Biodivers Conserv (2015) 24:2199–2212
DOI 10.1007/s10531-015-0979-4

ORIGINAL PAPER

Bryoflora of the Itatiaia National Park along an elevation gradient: diversity and conservation

Denise Pinheiro da Costa[1] · Nivea Dias dos Santos[2] · Maria Alice de Rezende[1] · William R. Buck[3] · Alfons Schäfer-Verwimp[4]

Received: 24 October 2014 / Revised: 3 August 2015 / Accepted: 10 August 2015 / Published online: 19 August 2015

Abstract (Bryoflora of the Itatiaia National Park along an elevational gradient: diversity and conservation). Itatiaia National Park harbors a unique bryoflora due to presence of different forest formations and well-defined climatic and vegetation bands: Montane Forest, Upper Montane Forest, and High-Altitude Fields (*Campos de Altitude*). Analysis of bryophyte diversity was undertaken to elucidate the richness and floristic composition of the different Atlantic Forest formations and to investigate the influence of elevation gradients on the bryoflora. Data from literature, herbarium samples, and data banks of the state's flora were consulted. Ten representative elevations were examined. The bryophyte diversity was high, comprising 519 taxa in 213 genera and 81 families (57 % of the total bryophyte flora known to Rio de Janeiro State, and 34 % of the Brazilian bryoflora). Bryoflora distribution was not uniform, showing differences in both species richness and floristic composition along an elevation gradient. The Montane Forest had the highest species richness (296), and numbers of exclusive taxa (172) and the Upper Montane Forest had more endemics species (47), which could be explained by its diversity of climatic, edaphic, and physiographic parameters. The 15 families with 59 % of the total number of species are also among the most species-rich families found in tropical America inventories. The species richness of mosses and liverworts reached their peaks at the mid-

Communicated by Jefferson Prado, Pedro V. Eisenlohr and Ary T. de Oliveira-Filho.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-015-0979-4) contains supplementary material, which is available to authorized users.

✉ Denise Pinheiro da Costa
denisepinheirodacosta@gmail.com; dcosta@jbrj.gov.br

1 Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão 915, Rio de Janeiro, RJ 22460-030, Brazil

2 Departamento de Botânica, Centro de Ciências Biológicas, Cidade Universitária, Universidade Federal de Pernambuco, Recife 50670-901, Brazil

3 Institute of Systematic Botany, New York Botanical Garden, Bronx, NY 10458-5126, USA

4 Mittlere Leiten 11, 88634 Herdwangen-Schönach, Germany

altitudinal range (2100–2200 m). The numbers of threatened species increased along the elevation gradient. These results emphasize the importance of the Atlantic Forest in southeastern Brazil to the conservation of bryophyte diversity, as well as the need to give priority to the protection of Upper Montane Forests and High-Altitude Fields.

Keywords Species richness · Endemism · Elevation gradient · Tropical rainforest · Southeastern Brazil · Itatiaia National Park

Introduction

Tropical rainforests harbor the richest bryofloras in the world due to their structural complexities and the diversities of their microhabitats (Pócs 1982; Gradstein 1995). The Atlantic Forest extends further inland in the southeastern region of Brazil, where the mountains can reach 2787 m in Itatiaia (Rio de Janeiro State) and 2890 m on the Pico da Bandeira (Minas Gerais State). The original vegetation of this region was tropical rainforest, with small enclaves of *Araucaria* forest at higher altitudes and shrubby vegetation covering lower inland areas. The soils associated with the eastern Atlantic Forest are principally yellowish-red latosols with clayey textures. They occur on half of the Orange Mountains as well as in the watersheds of the principal hydrographic basins. Yellowish-red clayey podzols occur along the valleys in areas with more pronounced dry seasons (Fundação SOS Mata Atlântica 2002; Leitão-Filho 1993). The Atlantic Forest is the most important ecosystem in Rio de Janeiro State, with its remnants covering 19 % of the total area of that state (Fundação SOS Mata Atlântica 2002)—and although exposed to severe anthropogenic pressures, the forest still maintains considerable bryophyte richness (Gradstein and Costa 2003; Costa et al. 2011; Costa and Lima 2005; Santos 2008; Santos and Costa 2010a; Costa 2013).

Bryophytes (hornworts, liverworts, and mosses) are sensitive to environmental changes (due to their poikilohydric nature) and can be used as bioindicators of local environmental and microclimatic conditions (Vanderpoorten and Goffinet 2009). Bryophyte diversity in tropical rainforests varies considerably with elevation, in terms of both its structure and floristic composition, with different taxa being characteristic of different elevation belts (Ah-Peng et al. 2012; Chantanorrapint 2010; Frahm and Gradstein 1991; Gradstein 1995; Gradstein et al. 2001; Grau et al. 2007; Gyrtnes et al. 2006; Pócs 1994; Wolf 1993). Climatic variations, the types of substrates available, and latitude, whoever, can alter the elevation limits of these belts in different regions (Frahm and Gradstein 1991; Gradstein et al. 2001), and the low elevational occurrences of montane species in southeastern Brazil accompany the general lowering of the altitudinal belts of the rain forests in southeastern Brazil (Gradstein and Costa 2003).

Four previous studies have focused on the elevational zonation of bryophytes in southeastern Atlantic Forest areas of Brazil: Visnadi (1998)—in the Serra do Mar State Park in São Paulo state; Costa and Lima (2005)—with the mosses in Rio de Janeiro State; Santos and Costa (2010a)—analyzing the phytogeographic patterns of liverworts in Rio de Janeiro State; and Santos and Costa (2010b)—analyzing the elevational zonation of liverworts in Rio de Janeiro State. All of these studies focused on primary rain forest in southeastern Brazil like our study, examining elevational zonation as a contribution to the knowledge of bryophyte distributions in tropical forests and demonstrating that these plants respond to elevational gradient in terms of species richness, floristic composition, and phytogeographical patterns.

The Itatiaia National Park (INP), located in Rio de Janeiro State, is the most important bryoflora conservation area in Brazil, with high levels of diversity, endemism, and threatened species (Costa et al. 2005a, b; Costa and Lima 2005; Costa and Faria 2008; Costa and Santos 2009; Santos and Costa 2010a). The high peaks and open High-Altitude Fields (*Campos de Altitude*) formations of the INP likewise harbor the largest number of examples of Andean or temperate taxa disjunctions (Costa et al. 2003; Santos and Costa 2010a). Costa and Santos (2009) analyzed liverwort conservation in Rio de Janeiro State and found that 68 % of threatened species occurred in INP, with 38 species being found exclusively in that reserve. Despite the importance of the INP, information concerning its bryoflora is scattered among various floristic surveys and regional diagnostic treatments, and herbarium samples are distributed around the world.

Itatiaia means "many-pointed-rock" in the Amerindian Tupi dialect. The park was created by Federal Decree N° 1713 on June 14, 1937 IBDF (1982) to preserve part of the biological heritage of the Serra da Mantiqueira. The park is located in southeastern Brazil and covers an area of approximately 30,000 hectares (22°19′–22°45′S and 44°45′–44°50′W) between southwest Rio de Janeiro (the municipalities of Resende and Itatiaia) and southern Minas Gerais State (near the towns of Alagoa, Bocaina, and Itamonte). The following types of rocks are found there: gneiss, nepheline, syenite-foidite, quartz syenite, alkaline granite, brecha magma, sediments, and sediment alluvial colluviums (FBDS 2000). The land originally belonged to Irineu Evangelista de Souza, the Visconde de Mauá, but was acquired by the "Fazenda Federal" in 1908 to establish two colonial settlements. A Biological Station was constructed in 1929 and administered by the Rio de Janeiro Botanical Garden. The idea of the area becoming a national park originated with the botanist Alberto Loefgren in 1913, and the INP was finally created in 1937—the first National Park in Brazil.

Müller (1898) was the first to study the bryophytes of Itatiaia, publishing the "*Bryologia Serra Itatiaiae*" that described 154 species of mosses, of which 115 species and one genus were new to science. Dusén published "*Sur la Flore de la Serra do Itatiaya*" in 1903, in which Stephani considered the hepatics, citing 58 species (of which four were new to science). Warnstorf's (1911) treatment of the family Sphagnaceae cited 342 species worldwide, many of which were from Itatiaia. Recent papers that cited species from Itatiaia include: Schäfer-Verwimp and Vital (1989); Frahm (1991); Schäfer-Verwimp (1992); Yano (1992); Reese (1993); Schäfer-Verwimp and Giancotti (1993); Gradstein and Costa (2003); Costa and Lima (2005); Costa (2008); Santos and Costa (2010b).

We present here for the first time a complete inventory of the bryophytes found in the INP, one of the major Atlantic Forest remnants in southeastern Brazil, and analyze the influence of elevation gradients on the richness, floristic composition, and numbers of endemic and threatened species of this group. We also stress the need for priority in adequately protecting mountain environments in light of the probable role of global warming in accelerating their destruction.

Materials and methods

Study area

Itatiaia was the first National Park established in Brazil, in a region of Atlantic Rainforest in the "Serra da Mantiqueira" range in northwestern Rio de Janeiro State (22°19′–22°45′S and 44°45′–44°50′W); it comprises an area of approximately 30,000 ha. (Fig. 1). The elevations vary

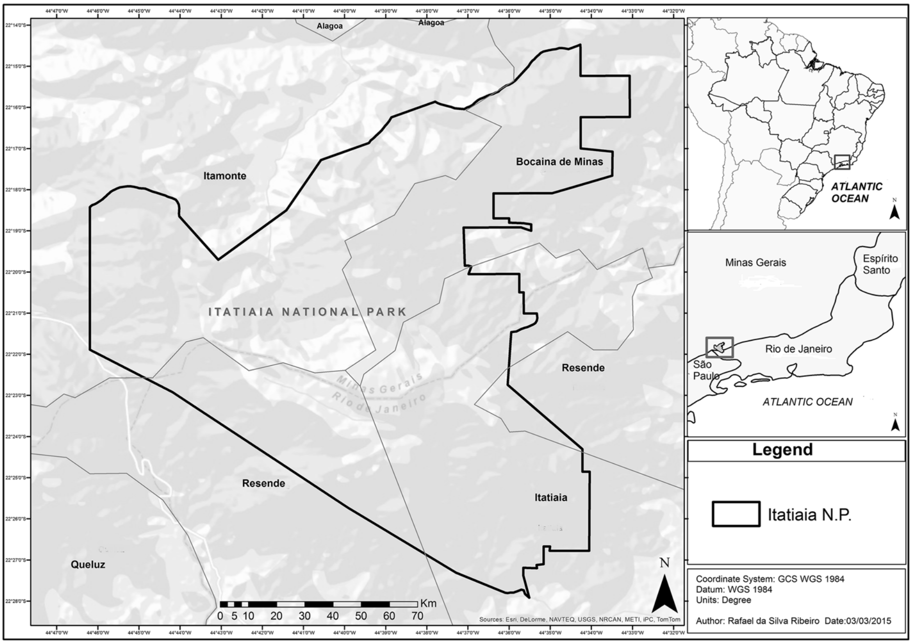

Fig. 1 Map illustrating the location of the Itatiaia National Park, Rio de Janeiro State, Brazil (source: Center for Scientific Computing and GIS-NCCG/JBRJ)

between 600 and 2787 meters above sea level, with the highest peaks reaching 2408 m (Cabeça do Leão), 2500 m (Dois Irmãos), and 2787 m (Pico do Itatiaiaçu). Air humidity averages 85 %. Local rainfall averages 2100 mm annually, the mean temperature is 11 °C, ranging from 6 °C to a maximum of 27 °C (Brade 1956; Hueck 1972; Pádua and Coimbra-Filho 1979).

Literature review and herbarium surveys

A review of the literature and complete surveys of specimens deposited in the Rio de Janeiro Botanical Garden (RB), the New York Botanical Garden (NY), and the Schäfer-Verwimp Herbarium (SV) were carried out. The classification of the phylum Marchantiophyta follows Crandall-Stotler et al. (2009) and that of the phylum Bryophyta follows Buck and Goffinet (2009).

Vegetation classification

The vegetation classification adopted here follows Veloso et al. (1991), and includes the vegetation types of Montane Forest = 500–1500 m, and Upper Montane Forest = >1500 m (the latter includes High-Altitude Fields—open, humid formations dominated by grasses and occurring above 2300 m) (Safford 1999).

Dataset

The floristic data used here was derived from published articles (Costa and Lima 2005; Lüth and Schäfer-Verwimp 2004; Schäfer-Verwimp 1992; Schäfer-Verwimp and Giancotti

1993; Schäfer-Verwimp and Vital 1989; Santos and Costa 2010a) and databases from floristic surveys undertaken by project team members (employing random sampling along trails and in forest areas during the years 1988–2012). These collections are deposited at NY, RB, and SP (G). Elevation data was obtained from the herbarium labels. We analyzed species richness as well as threatened and endemic species along an elevation gradient, considering elevation intervals of 100 m. Elevation belts of 200 m were used, however, to increase the accuracy of the similarity analysis, following Veloso et al. (1991): 600–800, 800–1000, 1000–1200, 1200–1500 m (Montane Forests), and 1500–1700, 1700–1900, 1900–2100, 2100–2300, 2300–2500, and 2500–2700 m (Upper Montane Forests).

Data analysis

The floristic matrix was submitted to outlier analyses and the samples with more than 2.0 standard deviations away from the mean were removed, and nonmetric multidimensional scaling ordination (NMDS) was subsequently applied using the Sørensen similarity coefficient. The ordination results were not modified when the rare species were not included in the calculations (those recorded in only a single elevation belt). We therefore chose to work with all of the taxa inventoried (230 liverworts and 289 mosses). Multiresponse permutation procedures (MRPP) were used to test whether a priori defined groups of samples (vegetation types) differed from those expected by chance. MRPP (Mielke and Berry 2007) is a nonparametric method that utilizes the Sørensen similarity coefficient to test the null hypothesis that two or more predefined groups have equal compositions. In this test, the A index describes the homogeneity within these groups (and varies from 0 to 1), where $A = 0$ signifies that the heterogeneities within and between the groups are equal; $A = 1$ signifies that all the members of each group are identical among themselves and different from members of the other groups (McCune and Grace 2002). All analyses were performed using PCOrd 4.1 software (McCune and Mefford 1999). The relationships between altitude and species richness and the numbers of endemic and threatened species were analyzed using regression models (generalized linear models—GLM), with Gaussian distribution. The species data were square-root transformed prior to statistical analyses (Zar 1999), conducted with R 3.1.2 software (R Development Core Team 2014).

Results

Species richness

The present study recognized 81 families, 213 genera, and 519 species of bryophytes in the INP (Supplementary Table S1). This represents 34 % of the total bryoflora of Brazil, and 58 % of the total bryoflora of Rio de Janeiro State (Table 1), demonstrating that the INP bryoflora is rich and well-studied as compared to other areas.

The 519 species of bryophytes included 289 mosses (135 genera and 51 families) and 230 liverworts (200 leafy liverworts and 30 thalloids, included in 78 genera and 30 families), with the total number of mosses being higher than liverworts (Supplementary Table S1).

The greatest bryophyte species richness was found in the Upper Montane Forest (Supplementary Fig. S1a) at 2100 m (145 taxa). The species richness of mosses was greater than that of liverworts in a majority of the elevation belts. Low species richness was

Table 1 Species richness of bryophytes in different regions of the world. The numbers in parentheses represent the percentages related to Itatiaia bryophytes

Area	Mosses	Liverworts	Reference
Itatiaia	289	230	This study
Rio de Janeiro state	519 (56 %)	370 (62 %)	Costa (2014), Costa and Peralta (2014)
Atlantic Forest	756 (38 %)	464 (50 %)	Costa (2009)
Brazil	878 (32 %)	638 (36 %)	Costa (2014), Costa and Peralta (2014)
Tropical America	2600 (11 %)	1350 (17 %)	Gradstein et al. (2001)
World	13000 (2 %)	5000 (5 %)	Gradstein et al. (2001)

observed between 1200 and 2000 m, which may indicate that few surveys were undertaken at this elevation zone in the park. Similar patterns were found for threatened species and endemism (Supplementary Fig. S1b, c).

The elevation distributions of mosses and liverworts are presented in Supplementary Table S1. Moss and liverwort richness were similar along the gradient that defined three vegetation types (Supplementary Fig. S1): Type 1—Montane Forest at 500–1500 m; Type 2—Upper Montane Forest at 1500–2300 m; and Type 3—High-Altitude Fields at 2300–2800 m. Moss and liverwort richness show a peak between 2100 and 2300 m, although bryophyte richness per elevation gradient was not uniform, with the Upper Montane Forest (1500–2300 m) having the highest species richness and numbers of exclusive and endemic taxa (Supplementary Fig. S1). Moss richness increased with altitude ($F_{1.19} = 4.4633$, $p = 0.048$), a pattern not observed with liverworts ($F_{1.19} = 0.2785$, $p = 0.6$).

The elevation zonation revealed significantly higher numbers of species with the upper elevational limits at 2000–2100 m and the lower elevational limits at 800–1000 m. In contrast, there were significantly lower numbers of species at the highest elevation (2500–2600 m) and at the very lowest (500–700 m) (Supplementary Fig. S1).

Floristic composition

In terms of total number of species, the most common moss families were Leucobryaceae (5 genera, 31 species), Sphagnaceae (1 genus, 24 species), Pilotrichaceae (9 genera, 19 species), Orthotrichaceae (5 genera, 19 species), Bryaceae (8 genera, 14 species), Pottiaceae (8 genera, 15 species), Fissidentaceae (1 genus, 13 species), and Sematophyllaceae (6 genera, 13 species), accounting for 29 % (148 species) of the total number of taxa. The most common liverwort families were Lejeuneaceae (29 genera, 71 species), Metzgeriaceae (1 genus, 16 species), Plagiochilaceae (1 genus, 16 species), Radulaceae (1 genus, 16 taxa), Lepidoziaceae (5 genera, 14 species), Frullaniaceae (1 genus, 13 species), and Lophocoleaceae (3 genera, 13 species)—accounting for 31 % (159 species) of the total number of taxa (Supplementary Table S1). These are also the principle bryophyte families encountered in floristic surveys in tropical forests (Gradstein and Pócs 1989). A total of 86 bryophyte species are endemic to Brazil (16 %), including 62 species of mosses and 24 liverworts. The richest genera are *Sphagnum* (24 species), *Metzgeria, Plagiochila* and *Radula* (16 species each), *Frullania* and *Fissidens* (13 species each).

Leafy liverworts showed the greatest species richness, with Lejeuneaceae being the best represented, with 70 species (30 % of the total number of liverwort species). Generic diversity was also high (213), with 52 % of the genera (112) being represented by only a single taxon. The most species rich liverwort genera occurring in the Montane Forest were: *Radula* (13 sp.); *Plagiochila* and *Metzgeria* (12 each); *Frullania* (10); *Lejeunea* (7); and *Bazzania* (5). In the Upper Montane Forest, the most species rich genera were: *Cololejeunea* (7 sp.); *Frullania* (9); *Syzygiella* (5); and *Riccardia* (4); some species, including those of the genera *Lejeunea*, *Frullania,* and *Plagiochila*, where present in all of the different forest forms. The following moss genera had the most species occurring in the Montane Forest: *Lepidopilum* and *Leucobryum* (5 sp. each) and *Sematophyllum* (4); and in the Upper Montane Forest: *Campylopus* and *Sphagnum* (21 sp. each); *Fissidens* (10); *Macromitrium* (9); and *Leptodontium* (6); *Lepidopilum* was exclusive to the Montane Forest (5 spp.).

Analyses of the occurrence of bryophyte families in different elevation belts in the INP indicated that most of them exhibited wide distributions, occurring in both Montane and Upper Montane Forests (Fig. 2). The main families occurring along the elevation gradient (with high species richness) included Leucobryaceae, Polytrichaceae, Sematophyllaceae, and Sphagnaceae for the mosses, and Frullaniaceae, Lejeuneaceae, Lepidoziaceae, and Plagiochilaceae for the liverworts. Some moss families, however, occurred exclusively in only one type of vegetation, as for example Amblystegiaceae, Andreaeaceae, Bruchiaceae, Calliergonaceae, Catagoniaceae, Ephemeraceae, Grimmiaceae, Hylocomiaceae, Plagiotheciaceae, Rhabdoweisiaceae, Seligeriaceae, Splachnaceae, and Symphyodontaceae—which were restricted to the Upper Montane Forest; Diphysciaceae, Helicophyllaceae, Leucomiaceae, Racopilaceae, and Rhizogoniaceae occur exclusively in the Montane Forest. Only Arnelliaceae, Chonecoleaceae, Gymnomitriaceae, and Jungermanniaceae, among the liverworts, were exclusive to the Upper Montane Forest; Dumortieraceae, Geocalycaceae, Fossombroniaceae, Monocleaceae, and Porellaceae occurred only in the Montane Forest.

Many of the families that had the highest species richness (Lejeuneaceae, Lepidoziaceae, Plagiochilaceae, Radulaceae, among others) significantly contributed to the diversity of the Montane Forest (Fig. 2), reinforcing the importance of these families to the bryoflora of tropical forests. Lejeuneaceae was the family with the greatest species richness in the three elevation belts, with its highest number of species in the Montane Forest (88 taxa), followed by Lepidoziaceae (19 species); Jungermanniaceae had the greatest species richness in the Upper Montane Forest (14 species). This analysis also demonstrated that some families (including Arnelliaceae, Chonecoleaceae, and Jungermanniaceae [liverworts], and Andreaeaceae, Bruchiaceae, Ephemeraceae, and Grimmiaceae [mosses]) were restricted to the Upper Montane Forest.

Bryoflora X vegetational types

Outlier analyses did not identify any elevation belt as being discrepant within the total set, therefore all samples were included in the analyses. A 2-dimensional representation was chosen by NMDS for mosses and liverworts. The bryophyte communities separated along NMDS axis 2, revealing distinctly different assemblages in the Montane and Upper Montane vegetation types (Fig. 3). This representation provided a stable solution and significantly reduced stress compared with the randomized data (for mosses, final stress = 8.18, final instability = 0.00006; for liverworts, final stress = 11.95, final instability = 0.00006). MRPP tests confirmed significant differences in the identities of the moss and liverwort species composing the Montane and Upper Montane forest vegetations along the elevation gradient in the INP (MRPP A = 0.18, P = 0.007 for mosses; MRPP

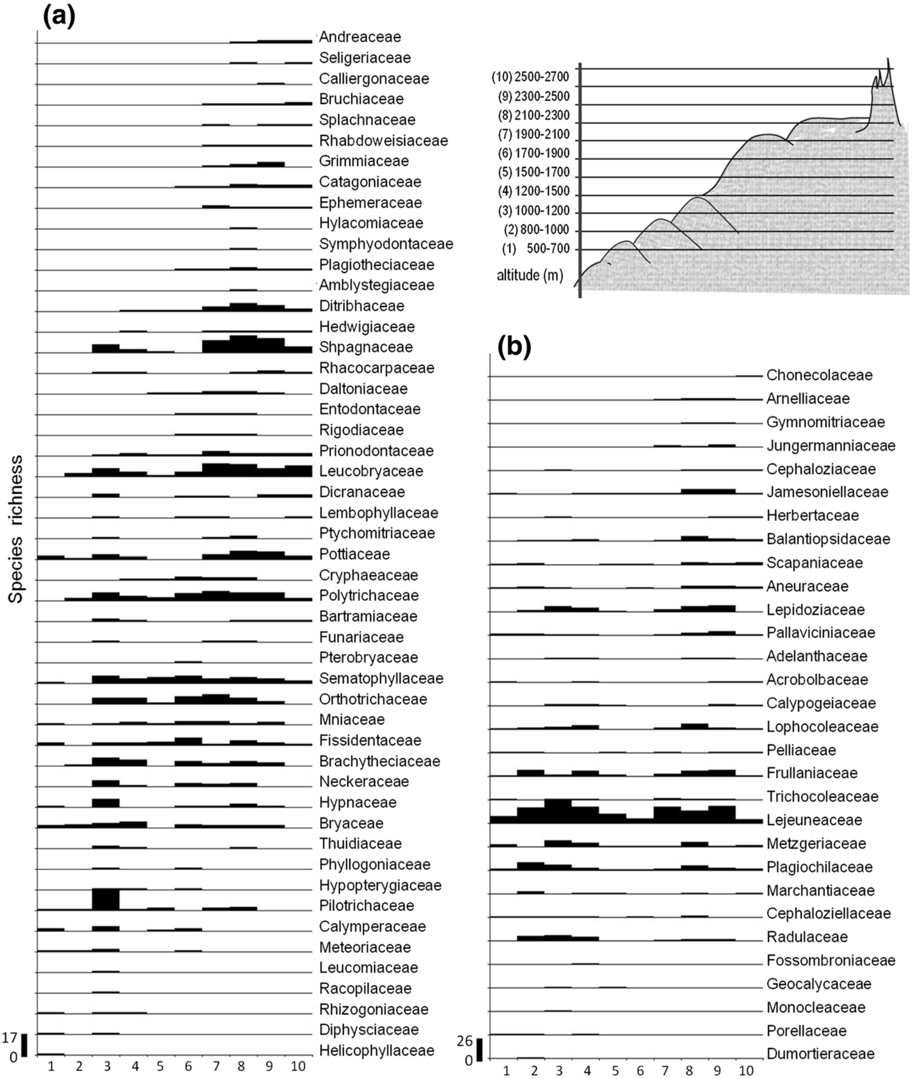

Fig. 2 Species richness of moss (**a**) and liverwort (**b**) families along an elevation gradient in Itatiaia National Park

A = 0.32, P = 0.003 for liverworts). This test indicated that heterogeneity was greater between the groups than within them, that is, the species compositions of the samples (elevation belts) within each vegetation type were different from those that would be expected purely by chance. However, the low A index values indicated that there were differences in composition within the elevation belts in the same vegetation type.

Bryophyte richness was not uniform in the vegetation types, with 296 taxa being found in the Montane Forest and 273 in the Upper Montane Forest (Supplementary Table S1). 172 taxa (58 %) were exclusive to the Montane Forest, whereas 102 taxa (37 %) were

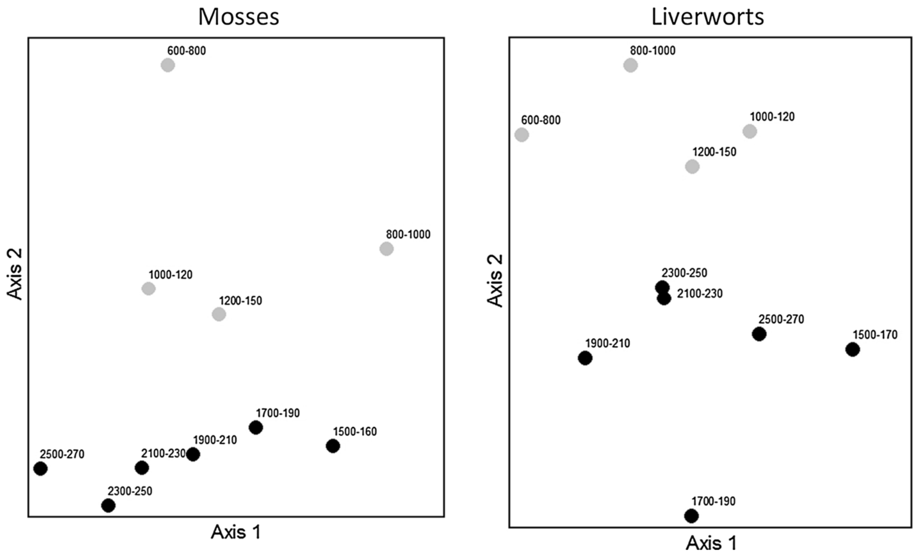

Fig. 3 Plot of two first axes of Nonmetric Multidimensional Scaling ordination (NMDS) of the floristic matrix of bryophyte communities in Itatiaia National Park. Colors distinguish the vegetation types (*gray* Montane Forest, *black* Upper Montane Forest)

found only in the Upper Montane Forest and High-Altitude Fields (Supplementary Table S1).

Many families found in the Upper Montane Forest and High-Altitude Fields are absent in the Montane Forest (e.g., Andreaeaceae, Splachnobryaceae, and Symphyodontaceae); Leucobryaceae was the largest family in the Montane and Upper Montane Forests. Among the liverworts, Lejeuneaceae dominated overall richness in both forest types (Supplementary Table S1).

Endemics (EN) versus non-endemics (NE)

A total of 76 bryophyte species are endemic to Brazil (14 %), including 51 species of mosses and 25 species of liverworts. Four of the seven species endemic to Rio de Janeiro State occur in the Upper Montane Forest, while two are unique to the High-Altitude Fields. Analyses of the distributions of endemic taxa along the elevation gradient in INP indicated that most of these species occurred in the Upper Montane Forest (47 species), followed by Montane Forest (40 species) and High-Altitude Fields (30 species). The number of endemic bryophyte species was higher in the Upper Montane Forest, declining with the elevation. The non-endemic species also decline with the elevation. Moss endemism increased with altitude ($F_{1.19} = 17.973$; $p = 0.0004$), reaching a maximum at 2100–2400 m (Supplementary Fig. S1c); this situation was not seen with liverworts ($F_{1.19} = 0.405$; $p = 0.53$).

Conservation

The INP contains a high number of threatened species on a regional scale (Rio de Janeiro State), with 28 moss species considered vulnerable (VU) and six endangered (EN); 46

liverworts found there are considered vulnerable and seven endangered. The numbers of threatened species of mosses ($F_{1.19} = 21.691$; $p = 0.0001$) and liverworts ($F_{1.19} = 5.8478$; $p = 0.026$) increased with increasing elevation (Supplementary Fig. S1b).

Discussion

Elevation patterns of species richness, endemism, and threatened species

Our data for the mosses corroborated the characteristic increase of bryophyte richness with altitude reported for the tropics (Ah-Peng et al. 2007, 2012; Wolf 1993; Santos et al. unpublished data). The same pattern was not identified with liverworts, probably as a result of the influence of biogeographic processes or the lack of microhabitat availability. Santos and Costa (2010b) reported an exceptional number of endemic mosses in the Montane and Upper Montane forests in the INP, in contrast to the Andean disjunctions of some liverworts. Moss species, due to their life forms and gametophyte morphologies, are able to colonize open environments such as rock outcrops, exposed soils, and banks—microhabitats that tend to increase in availability with increasing altitude. Bryophyte richness decreased, however, on the mountain top in the INP, probably due to the open, grass-dominated physiognomy of the High-Altitude Fields vegetation and the rigors of the cool-humid climate (Safford 1999). The open structures of High-Altitude Fields formations (without large trees), the absence of topographic relief (these are plateau areas), and high light intensities will affect the internal microclimates within the vegetation, directly affecting bryophyte communities. The greatest bryophyte species richness was found at 2100 m in the Upper Montane Forest, near the transition to High-Altitude Fields vegetation. This transition zone comprises species typical of both Upper Montane Forests and High-Altitude Fields, resulting in high species richness.

The species richness of mosses was greater than that of liverworts in the majority of the elevation belts examined. Low species richness was observed between 1200 and 2000 m, apparently reflecting the lack of surveys in these ranges in the park. Most of the families demonstrated wide elevation distributions, occurring in both Montane and Upper Montane Forests, although some genera had higher numbers of species occurring in either the Montane Forest or Upper Montane Forest, while others were exclusive to just one forest type. Meteoriaceae is an important family in the Montane Forest, but its importance decreases significantly in other vegetation types as this family consists of predominantly pendent species that require low temperatures, high light levels, and high atmospheric humidity (Richards 1984).

The observation that the highest species richness occurred in the Upper Montane Forest did not corroborate reports from other tropical America sites, such as Gradstein and Salazar Allen (1992) in Panama and Santos and Costa (2010a) in the Atlantic Rainforest of Rio de Janeiro State that found the highest richness occurring in the Montane Forests. The same patterns were found for endemic and threatened species. Like the non-endemic species, the numbers of endemic species declined in the top of mountain (High-Altitude Fields vegetation). The decrease of the species richness along elevational gradients is a common pattern described in nonnative floras from around the world (Alexander et al. 2011; Seipel et al. 2012).

Among the families that contributed to the high species richness of mosses in the Upper Montane Forest and High-Altitude Fields, were Sphagnaceae (its species generally growing on humid soils in open areas—an environment common in the transition zone between forest vegetation and High-Altitude Fields) and Leucobryaceae, Polytrichaceae, and Pottiaceae (acrocarpous mosses, that grow in turfs on banks, rocks, and rock outcrops). The richest liverwort families, such as Frullaniaceae and Lejeuneaceae, on the other hand, had their highest diversity in forest vegetation, growing on the trunks and branches of trees.

The peaks of both bryophyte endemism and species richness occurred at high elevations (2100 m) in the Upper Montane Forest in INP (Serra da Mantiqueira); this situation is different from spore producing plants (ferns) in Neotropical mountains—which have peaks of endemism that appear above their peaks of richness in relation to the elevation gradient (Kluge and Kessler 2006; Kessler 2002). Similar results were reported by Santos et al. (unpublished data) for the bryophytes on a small mountain (1170 m) in Serra do Mar National Park in the Atlantic Forest of southeastern Brazil, where the peaks of richness and endemism coincided at 950 m.

The endemic species that occur in the Upper Montane Forest and High-Altitude Fields show narrow elevation ranges (e.g., *Brachydontium notorogenes* and *Paraleucobryum longifolium* spp. *brasiliense*) and are best adapted to summit climates. The observed decreases in the species richness of endemic species in the Submontane Forest probably reflected the effects of ecological processes (such as climatic filtering), human interference (land-use), or biogeographic processes (historical refuges). Schuster (1983) highlighted that montane regions represent "biotic islands", where bryophyte populations were isolated and restricted due to Pleistocene climate changes.

Endemism and species richness are highly relevant to prioritizing conservation efforts (Kier et al. 2009) and our results emphasize the importance of the INP in conserving bryophyte diversity (and threatened and/or endemic species) in the Atlantic Forest. The high degrees of endemism found above 2000 m imply high phylogenetic diversity there.

The non-endemic species that grow at high elevations (Upper Montane Forest and High-Altitude Fields) are largely generalist species with wide tolerances to more extreme environmental conditions (such as low temperatures and high light levels), and many of them show disjunctions with respect to other high Neotropical mountains.

Our study suggests that the combined interactions of climatic factors (such as mean annual temperature and precipitation rates) apparently limit moss and liverwort species' richness patterns along elevation gradients. The high temperatures and low precipitation rates found there (generating high evapotranspiration rates and low humidity) limit liverwort growth at high elevations, while species richness in low land areas is limited by low temperatures. The more optimal ranges of temperature and precipitation at mid elevations in the INP create favorable conditions for higher species richness.

Our data also demonstrated that the bryoflora of the INP is rich and well-studied as compared to other areas in the state, emphasizing that this park is one of the most important Atlantic Forest remnants in Rio de Janeiro State (and the country) for the conservation of bryophyte species diversity.

Floristic composition x vegetation types

Marked heterogeneity was observed in terms of species composition among mosses and liverworts in elevation belts within the same vegetation type. There were significant differences in the identities of the moss and liverwort species growing in the Montane and Upper Montane Forests in INP as well as within the different elevation belts of those same vegetation types. Similar patterns were found by Santos et al. (2014) in their study of the liverwort flora of the Atlantic Forest in southeastern Brazil, as those authors detected groups of areas at the same altitudes with similar liverwort floras, suggesting that these plants have deterministic distributions related to environmental filtering driven by climatic variables associated with altitude.

The main bryophyte families (those having high species richness) occurred along the entire elevation gradient, while other smaller families occurred exclusively in only one type of vegetation. The families with the highest species richness contributed significantly to diversity in the Montane Forest, and are considered important components of the bryoflora of tropical forests (Gradstein et al. 2001).

Implications for conservation

Descriptions of diversity along elevation gradients are crucial for conservation management and for understanding the ecologies of montane environments. In their study of priority areas for conservation efforts in Rio de Janeiro State, Costa and Faria (2008) cited examples of areas under anthropogenic pressure with numerous threatened species. They included INP as a priority area because of its high species diversity and high numbers of endemic and threatened taxa—with its major threats involving questions of private lands within the park, and pasture and agriculture uses (Rocha et al. 2003). Costa and Santos (2009) considered 75 liverwort taxa to be threatened in Rio de Janeiro State, of which 53 species (71 %) occur in INP, including 38 exclusive taxa. Our data confirms the importance of the INP as one of the major Atlantic Forest remnants in southeastern Brazil and one of the major sites of bryophyte species diversity in the country, with the combination of relief (different microhabitats), altitude (high elevations), and climatic conditions (low temperatures and high humidity and light intensity) contributing to the high diversity of bryophytes. Adequate protection for endemic or endangered species and the Upper Montane Forests and High-Altitude Fields is still lacking, however, and must be given priority, as the consequences of global warming will accelerate the destruction of mountain environments.

Acknowledgments This research represents a joint collaboration among different specialists from the following institutions: the Rio de Janeiro Botanical Garden (Brazil), the University of Pernambuco (Brazil), the New York Botanical Garden (USA), and the bryologist Alfons Schäfer-Verwimp from Germany.

References

Ah-Peng C, Chualh-Petiot M, Descamps-Julien B, Bardat J, Stamenoff P, Strasberg D (2007) Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Réunion. Divers Distrib 13:654–662

Ah-Peng C, Wilding N, Kluge J, Descamps-Julien B, Bardat J, Chuah-Petiot M, Strasberg D, Hedderson TAJ (2012) Bryophyte diversity and range size distribution along two altitudinal gradients: Continent vs. island. Acta Oecol 42:58–65. doi:10.116/j.actao.2012.04.010

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard AB, Seipel T, MIREN Consortium (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. Proc Nat Acad Sc USA 108:656–661

Brade AC (1956) A flora do Parque Nacional do Itatiaia. Bol Parq Nac Itatiaia 5:1–92

Buck WR, Goffinet B (2009) Morphology and classification of mosses. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambridge University Press, New York, pp 55–138

Chantanorrapint S (2010) Ecological studies of epiphytic bryophytes along altitudinal gradients in Southern Tahoiland. Fakultät der Rheinischen-Friedrich-Wilhelms-Univeritält Bonn, Bonn
Costa DP (2008) Metzgeriaceae. Fl Neotr Monogr 102: 1–169 (ISSN 0071-5794)
Costa DP (2009) Briófitas. In: Stehlmann JR, Forzza RC, Salino A, Cabral M, Costa DP, Kamino LHY (eds) Plantas da Floresta Atlântica. Jardim Botânico do Rio de Janeiro, Rio de Janeiro, pp 13–17
Costa DP (2013) Briófitas. In: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB128472. Accessed 26 June 2014
Costa DP (2014) Hepáticas. In: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB128472. Accessed 26 June 2014
Costa DP, Faria CP (2008) Conservation priorities for the bryoflora of Rio de Janeiro state, Brazil. J Bryol 30:133–142
Costa DP, Lima FM (2005) Moss diversity in the tropical rainforests of Rio de Janeiro, southeastern Brazil. Braz J Bot 28(4):671–685. doi:10.1590/S0100-8404.2005000400003
Costa DP, Peralta DF (2014) Musgos. In: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB128472. Accessed 26 June 2014
Costa DP, Santos ND (2009) Conservação de hepáticas na Mata Atlântica do sudeste do Brasil: uma análise regional no estado do Rio de Janeiro. Acta Bot Bras 23(4):913–922
Costa DP, Imbassahy CAA, Silva VPAV (2005a) Checklist and distribution of mosses, liverworts and hornworts of Rio de Janeiro state, Brazil. J Hattori Bot Lab 98:259–298. doi:10.1590/S1679-87592006000300006
Costa DP, Imbassahy CAA, Silva VPAV (2005b) Diversidade e importância das espécies de briófitas na conservação dos ecossistemas do estado do Rio de Janeiro. Rodriguésia 56:13–49
Costa DP, Pôrto KC, Luizi-Ponzo AP, Ilkiu-Borges AL, Bastos CJP, Câmara PE, Peralta DF, Boas-Bastos SV, Imbassahy CAA, Henriques DK, Gomes HCS, Rocha LM, Santos ND, Silviero TS, Vaz-Imbassahy TF, Churchill S (2011) Synopsis of the Brazilian moss flora: checklist, distribution and conservation. Nova Hedwig 93:277–334
Crandall-Stotler B, Stotler RE, Long DG (2009) Morphology and classification of the Marchantiophyta. In: Goffinet B, Shaw AJ (eds) Bryophyte biology. Cambridge University Press, New York, pp 1–54
Dusén P (1903) Sur la flore de la Serra do Itatiaia. Arq. Mus. Nac. Rio de Janeiro 13:1–119
FBDS (2000) Cadernos FBDS. Rio de Janeiro: Fundação Brasileira para o Desenvolvimento Sustentável, n.3. http://www.fbds.org.br/IMG/doc-15.pdf. Accessed 1 out 2007
Frahm J-P (1991) Dicranaceae: Campylopodioideae, Paraleucobryoideae. Fl Neotr Monogr 54: 1–238 (ISSN 0071-5794)
Frahm J-P, Gradstein SR (1991) An altitudinal zonation of tropical rain forests using bryophytes. J Biogeogr 18:669–678
Fundação SOS Mata Atlântica (2002) Atlas da evolução dos Remanescentes Florestais da Mata Atlântica, período 1995–2000: relatório final. Fundação S.O.S. Mata Atlântica/INPE, São Paulo
Gradstein SR (1995) Bryophyte diversity of the tropical rainforest. Arch Sc (Geneva) 48:91–96
Gradstein SR, Costa DP (2003) The hepaticae and anthocerotae of Brazil. Mem New York Bot Gard 87: 1–336 (ISBN-0-89327-448-8)
Gradstein SR, Pócs T (1989) Bryophytes. In: Lieth H, Werger MJA (eds) Tropical rain forest ecosystems. Elsevier, Amsterdan, pp 311–325
Gradstein SR, Salazar Allen N (1992) Bryophyte diversity along an altitudinal gradient in Dárien National Park, Panama. Trop Bryol 5:61–71
Gradstein SR, Churchill SP, Salazar-Allen N (2001) Guide to the bryophytes to Tropical America. Mem New York Bot Gard 86: 1–577 (ISBN-0-89327-435-6)
Grau O, Grytnes JA, Birks HJB (2007) A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. J Biogeogr 34:1907–1915
Gyrtnes JA, Heegaard E, Ihlen PG (2006) Species richness of vasvcular plants, bryophytes and lichens along an altitudinal gradient in western Norway. Acta Oecol 29:241–246
Hueck K (1972) As florestas da América do Sul: ecologia, composição e importância econômica. Polígono, São Paulo
Instituto Brasileiro de Desenvolvimento Florestal (IBDF), Fundação Brasileira para a Conservação da Natureza (FBCN) (1982) Plano de manejo Parque Nacional do Itatiaia. IBAMA, Brasília
Kessler M (2002) The elevational gradient of Andean plant endemism, varying influences of taxon-specific traits and topography at different taxonomic levels. J Biogeogr 29:1159–1166
Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. Proc Nat Acad Sc USA 106:9322–9327

Kluge J, Kessler M (2006) Fern endemism and its correlates: contribution from an elevational transect in Costa Rica. Divers Distrib 12:535–545

Leitão-Filho HF (1993) Ecologia da Mata Atlântica em Cubatão. Edunesp-EduUnicamp, São Paulo

Lüth M, Schäfer-Verwimp A (2004) Additions to the bryophyte flora of the neotropics. Trop Bryol 25: 7–17 (ISSN 2381-9677)

McCune B, Grace JB (2002) Analysis of ecological communities. MJM Press, Oregon

McCune B, Mefford MJ (1999) PC-ORD: multivariate analysis of ecological data, version 4.10. Gleneden Beach: MjM Sofware Design

Mielke PW, Berry KJ (2007) Permutation methods: a distance function approach, vol 2. Springer, New York

Müller C (1898) Bryologia Serrae Itatiaiae. Bull Herb Boissier 6:18–48

Pádua JMT, Coimbra-Filho AF (1979) Os parques nacionais do Brasil. Instituto Brasileiro de Desenvolvimento Florestal, Brasília

Pócs T (1982) Tropical Forest Bryophytes. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London/New York, pp 59–103

Pócs T (1994) The altitudinal distribution of Kilimanjaro bryophytes. In: Seyani JH, Chikuni AC (eds) XIIIth Plenary meeting. AETFAT, Zomba, pp 797–812

Reese WD (1993) Calymperaceae. Fl Neotr Monograph 58: 1–102 (ISSN 0071-5794)

Richards PW (1984) The ecology of tropical forest bryophytes. In: Schuster RM (ed) New manual of bryology. The Hattori Botanical Laboratory, Nichina, Japan, pp 1233–1270

Rocha CFD, Bergallo HG, Alves MAS, Sluys MV (2003) A biodiversidade nos grandes remanescentes de florestais do estado do Rio de Janeiro e nas restingas da Mata Atlântica. RiMa, São Carlos

Safford H (1999) Brazilian Páramos I. An introduction to the physical environment and vegetation of the campos de altitude. J Biogeogr 26:693–712

Santos ND (2008) Hepáticas da Mata Atlântica do estado do Rio de Janeiro: diversidade, fitogeografia e conservação. M.Sc. Thesis. Rio de Janeiro: Instituto de Pesquisas Jardim Botânico do Rio de Janeiro/ Escola Nacional de Botânica Tropical

Santos ND, Costa DP (2010a) Phytogeography of the liverwort flora of the Atlantic Forest of southeastern Brazil. J Bryol 32:9–22

Santos ND, Costa DP (2010b) Altitudinal zonation of liverworts in the Atlantic Forest, Southeastern Brazil. Bryologist 113:631–645

Santos ND, Costa DP, Kinoshita LS, Shepherd GJ (2014) Windborne: can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? Ecol Indic 36:431–440

Schäfer-Verwimp A (1992) New or interesting records of Brazilian bryophytes, III. J Hattori Bot Lab 71: 55–68 (ISSN 0073-0912)

Schäfer-Verwimp A, Giancotti C (1993) New or interesting records of Brazilian bryophytes, IV. Hikobia 11: 285–292 (ISSN 0073-0912)

Schäfer-Verwimp A, Vital DM (1989) New or interesting records of Brazilian bryophytes. J Hattori Bot Lab 66: 255–261 (ISSN 0073-0912)

Schuster RM (1983) Phytogeography of bryophytes. In: Schuster RM (ed) New manual of bryophytes. Hattori Botanical Laboratory, Nichinan, pp 463–626

Seipel T, Kueffer C, Rew L, Daehler C, Pauchard A, Naylor B, Alexander J, Parks C, Edwards P, Arévalo JR, Cavieres L, Dietz H, Jakobs G, McDougall K, Otto R, Walsh N (2012) Processes at multiple scales affect richness and similarity of non-native plant species in mountains around the world. Glob Ecol Biogeogr 21:236–246

R Development Core Team (2014) R a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Vanderpoorten A, Goffinet B (2009) Introduction to bryology. Cambridge University Press, New York

Veloso HP, Rangel Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira adaptada a um sistema universal. IBGE/CDDI, Departamento de Documentação e Biblioteca, Rio de Janeiro

Visnadi SR (1998) Briófitas em ecossistemas costeiros do Núcleo Picinguaba do Parque Estadual da Serra do Mar,Ubatuba, SP. Ph.D. Thesis, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro

Warnstorf C (1911). Sphagnales, Sphagnaceae (Sphagnologia Universalis). In: Engler A. Das Pflanzenreich, W. Engelmann, Leipzig

Wolf JHD (1993) Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. Ann Missouri Bot Gard 80:928–960

Yano O (1992) Leucobryaceae (Bryopsida) do Brasil. Tese de Doutorado. Univ. São Paulo, São Paulo

Zar JH (1999) Biostatistical analysis, vol 4[a]. Prentice-Hall Inc., New Jersey