species found only once or twice in subplots in the elevational belt) was slightly greater at higher altitudes (950 m and 1170 m).

Endemism

Fourteen species endemic to the Atlantic Forest were encountered (Table 6 in Supplementary Material, doi/10.7872/cryb/v38.iss2.2017.Suppl.Mat.2). The endemism ratio demonstrated a positive correlation with elevation (Spearman's coefficient = 0.97; $p < 0.005$), with the peak of endemism occurring together with that of richness (Table 1).

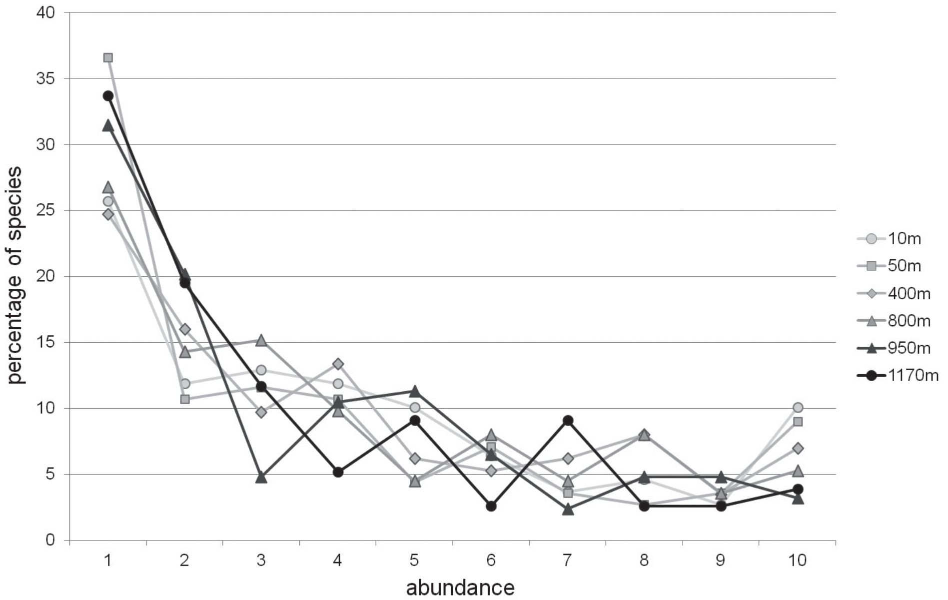

Fig. 3. Variations in the abundance (frequency based in replicated incidence data) of bryophyte species in the elevational belts examined in Serra do Mar State Park.

Floristic composition and beta diversity

Analyses of the occurrence of different families of bryophytes at the different elevational belts in the Atlantic Forest indicated that most families had wide distributions, occurring in at least three of the belts (Fig. 4). On the other hand, some families occurred exclusively in distinct belts, as for example Herbertaceae, Polytrichaceae, Scapaniaceae, and Sphagnaceae, which were restricted to the Mountaintop forest; Bartramiaceae, Jamesoniellaceae, and Trichocoleaceae occurred in at least two elevational belts of the Montane and Mountaintop forests.

The elevational belts studied shared many species and demonstrated floristic similarities generally greater than 50% (Table 2). Only the Mountaintop band demonstrated low similarity (< 35%) in relation to the other sites. Classification

Table 2. Comparison between bryophyte species richness in six elevational belts of the Atlantic Forest of Serra do Mar State Park. Bold = species richness per belt, normal font = number of species shared between the belts; italic = Sørensen similarity

Elevational belt (m)	*10*	*50*	*400*	*800*	*950*	*1170*
10	**109**	*0.62*	*0.59*	*0.52*	*0.53*	*0.29*
50	69	**112**	0.6	*0.59*	*0.53*	*0.23*
400	66	68	**113**	*0.69*	*0.56*	*0.23*
800	58	66	78	**112**	*0.67*	*0.31*
950	62	63	66	79	**124**	*0.33*
1170	27	22	22	29	33	**77**

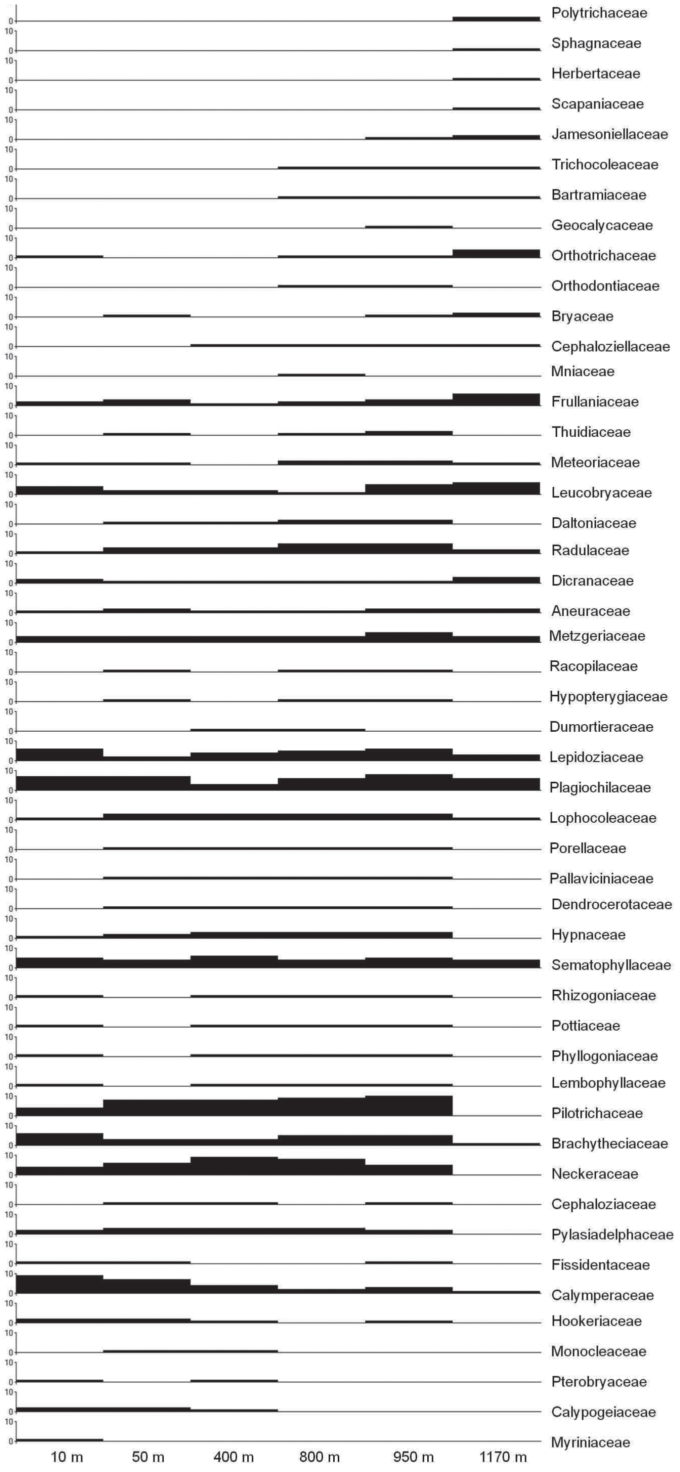

Fig. 4. Elevational distribution of bryophyte families (except Lejeuneaceae) in the Serra do Mar State Park. The width of the bars denotes the number of species per family.

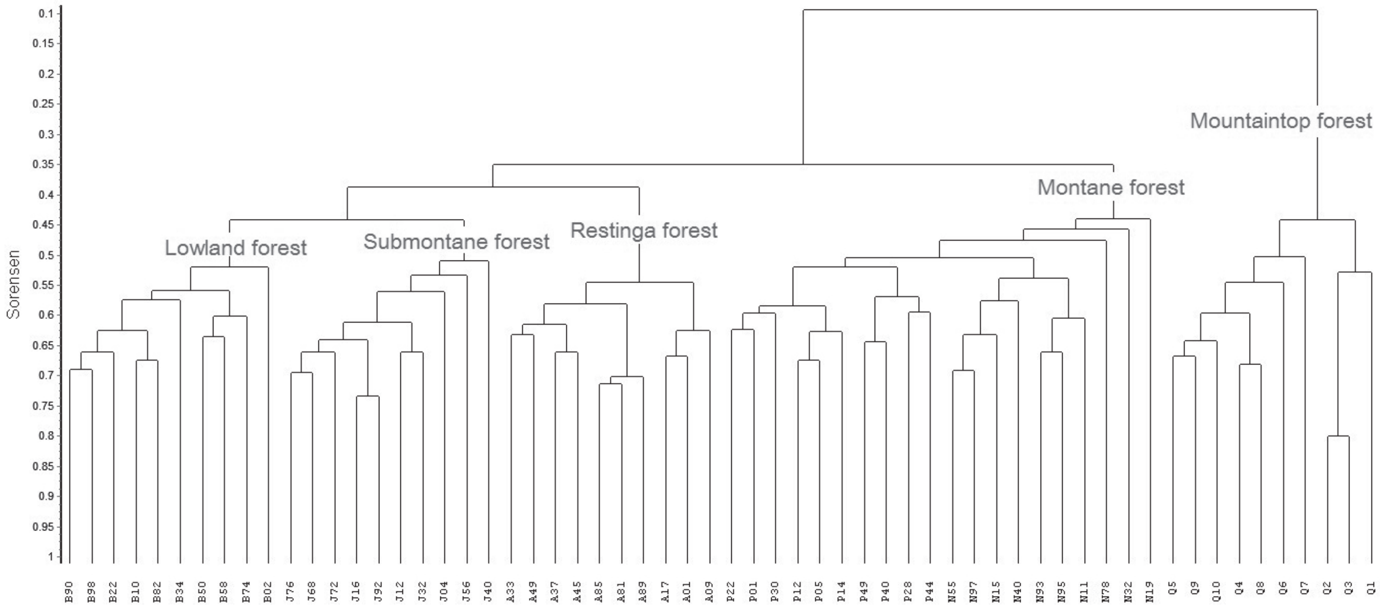

Fig. 5. Dendrogram that resulted from the cluster analyses using the Sørensen coefficient showing the patterns of similarity across elevations for the bryophyte communities.

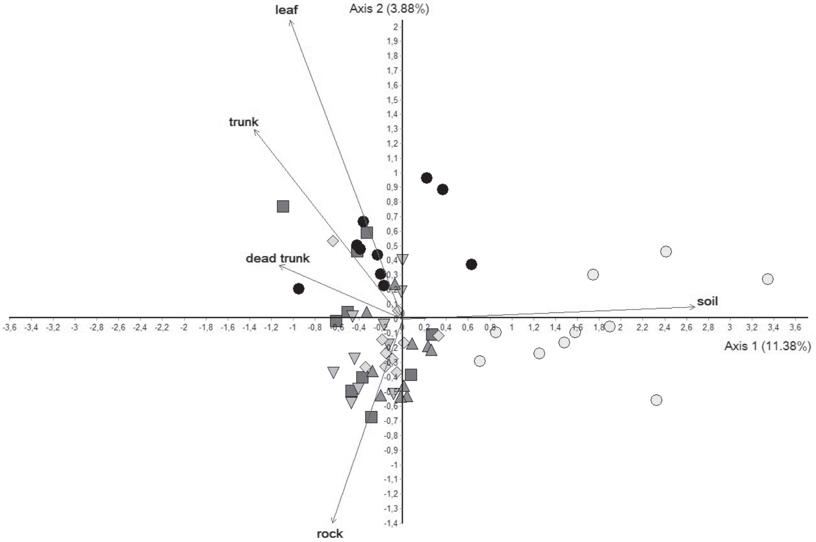

Fig. 6. Plot of two first axis of a Canonical Correspondence Analysis (CCA) of floristic and substrate matrices.

analyses using UPGMA (cophenetic correlation 0.91) indicated that the 10 subplots formed groups defined by Atlantic Forest vegetation types, with the two elevational belts of Montane forest (800 m in plot P and 950 m in plot N) grouping together (Fig. 5). Similar results were found using DCA (data not shown). These groupings are consistent and significant, as MRPP indicated that heterogeneity was greater between groups than within them ($A = 0.7$; $p < 0.001$). In terms of the influences of substrate availability on species compositions, the CCA (Fig. 6) demonstrated 15.2% of cumulative variance on the first two axes (Axis 1 = 11.38%, eigenvalue = 0.49 and Axis 2 = 3.9%; eigenvalue = 0.17). The Monte Carlo test was significant for those axes ($p = 0.001$). The soil (0.94) was the substrate most correlated with the first environmental axis (LC scores), where the Mountaintop subplots were grouped, while the Axis 2 was positively associated with the presence of leaves (0.72) and tree trunks (0.46), where the Restinga forests subplots were grouped, and negatively correlated with the presence of rocks (–0.49).

Thirty-one indicator species (IndVal ≥ 50; $p \leq 0.05$) were found in the groupings identified, *i.e.* vegetation types of Atlantic Forest (Table 3); the Mountaintop site demonstrated an especially high number of indicators (14 taxa).

Phytogeographical patterns

Parallel to changes in floristic compositions along the elevational gradient, there were variations in the phytogeographical patterns of the bryophytes, with a Neotropical pattern predominating in all of the elevational belts (Table 4). Pantropical and Tropical amphi-Atlantic (Afro-American) patterns stood out in Restinga forests, the Montane forests had high numbers of endemic species of Atlantic Forest, while the Mountaintop had many “Disjunct” patterns, as disjunctions between the high mountains of Central America, Andes and southeastern Brazil.

Table 3. Indicator species of bryophytes (IndVal ≥ 50) and p value from five vegetation types of Atlantic Forest in Serra do Mar State Park

Vegetation type	*Indicator species*	*Indicator value (IndVal)*	*P value*
Restinga forest	*Bazzania phyllobola*	90.9	0.001
	Leptolejeunea elliptica	85.3	0.001
	Cololejeunea obliqua	62.5	0.001
	Syrrhopodon incompletus	62.5	0.001
	Plagiochila disticha	54.1	0.001
	Harpalejeunea oxyphylla	50	0.001
Lowland forest	*Crossomitrium patrisiae*	66.7	0.001
Submontane forest	*Bryopteris filicina*	57.1	0.001
	Homalia glabella	57.1	0.001
	Ceratolejeunea rubiginosa	55.7	0.001
	Tortella sp.	51.6	0.001
	Homaliodendron piniforme	50.6	0.001
Montane forest	*Porotrichum longirostre*	90.9	0.001
	Radula nudicaulis	68.8	0.001
	Racopilum tomentosum	61.2	0.001
	Thamniopsis langsdorfii	53.3	0.001
	Bazzania stolonifera	50	0.003
Mountaintop forest	*Jamesoniella rubricaulis*	100	0.001
	Schlotheimia tecta	100	0.001
	Leucolejeunea xanthocarpa	80	0.001
	Frullania atrata	75.3	0.001
	Frullaniza kunzei	73.6	0.001
	Campylopus heterostachys	70	0.001
	Frullania apiculata	70	0.001
	Herbertus juniperoideus subsp. *bivittatus*	70	0.001
	Macromitrium cirrosum	70	0.001
	Plagiochila bifaria	65.3	0.001
	Camylopus griseus	60	0.001
	Campylopus pilifer	50	0.001
	Polytrichum juniperinum	50	0.002
	Schlotheimia jamesonii	50	0.001

Table 4. Phytogeographic pattern of bryophytes in the elevational belts of the Serra do Mar State Park, with their acronyms and taxa number

Phytogeographic pattern	*Acronym*	*Altitude (m)*					
		10	*50*	*400*	*800*	*950*	*1170*
Cosmopolitan (found at least in three continents)	Cos	5	8	3	7	9	6
Pantropical (wide tropical)	Pan	18	15	11	10	10	9
Tropical and subtropical America	TSA	3	2	2	3	4	2
Neotropical	Neo	63	68	72	65	67	44
Tropical amphi-Atlantic (disjunct between Africa and America)	Af-Am	14	10	11	11	11	2
Disjunct between the high mountains of Central America, Andes and southeastern Brazil	CAA	0	0	0	0	0	3
Southern temperate element (disjunct between temperate regions of southern hemisphere and south-eastern Brazil)	sT	0	1	1	1	1	0
Other disjunctions	Disj	0	1	1	1	1	4
Endemic of Brazil (not restricted to Atlantic Forest)	Bra	1	1	1	1	2	2
Atlantic element (restricted to Atlantic Forest)	Atl	2	6	8	8	11	1
Pattern not identified	Other	3	0	3	5	8	4

The Neotropical taxa, combined with those demonstrating wider distribution patterns (Tropical and subtropical American, Afro-American, Pantropical, and Cosmopolitan patterns, considered “Amply” distributed from here forward), comprised 94% of all the species in the Restinga forest (103 species), 92% in the Lowland (103), 87% in the Submontane (99), 86% in the 800 m Montane (96), 81% in the 950 m Montane (101), and 82% in the Mountaintop forest (63). As such, there was a negative correlation between elevation and the amplitude of geographical distributions (Spearman’s coefficient = –0.94; $p < 0.005$), with the greatest percentages of widely distributed species occurring at low altitudes.

Sexual systems

The dioicous condition predominated in all of the elevational belts (Table 5), although a tendency of diminishing degrees of dioicous with increasing altitude was confirmed using Linear Regression analysis ($R^2 = 0.59$; $p = 0.04$). The numbers of monoicous taxa, on the other hand, increased with altitude, with the exception of the Mountaintop forest. When this latter vegetation type was removed from analysis (as an outlier), there was an obvious positive correlation between the monoicous condition and altitude ($R^2 = 0.78$; $p = 0.03$). The data for the different phylum were considered together (liverwort + mosses + hornworts), but they demonstrated the same pattern when analyzed separately.

The dioicous/monoicous ratio of total bryophytes demonstrated a distribution in the form of an inverted parabola, with the highest values at the extremes of the gradient; this same result was seen with liverworts and mosses when considered separately (although the curve was more exaggerated for liverworts) (Fig. 7). Hornworts were not considered in these analyses as only a single species was encountered.

Table 5. Sexual system of bryophytes in the elevational belts of the Serra do Mar State Park

Sexual system	*Altitude (m)*					
	10	*50*	*400*	*800*	*950*	*1170*
Dioicous	86	82	80	74	79	59
Monoicous	20	27	28	32	38	10
Monoicous and dioicous	0	0	0	0	1	0
Pseudo-autoicous	2	0	0	1	1	7
Unknown	1	3	5	5	5	1
Sexual ratio (dioicous/monoicous)	4.3	3.04	2.86	2.31	2.08	5.9

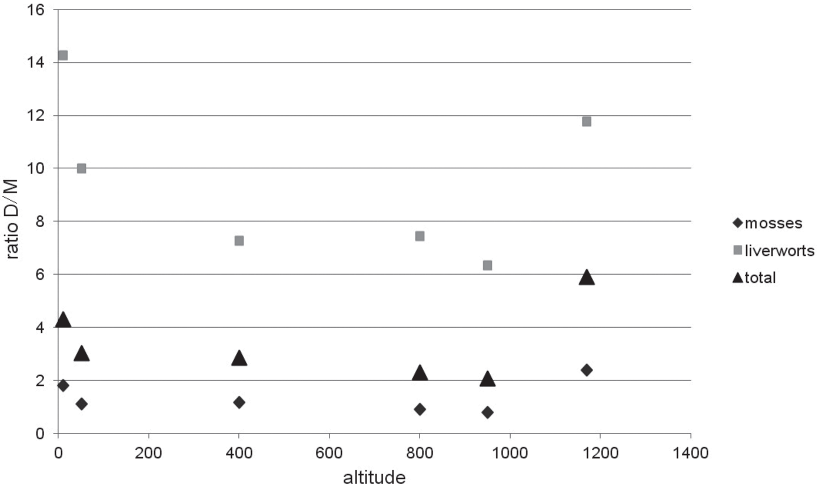

Fig. 7. Dioicous/monoicous ratio for total bryophyte community and for each phyllum separately (mosses and liverworts).

DISCUSSION

Bryophyte community attributes along the elevational gradient

The patterns of bryophyte species richness in the Serra do Mar study area differed from our original expectations of a peak of richness at mid-altitude, a pattern found for trees on this same mountain (Eisenlohr *et al.*, 2013) and for cryptogamic plants in tropical forests (Wolf, 1993; Grau *et al.*, 2007; Kessler *et al.*, 2011). The species richness did not vary significantly with elevation, but was higher in Montane forests (950 m), as had been observed in other studies in the Atlantic Forest (Costa & Lima, 2005; Santos & Costa, 2010b). In this region of the Atlantic Forest (*i.e.* Serra do Mar) bryophytes are greatly influenced by local abiotic conditions, such as small elevational variations, the mountainous topography, the occurrence of orographic rains, the high latitude, and by the strong influence of winds due to the close proximity of the sea. The importance of these intrinsic local characteristics became evident in analyses of the floristic affinities of liverworts in the Atlantic Forest (Santos *et al.*, 2014), with the areas of the Serra do Mar State Park grouping among themselves, with low similarity with other areas in southeastern Brazil. It is worth emphasizing that the processes that act on species distributions and define their species richness patterns include important ecological and historical filters, such as the local climatic regime and historical/biogeographical process (Sanders & Rahbek, 2012). The pattern of species richness observed in the present study reflect the “Massenerhebung” effect, which predicts that elevational belts in low mountains will be compressed (Grubb & Whitmore, 1966; Grubb, 1971), and the latitude effects, in which plants tend to shift toward lower elevations with increasing latitude (Frahm & Gradstein, 1991; Gradstein & Costa, 2003).

Rarity and high species richness are marked characteristics of tropical forests, and their species accumulation curves do not usually flatten (even with large sample sizes) (Schilling & Batista, 2008). This pattern was also found in our study, especially for the highest belts (950 m and 1170 m), where more than 50% of species are rare. Bryophyte species with restricted distributions (rare, endemics, or with disjunct distribution) are typical of Montane tropical forests (Gradstein, 1995; Santos & Costa, 2010a).

The peaks of endemism and species richness among the bryophytes in the area studied both occurred in the Montane forest (950 m), which did not confirm our initial expectations of a peak of endemism situated above the peak of richness in relation to the elevational gradient, as was reported by Kluge & Kessler (2006) and Kessler (2002a) for fern in Neotropical mountains and by Santos & Costa (2010a, 2010b) for liverworts in the Atlantic Forest of Rio de Janeiro. Favorable climatic conditions (high humidity and constant but moderate temperatures) are strictly linked to the high endemism seen in montane regions, as reported for angiosperms by Kruckeberg & Rabinovitz (1985). Climatic and biogeographical changes have supporting roles in the high ratios of fern endemism observed on mountain tops (Kluge & Kessler, 2006). Schuster (1983) likewise identified montane regions as biotic islands, as the plant species there occupy only small areas with small populations, and are naturally subject to environmental stress, genetic drift, and rapid evolution, which would all have been accentuated by the climatic fluctuations that occurred during the Pleistocene. As such, the present distributions of endemic bryophyte species might be related to historical processes (*e.g.*, climate change, refuge theory) and are currently influenced principally by the more amenable climatic conditions in montane regions (*e.g.*, low temperatures and high humidity). As was pointed out by Santos *et al.* (2011), the climatic conditions of lowland areas (low humidity, higher temperatures) probably restrict the establishment of the spores of endemic species. The spores of species showing restricted distributions (as is the case of endemic species) are generally less tolerant to the stresses involved in long-distance dispersal (e.g., desiccation and UV irradiation) than are species having transoceanic distributions (van Zanten & Pócs, 1981).

As temperature and forest structures are not homogeneous along this elevational gradient (see Alves *et al.*, 2010; Joly *et al.*, 2012), and bryophytes demonstrate deterministic distributions in the Atlantic Forest (Santos *et al.*, 2014), the bryophyte composition would be expected to be distinct in each elevational belt. However, the elevated numbers of shared species among the different elevational belts partially refuted the initial expectation of high beta diversity. The principal floristic transition zone in our study (similarity < 35%) was located at Mountaintop forest, while the other belts demonstrated floristic gradients along the slope in the

Serra do Mar Atlantic Forest, with many shared species of bryophytes, but also some that were exclusive and indicators to specific belts. The classification and ordination analyses showed major floristic similarities between subplots located in the same vegetation type (with 800 and 950 m forming a single group: Montane forest). The high similarities between the elevational belts on the mountain slope (the 50-950 m belts) reflected the types of available microhabitats within the forests studied (bark of trees and shrubs, dead woods, wet rocks, moist soils and leaving leaves), as well as spores capacity for long distance dispersal. The main floristic transition zone identified in our study, the Mountaintop located at 1170 m (Corcovado Peak), has few available microhabitats for bryophyte colonization (manly exposed soil and trunks and branches of shrubs). The high representativity of terrestrial bryophytes could explain the high beta diversity found in that area, although additional studies will still be necessary to better understand the relationships between substrate availability and beta diversity in tropical forests.

The Mountaintop of Corcovado Peak has strong floristic affinities with High Montane forests found in southeastern Brazil (Santos *et al.*, 2014). Similar result was found by Bertoncello *et al.* (2011) for the vascular flora located at 820-1277 m (Cuscuzeiro Peak) in the Serra do Mar State Park, with an abrupt change in floristic composition at 1120 m, above the Nebular forest, which is more similar to High Montane forests than to the coastal forests of southeastern and southern Brazil.

Species that demonstrate preferences for certain environmental conditions can be used as ecological indicators of vegetation types and/or of environmental change (Heink & Kowarick, 2010). Our analysis identified 31 bryophyte species (12% of the total) as indicators of groups formed by Atlantic Forest vegetation types in the Serra do Mar, with many species having high IndVal (≥ 70) that demonstrate their selective natures and the potential as bioindicators. Indicator species will react predictably and measurably to environmental alterations (Vanderpoorten & Goffinet, 2009) and can be used to monitor the effects of climate change on forests.

Bryophyte species attributes along the elevational gradient

As was expected, the species inhabiting lower altitude regions demonstrated more wide phytogeographical patterns than those found at higher altitudes, which corroborates the results of other surveys undertaken in the Atlantic Forest of southeastern Brazil (Santos & Costa, 2010a; Santos *et al.*, 2011). Different from angiosperms, endemic taxa of bryophytes and fern are relatively rare, while transoceanic taxa (e.g., Afro-American, Pantropical, and Cosmopolitan) are quite common (Schofield, 1992; Kessler, 2010). In the case of bryophytes, their wide ranges are considered to be the result of two principal biological and geographical processes: (1) historical patterns of vicariance and low evolutionary rates; and (2) long distance wind dispersal (as since they produce large quantities of small spores that are resistant to desiccation) (van Zanten & Pócs, 1981; Shaw, 2001). This second hypothesis has been corroborated by recent molecular data, indicating dispersal as the main cause of the intercontinental distribution ranges of bryophytes (Shaw *et al.*, 2003; Heinrichs *et al.*, 2009).

The existence of more dioicous than monoicous species in the survey area was expected, as most bryophytes are dioicous (Wyatt, 1982), with even greater proportions of pleurocarpic mosses (60%, Hedenäs & Bisang, 2011) and liverworts (67%, Wyatt, 1982), the main groups encountered in our survey. However, with respect to the relationships between the sexual systems and altitude, we encountered a pattern contrary to our expectations, and the premise that more humid environments would favor the occurrence of sexual reproduction with the occurrence of more dioicous species (as bryophytes require water for the masculine gamete to reach and fertilize the female gamete), was not confirmed because the proportions of dioicous species diminished with altitude; while monoicous species demonstrated the opposite tendency. The dioicous/monoicous ratio demonstrated greater values at the extremes of the gradient, where the environments were more stressful to bryophytes, whether due to high temperature conditions and annual flooding in the Restinga forest, or the high incidence of solar radiation and high wind (which increased the possibility of desiccation) in the Mountaintop forest site.

The external environment directly effects sexual expression in bryophytes and can impose strong selection pressures on the genes that control plant phenology (Glime, 2007). In addition to humidity gradients, tropical mountains demonstrate temperature gradients, as well as variations of the duration of the dry season and photoperiod that will have strong effects on bryophyte phenology (Stark, 2002; Glime, 2007; Maciel-Silva & Válio, 2011) and reproductive performance (Maciel-Silva *et al.*, 2012). As such, even dioicous species can maintain viable populations in stressful environments by expressing only one of the sexes and reproducing exclusively asexually (*e.g.*, by way of vegetative propagules), a successful strategy of tropical bryophytes (Maciel-Silva, 2016).

Additionally, asexual production of propagules is quite common among dioicous mosses, permitting the maintenance and growth of populations even when sexual reproduction is not possible (Longton, 1992); this pattern has not been confirmed for liverworts, however (Laaka-Lindberg, 2000). The occurrence of asexual reproduction is a strategy that allows dioicous plants to survive conditions (such as drying and freezing) that are unfavorable to fertilization processes (Longton, 1990). Another important factor is that even though both sexes may be represented in populations of dioicous species, feminine and masculine gametophytes may be spatially segregated, which would make sexual reproduction difficult even with local. Studies examining the sexual systems of angiosperms along elevational gradients have reported a number of different patterns, including increasing portions of dioicous species with altitude (Baker & Cox, 1984; Arroyo & Squeo, 1990), the existence of a unimodal curve for dioicous species (with a peak at mid-elevations), a negative association between altitude and the portions of monoicous species (Vamosi & Queenboroug, 2010), and greater self-pollination indices at higher elevations (Jacquemyn *et al.*, 2005). A better understanding of the patterns and mechanisms associated with the distributions of monoicous and dioicous species along tropical mountain gradients would increase our knowledge of species interactions and the functioning of those ecosystems. Is important to note that the reproductive biology of bryophytes is quite distinct from that of angiosperms, as bryophytes do not depend on pollinators or animal dispersal, so that the mechanisms that determine their species distributions along elevational gradients are principally influenced by abiotic variables (*i.e.* wind for dispersal and water for fertilization).

Our results show that environmental changes related to elevation alter the attributes of bryophyte communities and species, in spite of the fact that some of our hypotheses were not sustained. The present study represents the first systematic survey of bryophytes along an Atlantic Forest elevational gradient, and the analysis of their patterns of species distributions in this endangered ecosystem. Future studies directed toward elucidating historical factors and environmental filters that act (and have acted) upon bryophyte communities and species will be necessary in order to more fully understand the processes that shaped the patterns currently seen.

Bryophytes represent a viable tool for environmental monitoring and for gauging the effects of climatic change due to their rapid responses to fluctuations in the external environment (Tuba *et al.*, 2010). Studies investigating the influence of global warming on bryophyte communities have demonstrated that temperature increases have diminished species richness and altered the distributions of indicator species in cold environments (cryophilous), tending to expand their distributions to higher elevational areas (Gignac, 2001; Bergamini *et al.*, 2009). As such, data examining the richness and distributions of bryophyte species among the different vegetation types of Atlantic Forest should be useful in monitoring programs.

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REFERENCES

ALVES L.F., VIEIRA S.A., SCARANELLO M.A., CAMARGO P.B., SANTOS F.A.M., JOLY C.A. & MARTINELLI L.A., 2010 — Forest Structure and Live Aboveground Biomass Variation along an Elevational Gradient of Tropical Atlantic Moist Forest (Brazil). *Forest ecology and management* 260: 679-91.

ALVES L.F., ASSIS M.A., VAN MELIS J., BARROS A.L.S., VIEIRA S.A., MARTINS F.R., MARTINELLI L.A. & JOLY C.A., 2012 — Variation in liana abundance and biomass along an elevational gradient in the tropical Atlantic Forest (Brazil). *Ecological research* 27: 323-332.

ARROYO M.T.K. & SQUEO F.A., 1990 — Relationship between plant breeding systems and pollination. *In*: Kawano S. (ed.), *Biological approaches and evolutionary trends in plants.* London, Academic Press, pp. 205-227.

ASSIS M.A., PRATA E.M.B., PEDRONI F., SANCHEZ M., EISENLOHR P.V., MARTINS F.R., SANTOS F.A.M., TAMASHIRO J.Y., ALVES L.F., VIEIRA S.A., PICCOLO M.C., MARTINS S.C., CAMARGO P.B., CARMO J.B., SIMÕES E., MARTINELLI L.A. & JOLY C.A 2011 — Florestas de Restinga e de Terras Baixas na Planície Costeira do sudeste do Brasil: vegetação e heterogeneidade ambiental. *Biota neotropica* 11 (2): 103-121.

AYRES M., AYRES J.R.M., AYRES D.L. & SANTOS A.A., 2007 — *BIOESTAT – Aplicações estatísticas nas áreas das ciências biológicas e médicas.* Belém, ONG Mamiraua.

BADER M.Y., REICH T., WAGNER S., GONZÁLEZ GONZÁLEZ A.S. & ZOTZ G., 2013 — Differences in desiccation tolerance do not explain altitudinal distribution patterns of tropical bryophytes. *Journal of bryology* 35: 47-56.

BAKER H.G. & COX P.A., 1984 — Further thoughts on dioecismand islands. *Annals of the Missouri botanical garden* 71: 244-253.

BERGAMINI A., UNGRICHT S. & HOFMANN H., 2009 — An elevational shift of cryophilous bryophytes in the last century–an effect of climate warming? *Diversity & distribution* 15: 871-879.

BERTONCELLO R., 2009 — *A vegetação arbórea em um gradiente altitudinal no Morro do Cuscuzeiro, Ubatuba (SP): uma análise florística, fitossociológica e fitogeográfica.* Dissertation thesis. Campinas, Universidade Estadual de Campinas.

BERTONCELLO R., YAMAMOTO K., MEIRELES L.D. & SHEPHERD G.J., 2011 — A phytogeographic analysis of cloud forests and other forest subtypes amidst the Atlantic forests in south and southeast Brazil. *Biodiversity and conservation* 20: 3413-3433.

BUCK W.R., 1998 — Pleurocarpous mosses of the West Indies. *Memoires New York botanical garden* 82: 1-400.

CABRERA A.L. & WILLINK A., 1980 — *Biogeografia de América Latina*. 2ª edición corregida. Monografía 13, Serie de Biología. Washington DC, Secretaría General de La Organización de los Estados Americanos.

CÉSAR O. & MONTEIRO R., 1995 — Florística e fitossociologia de uma floresta de restinga em Picinguaba (Parque Estadual da Serra do Mar), Município de Ubatuba/SP. *Naturalia* 20: 89-105.

COLWELL R.K. & LEES D.C., 2000 — The mid–domain effect: geometric constraints on the geography of species richness. *Trends in ecology and evolution* 15: 70-76.

COSTA D.P. & LIMA F.M., 2005 — Moss diversity in the tropical rainforest of Rio de Janeiro, Southeastern Brazil. *Revista Brasileira de botânica* 28: 671-685.

COSTA D.P., SANTOS N.D., IMBASSAHY C.A.A. & LOPES D.J., 2009a — Briófitas – Hepáticas. *In*: Stehmann J.R., Forzza R.C., Salino A., Sobral L.M., Costa D.P. & Kamino L.H.Y. (eds), *Plantas da Floresta Atlântica*. Rio de Janeiro, Jardim Botânico do Rio de Janeiro, pp. 43-56.

COSTA D.P., PÔRTO K.C., LUIZI-PONZO A.P., ILKIU-BORGES A.L., BASTOS C.J.P., CÂMARA P.E.A.S., BÔAS-BASTOS S.V., VAZ-IMBASSAHY T.F., IMBASSAHY C.A.A. & LOPES D.J., 2009b — Briófitas – Musgos. *In*: Stehmann J.R., Forzza R.C., Salino A., Sobral L.M., Costa D.P. & Kamino L.H.Y. (eds), *Plantas da Floresta Atlântica*. Rio de Janeiro, Jardim Botânico do Rio de Janeiro, pp. 57-80.

COSTA D.P., PÔRTO K.C., LUIZI-PONZO A.P., ILKIU-BORGES A.L., BASTOS C.J.P., CÂMARA P.E.A.S., PERALTA D.F., VILAS BÔAS-BASTOS S.B.V., IMBASSAHY C.A.A., HENRIQUES D.K., GOMES H.C.S., ROCHA L.M., SANTOS N.D., SIVIERO T.S., VAZ-IMBASSAHY T.F. & CHURCHILL S.P., 2011 — Synopsis of the Brazilian moss flora: checklist, distribution and conservation. *Nova Hedwigia* 93: 277-334.

COSTA D.P. & PERALTA D.F., 2015 — Bryophytes diversity in Brazil. *Rodriguésia* 66: 1063-1071.

CRANDALL-STOTLER B., STOTLER R.E. & LONG D.G., 2009 — Morphology and classification of the Marchantiophyta. *In*: Goffinet B. & Shaw A.J. (eds), *Bryophyte Biology* 2nd ed. New York, Cambridge University Press, pp. 1-54.

DIAS R.L., 2006 — *Comunidata v 1.5*. Manaus, Amazonas, Brazil.

DUFRÊNE M. & LEGENDRE P., 1997 — Species assemblages and indicator species: the need for flexible asymmetrical approach. *Ecological monographs* 67: 345-366.

EISENLOHR P.V., ALVES L.F., BERNACCI L.C., PADGURSCHI M.C.G., TORRES R.B., PRATA E.M.B, SANTOS F.A.M., ASSIS M.A., RAMOS E., ROCHELLE A.L.C., MARTINS F.R., CAMPOS M.C.R., PEDRONI F., SANCHEZ M., PEREIRA L.S., VIEIRA S.A., GOMES J.A.M.A., TAMASHIRO J.Y., SCARANELLO M.A.S., CARON C.J. & JOLY C.A., 2013 — Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. *Biodiversity and conservation* 22: 2767-2783.

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

FRAHM J.-P., 2001 — *Biologie der Moose.* Heidelberg, Berlin, Spektrum Akademischer Verlag.

GINAC L.D., 2001 — Bryophytes as indicators of climate change. *The bryologist* 104: 410-420.

GIVNISH T.J., 1999 — On the causes of gradients in tropical tree diversity. *Journal of ecology* 87: 193-210.

GLIME J.M., 2007 — *Bryophyte Ecology. Volume 1. Physiological Ecology.* Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at http://www.bryoecol.mtu.edu/. Accessed 20 July 2011.

GOFFINET B., BUCK W.R. & SHAW A.J., 2009 — Morphology and classification of the Bryophyta. *In*: Goffinet B. & Shaw A.J. (eds), *Bryophyte Biology 2nd ed.*, New York, Cambridge University Press, pp. 55-138.

GRADSTEIN S.R., VAN REENEN G.B.A. & GRIFFIN III D., 1989 — Species richness and origin of the bryophyte flora of the Colombian Andes. *Acta botanica Neerlandica* 38: 439-448.

GRADSTEIN S.R., 1995 — Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. *In*: Churchill S.P., Balslev H., Forero E. & Luteyn J.L. (eds), *Biodiversity and conservation of the neotropical montane forest*. New York, 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: 1-336.

GRAU O., GRYTNES J.A. & BIRKS H.J.B., 2007 — A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of biogeography* 34: 1907-1915.

GRUBB P.J. & WHITMORE T.C., 1966 — A comparison of montane and lowland rain forests in Equador. II. The climate and its effects on the distribution and physiognomy of the forests. *Journal of ecology* 54: 303-333.

GRUBB P.J., 1971 — Interpretation of the 'Massenerhebung' Effect on Tropical Mountains. *Nature* 229: 44-45.

HEDENÄS L. & BISANG I., 2011 — The overlooked dwarf males in mosses – Unique among green land plants. *Perspectives in plant ecology, evolution and systematics* 13: 121-135.

HEINK U. & KOWARICK I., 2010 — What are indicators? On the definition of indicators in ecology and environmental planning. *Ecological indicators* 10: 548-598.

HEINRICHS J., GRADSTEIN S.R. & GROLLE R., 1988 — A revision of the neotropical species of *Plagiochila* (Dumort.) Dumort. (Hepaticae) described by Olof Swartz. *Journal of the Hattori botanical laboratory* 85: 1-32.

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

HEMP A., 2006 — Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant ecology* 184: 27-42.

HILL M.O. & GAUCH H.G., 1980 — Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.

JACQUEMYN H., MICHENEAU C., ROBERTS D. & PAILLER T., 2005 — Elevational gradients of species diversity, breeding system and floral traits of orchid species on Réunion Island. *Journal of biogeography* 32: 1751-1761.

JOLY C.A., ASSIS M.A., BERNACCI L.C. TAMASHIRO J.Y, CAMPOS M.C.R., GOMES J.A.M.A., LACERDA M.S., SANTOS F.A.M., PEDRONI F., PEREIRA L.S., PADGURSCHI M.C.G., PRATA E.M.B., RAMOS E., TORRES R.B., ROCHELLE A., MARTINS F.R, ALVES L.F., VIEIRA S.A., MARTINELLI L.A., CAMARGO P.B., AIDAR M.P.M., EISENLOHR P.V., SIMÕES E., VILLANI J.P. & BELINELLO R., 2012 — Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. *Biota neotropica* 12(1): 123-145.

KESSLER M., 2000a — Altitudinal zonation of Andean cryptogam communities. *Journal of biogeography* 27: 275-282.

KESSLER M., 2000b — Elevational gradients in species richness and endemism of selected plant groups in Central Bolivian Andes. *Plant ecology* 149: 181-193.

KESSLER M., 2002a — The elevational gradient of Andean plant endemism, varying influences of taxon–specific traits and topography at different taxonomic levels. *Journal of biogeography* 29: 1159-1166.

KESSLER M., 2002b — Range size and its ecological correlates among the pteridophytes of Carrasco National Park, Bolivia. *Global ecology and biogeography* 11: 89-102.

KESSLER M., 2010 — Biogeography of ferns. *In*: Mehltreter K., Walker L. & Sharpe J.M. (eds), *Fern Ecology.* New York, Cambridge University Press, pp. 22-60.

KESSLER M., KLUGE J., HEMP A. & OHLEMÜLLER R., 2011 — A global comparative analysis of elevational species richness patterns of ferns. *Global ecology and biogeography* 20: 868-880.

KLUGE J. & KESSLER M., 2006 — Fern endemism and its correlates: contribution from an elevational transect in Costa Rica. *Diversity and distributions* 12: 535-545.

KLUGE J., KESSLER M. & DUNN R., 2006 — What drives elevational patterns of diversity? A test of geometric constraints, climate, and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global ecology and biogeography* 15: 358-371.

KÖRNER C., 2007 — The use of 'altitude' in ecological research. *Trends in ecology and evolution* 22: 569-574.

KOTTEK M., GRIESER J., BECK C., RUDOLF B. & RUBEL F., 2006 — World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15: 259-263.

KRUCKEBERG A.R. & RABINOVITZ D., 1985 — Biological aspects of endemism in higher plants. *Annual review of ecology and systematics* 16: 447-479.

LAAKA-LINDBERG S., 2000 — Ecology of Asexual Reproduction in Hepatics. E–thesis. University of Helsinki. Available at http://ethesis.helsinki.fi/julkaisut/mat/ekolo/vk/laaka-lindberg/ecologyo.pdf. Accessed 10 July 2015.

LONGTON R.E., 1990 — Sexual reproduction in bryophytes in relation to physical factors of the environment. *In*: Chopra R.N. & Bhatla S.C. (eds), *Bryophyte Development: Physiology and Biochemistry*. Boca Raton, CRC Press, pp. 139-166.

LONGTON R.E., 1992 — Reproduction and rarity in British mosses. *Biological conservation* 59: 89-98.

LUIZI-PONZO A.P., BASTOS C.J.P., COSTA D.P., PÔRTO K.C., CÂMARA P.E., LISBOA R.C.L. & VILAS BOAS-BASTOS S., 2006 — *Glossarium polyglotum bryologiae: versão brasileira do glossário briológico*. Juiz de Fora, Editora da UFJF.

MACHAC A., JANDA M., DUNN R.R. & SANDERS N.T., 2011 — Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography* 34: 364-371.

MACIEL-SILVA A.S. & VÁLIO I.F.M., 2011 — Reproductive phenology of bryophytes in tropical rain forests: the sexes never sleep. *The bryologist* 114: 708-719.

MACIEL-SILVA A.S., VÁLIO I.F.M. & RYDIN H., 2012 — Altitude affects the reproductive performance in monoicous and dioicous bryophytes: examples from a Brazilian Atlantic rainforest. *AoB Plants* pls016. Available at: http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3401027. Accessed 05 October 2016.

MACIEL-SILVA A.S., 2016 — Asexual regeneration and its implications for local bryophyte establishment in a Brazilian tropical rain forest. *Botany* (online first). Available at: http://www.nrcresearchpress.com.sci-hub.cc/doi/abs/10.1139/cjb-2016-0114. Accessed 05 October 2016.

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

MCCUNE B. & GRACE J.B., 2002 — *Analysis of Ecological Communities*. Oregon, MJM Press.

MIELKE P.W. & BERRY K.J., 2007 — *Permutation Methods: a distance function approach.* 2nd ed., New York, Springer-Verlag.

MORELLATO L.P.C., TALORA D.C., TAKAHASHI A., BENCKE C.C., ROMERA E.C. & ZIPPARRO V.B., 2000 — Phenology of Atlantic Rain Forest trees: a comparative study. *Biotropica* 32: 811-823.

MICHELETTI NETO J.C.M.T., 2007 — Relações florísticas, estruturais e ecológicas entre as florestas do topo da Serra do Mar e as florestas de restinga do estado de São Paulo. Dissertation thesis. São Paulo, Universidade de São Paulo.

PADGURSCHI M.C.G., PEREIRA L.P., TAMASHIRO J.Y. & JOLY C.A., 2011 — Composição e similaridade florística entre duas áreas de Floresta Atlântica Montana, São Paulo, Brasil. *Biota neotropica* 11(2): 139-152.

PÓCS T., 1982 — Tropical Forest Bryophytes. *In*: Smith A.J.E. (ed.), *Bryophyte Ecology*. London, New York, Chapman and Hall, pp. 59-103.

RAHBEK C., 1995 — The elevational gradient of species richness: a uniform pattern. *Ecography* 18: 200-205.

REINER-DREHWALD M.E. & GODA A., 2000 — Revision of the genus *Crossotolejeunea* (Lejeuneaceae, Hepaticae). *Journal of the Hattori botanical laboratory* 89: 1-54.

RENZAGLIA K.S., VILLAREAL J.C. & DUFF R.J., 2009 — New insights into morphology, anatomy, and systematic of hornworts. *In*: Goffinet B. & Shaw A.J. (eds), *Bryophyte Biology 2nd ed.*, New York, Cambridge, University Press, pp. 139-171.

RICHARDS P.W., 1984 — The Ecology of Tropical Forest Bryophytes. *In*: Schuster R.M. (ed.), *New Manual of Bryology*. Nichinan, The Hattori Botanical Laboratory, pp. 1233-1270.

ROCHELLE A.L.C., CIELO–FILHO R. & MARTINS F.R., 2011 — Florística e estrutura de um trecho de Floresta Ombrófila Densa Atlântica Submontana no Parque Estadual da Serra do Mar, em Ubatuba/SP, Brasil. *Biota neotropica* 11(2): 337-346.

SANDERS N.J. & RAHBEK C., 2012 — The patterns and causes of elevational diversity gradients. *Ecography* 35: 1-3.

SANTOS N.D. & COSTA D.P., 2010a — Phytogeography of the liverwort flora of the Atlantic Forest of southeastern Brazil. *Journal of bryology* 32: 9-22.

SANTOS N.D. & COSTA D.P., 2010b — Altitudinal zonation of liverworts in the Atlantic Forest, Southeastern Brazil. *The bryologist* 113: 631-645.

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

SANTOS N.D., 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.

SCHILLING A.C. & BATISTA J.L.F., 2008 — Curva de acumulação e suficiência amostral em florestas tropicais. *Revista Brasileira de botânica* 31: 179-187.

SCHOFIELD W.B., 1992 — Bryophyte distribution patterns. *In*: Bates J.W. & Farmer A.M. (eds), *Bryophytes and lichens in a changing environment.* Oxford, Clarendon Press, pp. 103-130.

SCHUSTER R.M., 1983 — Phytogeography of bryophytes. *In*: Schuster R.M. (ed.). *New Manual of Bryology*. Nichinan, The Hattori Botanical Laboratory, pp. 463-626.

SENTELHAS P.C., PEREIRA A.R., MARIN F.R., ANGELOCCI L.R., ALFONSI R.R., CARAMORI P.H. & SWART S., 1999 — Balanços Hídricos Climatológicos do Brasil - 500 balanços hídricos de localidades brasileiras. ESALQ, Piracicaba. Available at: http://www.bdclima.cnpm.embrapa.br/index.php. Accessed 12 April 2014.

SHAW A.J., 2001 — Biogeographic patterns and cryptic speciation in bryophytes. *Journal of biogeography* 28: 253-261.

SHAW A.J., WERNER O. & ROS R.M., 2003 — Intercontinental Mediterranean disjunct mosses: morphological and molecular patterns. *American journal of botany* 90: 540-550.

SHEPHERD G.J., 2010 — *FITOPAC 2.1. Manual do Usuário*. Campinas, Departamento de Botânica, Universidade Estadual de Campinas.

SØRENSEN T.A., 1948 — A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Kongelige danske videnskabernes selskab* 5: 1-34.

STARK L.R., 2002 — Phenology and its repercussions on the reproductive ecology of mosses. *The bryologist* 105: 204-218.

STEVENS G.C., 1992 — The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude. *The American midland naturalist* 140: 893-911.

TUBA Z., SLACK N.G. & STARK L.R., 2010 — *Bryophyte Ecology and Climate Change*. New York, Cambridge Press.

TURETSKY M., 2003 — The Role of Bryophytes in Carbon and Nitrogen Cycling. *The bryologist* 106: 395-409.

VAMOSI S.M. & QUEENBOROUGH S.A., 2010 — Breeding systems and phylogenetic diversity of seed plants along a large–scale elevational gradient. *Journal of biogeography* 37: 465-476.

VAN ZANTEN B.O. & PÓCS T., 1981 — Distribution and dispersal of Bryophytes. *Advances in bryology* 1: 479-562.

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

VAZ-IMBASSAHY T.F., IMBASSAHY C.A.A. & COSTA D.P., 2008 — Sinopse de Pilotrichaceae (Bryophyta) no Brasil. *Rodriguésia* 59: 765-797.

VÁZQUEZ G.A. & GIVNISH T.J., 1998 — Altitudinal gradients in tropical forest composition structure, and diversity in the Sierra de Manantlán. *Journal of ecology* 96: 999-1020.

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, IBGE.

WAGNER S., ZOTZ G., SALAZAR-ALLEN N. & BADER M.Y., 2012 — Altitudinal changes in temperature responses of net photosynthesis and dark respiration in tropical bryophytes. *Annals of botany* 111: 455-465.

WHITMORE T.C., 1990 — *An introduction to tropical rain forests*. Oxford, Oxford University Press.

WOLF J.H.D., 1993 — Diversity patterns and biomass of epiphytes bryophytes and lichens along an altitudinal gradient in the Northern Andes. *Annals of the Missouri botanical garden* 80: 928-960.

WYATT R., 1982 — Population ecology of bryophytes. *Journal of the Hattori botanical laboratory* 52: 179-198.

YANO O., 1984 — Briófitas. *In*: Fidalgo O. & Bononi V.L.R. (eds.), *Técnicas de coleta, preservação e herborização de material botânico*. São Paulo, Instituto de Botânica, pp. 27-30.