

Geographical patterns of terrestrial herbs: a new component in planning the conservation of the Brazilian Atlantic Forest

Leandro Tavares Azevedo Vieira^{1,2}  ·
Rodrigo Trassi Polisel³ · Natália Macedo Ivanauskas⁴ ·
George John Shepherd⁵ · Jorge Luiz Waechter⁶ ·
Kikyo Yamamoto⁵ · Fernando Roberto Martins⁵

Received: 1 October 2014 / Revised: 30 June 2015 / Accepted: 16 July 2015 /

Published online: 22 July 2015

© Springer Science+Business Media Dordrecht 2015

Abstract The Brazilian Atlantic Forest (*sensu lato*) is constituted by Dense Ombrophilous Forest, Mixed Ombrophilous Forest and Seasonal Semideciduous Forest, in which tree species are distributed in gradients, whichever latitude, longitude, or altitude is considered. We investigated whether herb species living on the floor of these forests would have the same geographic distribution pattern. If tree and herb-layer species have coincident distribution patterns, the same conservation units can conserve both species sets; otherwise, specific conservation actions should be taken. We built a presence/absence matrix of 803 terrestrial native species in 80 surveys across the southern and southeastern Brazilian Atlantic Forest. We performed UPGMA, CA and RDA multivariate analyses in order to investigate the distribution patterns. The high degree of agreement among the analyses led us to assume that the geographic distribution of the herb-layer flora occurs as gradients among three main floristic groups: Tropical Ombrophilous forests (mostly lowland forests),

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/s10531-015-0967-8](https://doi.org/10.1007/s10531-015-0967-8)) contains supplementary material, which is available to authorized users.

✉ Leandro Tavares Azevedo Vieira
vieiralt@yahoo.com.br; leandro.vieira@mackenzie.br

¹ Ecology Graduate Course, Institute of Biology, University of Campinas – UNICAMP, P.O. Box 6109, Campinas, SP 13083-970, Brazil

² Present Address: Herbarium MACK, Mackenzie Presbyterian University, Rua Piauí, 181. 1st Floor, São Paulo, SP 01241-001, Brazil

³ Plant Ecology Graduate Course, Institute of Biology, University of Campinas – UNICAMP, P.O. Box 6109, Campinas, SP 13083-970, Brazil

⁴ Seção de Ecologia Florestal, Instituto Florestal, Rua do Horto 931, São Paulo, SP 02377-000, Brazil

⁵ Department of Plant Biology, Institute of Biology, University of Campinas – UNICAMP, P.O. Box 6109, Campinas, SP 13083-970, Brazil

⁶ Department of Botany, Institute of Biosciences, Federal University of Rio Grande do Sul – UFRGS, Porto Alegre, RS 91501-970, Brazil

Subtropical Ombrophilous forests (mostly montane and upper-montane forests in lower latitudes and sub-montane and lowland forests in higher latitudes, i.e., where temperature is lower), and Seasonal Semideciduous forests (with a marked dry season). Based on different patterns and processes between herbs and trees, and in order to encompass the highest flora diversity, we highlight the importance of creating more reserves in each one of the three main floristic groups of herb-layer species in the Brazilian Atlantic Forest.

Keywords Atlantic forest · Conservation units · Herb-layer · Floristic groups · Gradient distribution · Indicator species

Introduction

In the Brazilian Atlantic Forest, the tree flora suffers a gradual east–west differentiation between ombrophilous and seasonal forests influenced by rainfall regime (Salis et al. 1995; Torres et al. 1997; Oliveira-Filho and Fontes 2000; Oliveira 2006). Oliveira-Filho and Fontes (2000) also claimed the existence of a north–south gradient associated with both rainfall and temperature with increasing frequency of frosts towards the south. Latitudinal and altitudinal gradients are also found for both the seasonal and the ombrophilous forests in the southeast-northeastern direction (Oliveira-Filho et al. 2005). Ivanauskas et al. (2000) and Scudeller et al. (2001) found a gradual differentiation in species composition between lowland and upland rainforests, which were closely influenced by altitude. The seasonal forests also have an east–west gradient associated with altitude, soil fertility and fire frequency (Salis et al. 1995; Torres et al. 1997; Yamamoto et al. 2005; Oliveira-Filho et al. 2006; Oliveira 2006; Gonzaga et al. 2008). Summing up, tree species in the Brazilian Atlantic Forest are distributed in gradients, whichever latitude, longitude, or altitude is considered.

Although the distribution pattern of the tree flora across the Brazilian Atlantic Forest is rather well known, we are not aware of any study addressing this issue to herb species living on the floor of these forests. Due to their superficial root system and small size, terrestrial herbs in tropical forests are subjected to severe competition for water, nutrients, and light (Pearcy 1983; Raich 1989; Chazdon and Pearcy 1991; Mulkey et al. 1991; Chazdon et al. 1996). Because they struggle in particular ecological conditions, herbaceous plants on the forest floor present exceptionally interesting adaptations (Richards 1996) that reflect their environment in any forest type (Cestaro et al. 1986). However, it is still not clear what plays a major role in the distribution pattern of the herb species in Brazilian Atlantic Forest. Would the distribution of the herb species of southern/southeastern Atlantic Forest be limited because of the special microclimate each forest-type imposes upon them, thus indicating a higher level of specialization? Or would it be in accordance with a gradient pattern similar to that shown by the tree species, thus being mainly influenced by the macroclimate?

We investigated whether the herb-layer flora has a geographic distribution pattern similar to that already known for the tree flora in the southeastern and southern sectors of the Brazilian Atlantic Forest. A gradient should be identified if many herb species are common to different sites of the Atlantic Forest, with the species geographic ranges overlapping at least partially, thus characterizing a continuous species turnover along some spatial reference. A distribution pattern coherent with that of the tree flora would indicate

that ecological conditions act equally upon the herb-layer and the tree flora in the southern/southeastern Brazilian Atlantic Forest. If tree and herb-layer species have coincident distribution patterns, the same conservation units can conserve both species sets; otherwise, specific actions should be taken to effectively conserve both tree and herb-layer species sets. Since the tree flora distribution is well known in the southern and southeastern Brazilian Atlantic Forest, we based our analyses on herb-layer species distribution across the same region, and made a free comparison of patterns and processes between these two floras.

Materials and methods

Floristic data

We built a matrix of species presence or absence from floristic or phytosociological surveys including herbaceous terrestrial plants across the southern and southeastern Brazilian Atlantic Forest (between the states of Minas Gerais and Rio Grande do Sul). We considered the herb layer as the forest compartment occupied by terrestrial herbs, characterized as vascular, mechanically independent, and little lignified plants (Cestaro et al. 1986). We accepted every species identified to binomials that the authors of the original papers considered as a terrestrial herb, and we reviewed the literature to confirm the growth habit of each of these species.

To select the lists we applied the following criteria: (a) the survey was carried out in well preserved sites in different forest formations of the southern/southeastern Brazilian Atlantic Forest; (b) scientific papers, theses and dissertations published until June 2014; and (c) adequate information about the locality and geographical coordinates to locate the site in a given formation of the Brazilian Atlantic Forest. We conducted nomenclatural update and correction of binomials with the PlantMiner platform (Carvalho et al. 2010), which incorporates the databases List of Species of Flora of Brazil (Forzza et al. 2010), and MOBOT (Tropicos.org 2011). We gave priority to the accepted names found in Forzza et al. (2010) in order to keep standardized the information in Brazilian species lists. We adopted the classification system proposed by Smith et al. (2006) for ferns and APG III (2009) for angiosperms. Considering the low number of surveys that includes abundance data, we built our matrix with presence/absence information of the species to encompass the highest number of surveys.

We selected 80 surveys from 63 references (see supplementary material, Appendix 1). Most of surveys were published in non-indexed journals of restricted circulation or are MSc or PhD theses. Also, the surveys were done with different methods using different sampling designs, which yielded different sample sizes and numbers of species sampled (supplementary material, Appendix 1). For instance, 48 surveys only collected plants (floristics) and 32 used plots to quantitatively sample plants in different sampled areas (phytosociology). The mean richness in the 80 surveys was 27 species per survey, with a standard deviation of 22. This lack of uniformity is the panorama for all vegetation surveys done so far in Brazil, but Felfili et al. (2011) published a book in order to standardize the procedures and methods in phytosociological studies in Brazil. Caiafa and Martins (2007) discussed the implications arising from the heterogeneity of methods and criteria used in vegetation surveys in Brazil and the deficient taxonomic treatment. Facing this panorama, we adopted a cautious statistical approach using three complementary multivariate

techniques and using only species identified to binomials by specialists and that were recorded in more than one site. Thus, the current available data allows us to construct hypotheses about geographical patterns on a broad scale, which can support more accurate researches in the future.

We attributed each survey to a forest formation according to IBGE (2012), which essentially considers rainfall regime, altitude belts according to latitude, and vegetation characteristics. One important aspect of this classification is that the altitudinal belts changes southward. For example, lowland forests occur up to 100 m above sea level (a.s.l.) between 4°N and 16°S, up to 50 m a.s.l. between 16°S and 24°S, and up to 30 m a.s.l. between 24°S and 32°S. Hence, we divided the 80 surveys into: Deciduous Seasonal Montane Forest (DSM, 2 sites), Semideciduous Seasonal Submontane Forest (SSS, 4), Semideciduous Seasonal Montane Forest (SSM, 17), Dense Ombrophilous Lowland Forest (DOL, 18), Dense Ombrophilous Submontane Forest (DOS, 10), Dense Ombrophilous Montane Forest (DOM, 8), Dense Ombrophilous Upper-montane Forest (DOU, 3), Mixed Ombrophilous Montane Forest (MOM, 9), Mixed Ombrophilous Upper-montane Forest (MOU, 9). In Fig. 1, the sites are numbered and ordered by decreasing latitude, and the

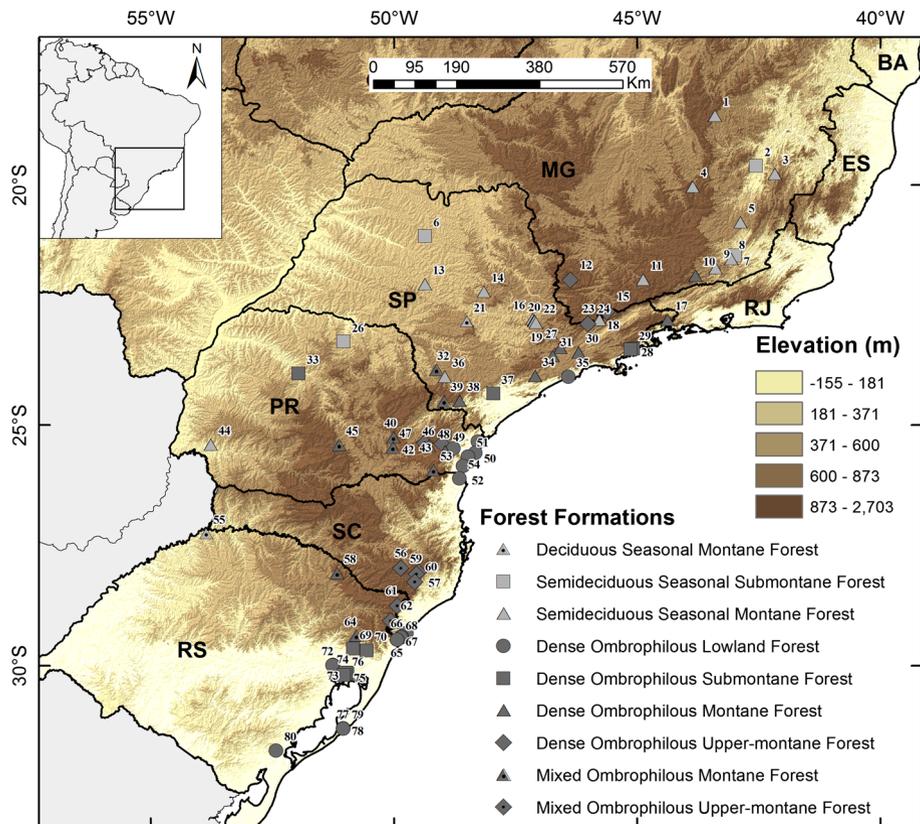


Fig. 1 Location of the sites considered in this study. The *symbols* indicate the forest types numbered and ordered by decreasing latitude. Elevation ranges are shown. See supplementary material, Appendix 1 for site references

forest sub-types of the sites are indicated by their abbreviations (supplementary material, Appendix 1).

Primary matrices

Our databank had 845 species, out of which 42 were exotic species, but we only included native terrestrial herbs in our primary matrix. Out of the 803 species left, 394 species were recorded at a single site and were excluded from our analyses to diminish noise, which could mask patterns (ter Braak 1995). After this exclusion, the localities Potirendaba (SSS6), Ubatuba (DOS28) and Juitiba (DOM34) were represented by only one species, and these sites were also excluded from our analyses. Four localities of Urubici-SC (MOU57, MOU59, MOU60 and MOU61) were considered outliers in our exploratory Correspondence Analysis (CA, detailed below), masking general patterns, and were also excluded with their 41 exclusive species. These four localities were grouped as a disjunct block and this can be considered an outlier (Gauch 1982). Since the eigenvectors in a reduced space are normalized, as in Correspondence Analysis results (Legendre and Legendre 1998), we confirmed these outliers by fitting the frequency distribution of eigenvalues of first two axes with theoretical normal curve using 99 % of confidence level as a threshold. These localities are Cloud Forests, and concerning tree species this forest type is very different from all other Brazilian Atlantic Forests (Falkenberg 2003; Bertonecello et al. 2011). Thus, our primary binary floristic matrix had 73 sites as objects and 368 species as descriptors and was used in all multivariate analyses.

We constructed a primary environmental matrix using the geographical coordinates of the sites to extract the values of environmental variables from WorldClim 1.4 database (Hijmans et al. 2005). We used Arc-GIS 10.0 (ESRI 2010) to extract values of all 19 bioclimatic variables (BIOTIME) and elevation data with 30 arc-s of resolution (about 1 km spatial resolution). When using multiple environmental variables, multicollinearity is inevitable and in many cases cannot be “solved” (Dormann et al. 2013), but cannot be ignored (Eisenlohr 2014). Collinearity is the existence of correlation between covariates, and several methods for diagnostics can be used, such as variance inflation factor (VIF), variance decomposition proportions (VD), and PCA biplot (Zuur et al. 2010; Dormann et al. 2013). The easiest ways to avoid collinearity include dropping collinear covariates based on VIFs (Zuur et al. 2010), performing pairwise correlations (Dormann et al. 2013), or perhaps better, using common sense or biological knowledge to choose the most ecologically meaningful variables (Zuur et al. 2010). Thus, we performed pairwise correlations among all environmental variables and eliminated the variables whose correlation coefficients were greater than 0.80. We used Pearson correlation coefficient for normal distribution variables; otherwise, we used Spearman correlation coefficient. Thus, we selected the following variables: altitude, annual mean temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), temperature annual range (BIO7), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), annual precipitation (BIO12), precipitation of wettest month (BIO13), and precipitation of driest month (BIO14). This primary environmental matrix was used in the Redundancy Analysis (RDA). Both floristic and environmental matrices are available in supplementary material (Appendices 2 and 3).

Multivariate analyses

To assess the existence of a floristic gradient we adopted three complementary multivariate techniques: cluster analysis, CA, and RDA. To perform these analyses, we used the “Vegan package” (Oksanen et al. 2014) in the R statistical language and environment (R Development Core Team 2014).

With Jaccard’s distance coefficient, which is considered a metric coefficient and is indicated for binary data (Legendre and Legendre 1998), we chose the best agglomerative hierarchical classification among WPGMA, simple linkage, complete linkage, Ward grouping, and UPGMA. Borcard et al. (2011) remember that clustering is a heuristic procedure, not a statistical test, so that the dendrogram must be evaluated by the correlation between the original distances and the cophenetic distances, which estimates dissimilarity from a dendrogram for every pair of points. The method with the highest cophenetic correlation may be seen as the one that produces the best clustering model for the distance matrix (Borcard et al. 2011). Once chosen the best dendrogram, if there was a gradient, we would expect the dendrogram to display a series of steps; otherwise, the dendrogram would display distinct groups on the first divisions. We tested whether there was a significant difference between two or more groups indicated by the best clustering with the Multiple Response Permutation Procedure (MRPP), which compares dissimilarities within and among groups.

McCune (1997) suggested the application of a direct ordination method together with an indirect ordination method, where pure community structure is expressed. As an indirect gradient analysis technique, we applied the Correspondence Analysis (CA; Hill 1973), where environmental gradients are not studied directly but are inferred from species composition data (Palmer 1993). As a direct gradient analysis, we applied a Canonical Redundancy Analysis (RDA), in which the species composition is directly related to environmental variables.

The base of CA is the Chi square distance, which is a coefficient excluding double absences used to quantify the relationships among rows and columns, so that the distances among sites in ordination space preserve their Chi square distances. CA may be applied to any data table that is dimensionally homogeneous and only contains positive integers or zeros and is recommended when the data contain a large number of null values (Legendre and Legendre 1998), which is our case due to the low constancy of herbaceous species among sites. In CA, the first axis separates the species curves by maximizing the dispersion, thus producing a linear arrangement. The second CA axis does the same, but, since it is correlated with the first axis, a folding of the objects being ordinated is produced, thus generating the “arch effect” (ter Braak 1995), for which this method is criticized (Palmer 1993). Nevertheless, some authors (e.g. Wartenberg et al. 1987) did not consider the arch effect as an artifact of the method, but rather an attribute of the data structure. Then, the arch-like curvature is an important, inherent property of successive-replacement data, which must be considered in any discussion or analysis (Wartenberg et al. 1987). This means that, if a gradient existed in our data, we would expect a global curvilinear arrangement of the sites in the ordination provided by the CA first two axes.

To assess the influence of environmental factors on the distribution of the herb-layer species, we applied a Canonical Redundancy Analysis (RDA; Rao 1964). RDA is a constrained ordination method that preserves the Euclidean distances among sites in the full-dimensional space. However, for longer gradients, which is our case, many species are replaced by others along the gradient, which generates many zeros in the species data table

(Legendre and Gallagher 2001), even if the rare species are excluded. One alternative to minimize this issue is to compute a resemblance matrix among sites using Hellinger's transformation of species data (Legendre and Gallagher 2001). Hellinger's transformation results in a metric distance that can be performed on presence-absence data and is appropriate for the analysis of community composition (Legendre and Legendre 1998). In this case, RDA computes axes that are linear combinations of the explanatory variables (Borcard et al. 2011). This is equivalent to a series of multiple linear regressions (Legendre and Legendre 1998). Thus, in order to estimate the approximated significance of the relationship between the floristic data set and the environmental variables, we applied a Monte Carlo test with 5000 random permutations, assuming H_0 as a non-linear relationship between the matrices. Prior, we performed a standardization on the environmental matrix by scaling each datum to zero mean and unit variance.

Indicator species

In order to assess whether there are species associated with potential groups formed in the multivariate analyses, we performed the Indicator Value (IndVal) analysis, initially proposed by Dufrene and Legendre (1997) and modified by Cáceres and Legendre (2009). Indicator species are determined by analyzing the relationship between the species occurrence or abundance values from a set of surveyed sites and the classification of these sites into groups (Dufrene and Legendre 1997). The interpretation of components depends on whether species presence-absence or abundance data are considered (Cáceres and Legendre 2009). Since we had presence-absence data, two components were used to compute IndVal. Component "A" is the probability that the surveyed site belongs to the target site group given the fact that the species has been found, expressing the specificity of the species. Component "B" is the probability of finding the species when the site belongs to the target site group, thus expressing the sensitivity of the species as a bioindicator (Cáceres and Legendre 2009; De Cáceres et al. 2012). The IndVal statistical significance was tested using a permutation test for each species at 0.05 significance level. We used the floristic matrix and the groups of sites produced by all the multivariate analyses considered together. We used the "indicspecies package" (Cáceres and Legendre 2009) in the R statistical language and environment (R Development Core Team 2014).

Results

Multivariate analyses

Among the WPGMA, simple linkage, complete linkage, and Ward grouping procedures, UPGMA showed to be the best procedure, since it produced a cophenetic correlation of 0.717, greater than the other procedures (results not shown). The UPGMA analysis produced a dendrogram (Fig. 2) in which seven groups could be distinguished at the level of 0.965 of Jaccard's distance coefficient. The main groups were C, F and G. The group C included nine lowland, one submontane and one montane dense ombrophilous forests from northern Santa Catarina to São Paulo State. The group F included 11 mixed ombrophilous forests and 18 dense ombrophilous forests from northeastern São Paulo to southern Rio Grande do Sul, out of which six submontane, three montane, and eight lowland forests. These lowland forests located more southern than the ones of group C. Five seasonal

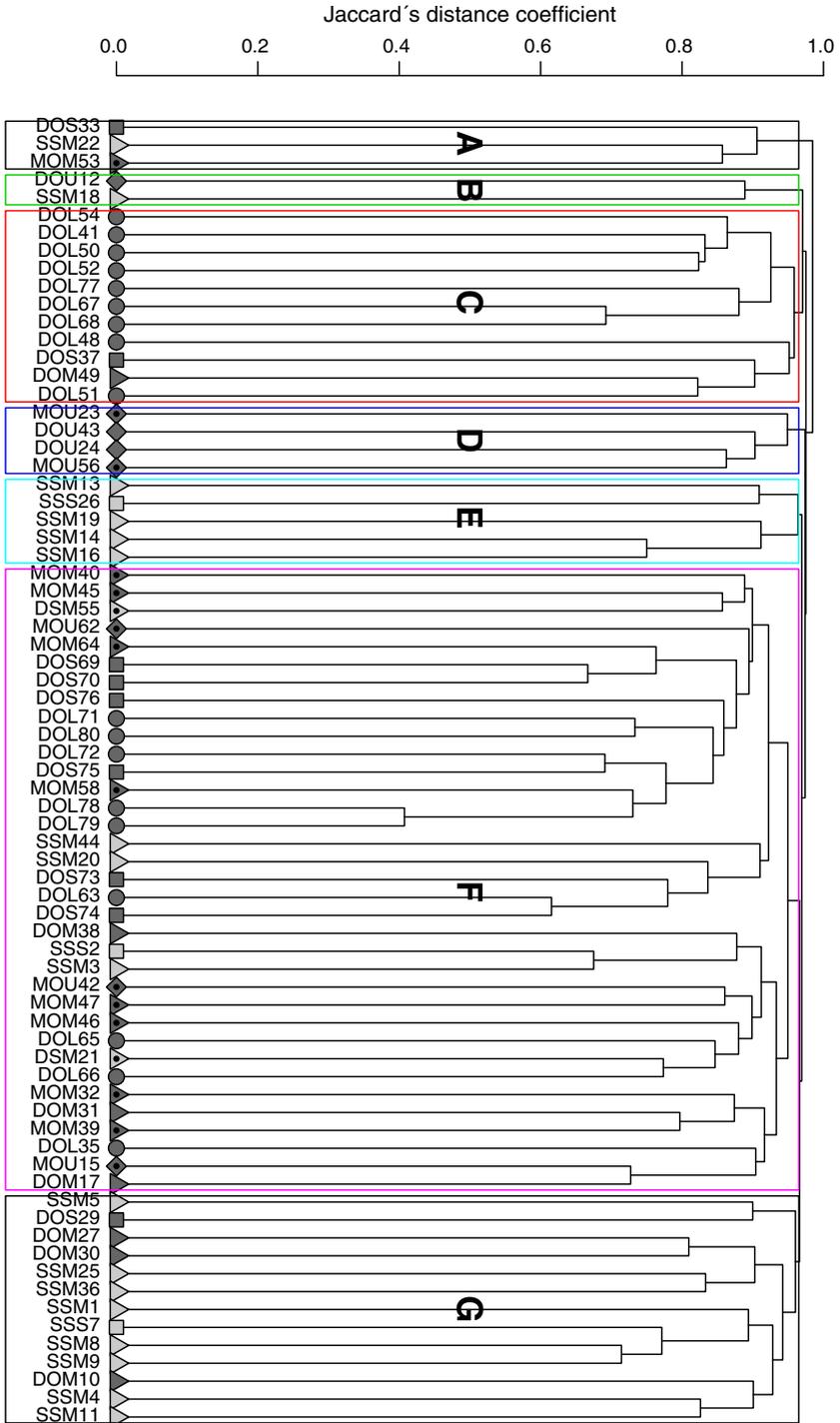


Fig. 2 Agglomerative hierarchical classification by the Unweighted Pair-Grouping Method by Arithmetic Averages (UPGMA) using Jaccard’s distance coefficient. Sites numbered and ordered by decreasing latitude. *DSM* Deciduous Seasonal Montane Forest, *SSS* Semideciduous Seasonal Submontane Forest, *SSM* Semideciduous Seasonal Montane Forest, *DOL* Dense Ombrophilous Lowland Forest, *DOS* Dense Ombrophilous Submontane Forest, *DOM* Dense Ombrophilous Montane Forest, *DOU* Dense Ombrophilous Upper-montane Forest, *MOM* Mixed Ombrophilous Montane Forest, *MOU* Mixed Ombrophilous Upper-montane Forest. See supplementary material, Appendix 1 and Fig. 1 for site references and symbols. The groups are detailed in the text

forests were present in group F. The group G was constituted by nine seasonal forests and four dense ombrophilous forest. The group E clustered five seasonal forests. The group D clustered four ombrophilous upper-montane forest, two mixed and two dense forests. The group A clustered only three sites, and group B only two sites, but in both groups, no pattern could be recognized. Broadly, the dendrogram (Fig. 2) indicates that the terrestrial herb species distributed into three main groups: lowland ombrophilous forests, non-lowland ombrophilous, and seasonal forests. According to MRPP analysis, these groups were statistically different from random association ($\Delta = 0.9271$, $p = 0.001$).

The eigenvalues for the first two CA axes were 0.57 and 0.50, respectively. Eigenvalue is the maximized dispersion of the species scores on the ordination axis, and values over 0.5 often denote a good separation of the species along the axis (ter Braak 1995). The CA first axis ordered the samples from montane (at left) to lowland (at right) forests, whereas the second axis ordered the samples from rain (top) to seasonal (bottom) forests, with the mixed forest in the middle (Fig. 3). The surveys were displayed in two straight lines forming a V-like figure, suggesting the existence of two great gradients: one referring to

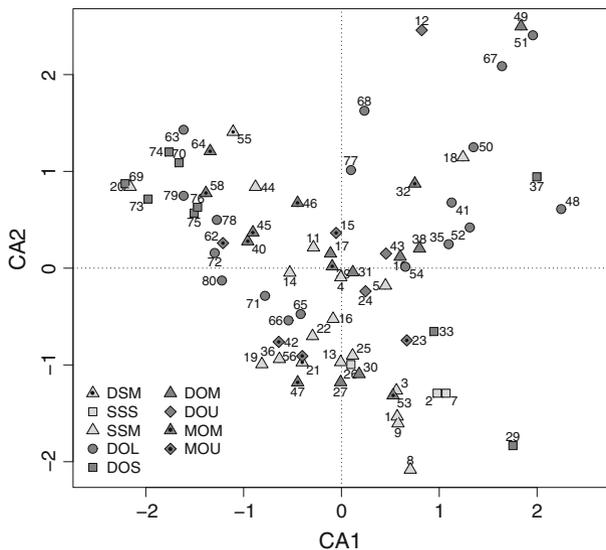


Fig. 3 Correspondence analysis ordination diagram with sites numbered and ordered by decreasing latitude. *DSM* Deciduous Seasonal Montane Forest, *SSS* Semideciduous Seasonal Submontane Forest, *SSM* Semideciduous Seasonal Montane Forest, *DOL* Dense Ombrophilous Lowland Forest, *DOS* Dense Ombrophilous Submontane Forest, *DOM* Dense Ombrophilous Montane Forest, *DOU* Dense Ombrophilous Upper-montane Forest, *MOM* Mixed Ombrophilous Montane Forest, *MOU* Mixed Ombrophilous Upper-montane Forest. See supplementary material, Appendix 1 and Fig. 1 for site references and symbols

rainfall seasonality along axis 2, and the other referring to altitude along axis 1. In spite of these two general gradients, three main floristic blocks are apparent: the non-lowland ombrophilous (top-left), the lowland ombrophilous (top-right), and seasonal forest (bottom).

In the Canonical Redundancy Analysis (RDA, Fig. 4), the total inertia was 0.91, and the inertia of the constrained axes was 0.19. Thus, the R^2 was 20.85 %, which is the proportion of total variance explained by constrained axes, i.e. environmental variables. For this constrained inertia, the proportion of variance explained by the first three axes were 0.23, 0.125, and 0.115 respectively. The relationship between the floristic data set and the environmental variables was significant ($F = 1.633$, $p = 0.005$). The first axis ordered the samples from seasonal and lowland ombrophilous forests (at left) to non-lowland ombrophilous (at right), and the second axis ordered the samples of the seasonal forests (at the top) to ombrophilous forests (at the bottom). The RDA ordination indicated two general gradients: one referring to rainfall seasonality (augmenting from top-left to center-right), the other referring to temperature (augmenting from bottom-left to center-right). Thus, dense ombrophilous lowland forests, in the bottom-left quarter (Fig. 4), were positively influenced by annual precipitation (*Precip*, BIO12 bioclimatic variable) and negatively by temperature annual range (*TRange*, BIO2). Dense ombrophilous montane and upper-montane forests were mostly influenced negatively by annual mean temperature (*MTemp*, BIO1), mean temperature of wettest quarter (*TWetQ*, BIO8), and positively by temperature

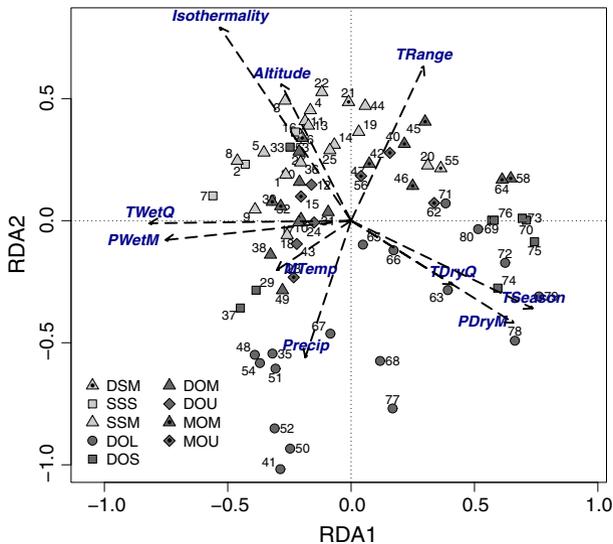


Fig. 4 Canonical Redundancy Analysis ordination diagram with sites numbered and ordered by decreasing latitude. *DSM* Deciduous Seasonal Montane Forest, *SSS* Semideciduous Seasonal Submontane Forest, *SSM* Semideciduous Seasonal Montane Forest, *DOL* Dense Ombrophilous Lowland Forest, *DOS* Dense Ombrophilous Submontane Forest, *DOM* Dense Ombrophilous Montane Forest, *DOU* Dense Ombrophilous Upper-montane Forest, *MOM* Mixed Ombrophilous Montane Forest, *MOU* Mixed Ombrophilous Upper-montane Forest. The vectors represent the following environmental variables: *Altitude*, *MTemp* annual mean temperature, *Isothermality*, *TSeason* temperature seasonality, *TRange* temperature annual range, *TWetQ* mean temperature of wettest quarter, *TDryQ* mean temperature of driest quarter, *Precip* annual precipitation, *PWetM* precipitation of wettest month, *PDryM* precipitation of driest month. See supplementary material, Appendix 1 and Fig. 1 for site references and symbols

seasonality (TSeason, BIO4) and precipitation in the driest month (PDryM, BIO14). Seasonal forests, on top-left quarter, were mostly influenced positively by isothermality (BIO3) and altitude, and negatively by annual mean temperature (MTemp, BIO1), temperature seasonality (TSeason, BIO4) and precipitation in the driest month (PDryM, BIO14).

Floristic patterns

The high degree of agreement between both ordination and cluster analyses led us to assume that the distribution of the herb-layer flora of the southern/southeastern Brazilian Atlantic Forest occurs in gradients among three floristic groups. These gradients are driven by the same variables driving tree gradients, mainly rainfall and temperature (Oliveira-Filho and Fontes 2000). The gradients occur among three floristic groups: Tropical Ombrophilous Forests (mostly lowland forests), Subtropical Ombrophilous Forests (mostly montane and upper-montane forests from lower latitudes and sub-montane and lowland forests from higher latitudes, i.e., where temperature is always lower than in others floristic groups), and Seasonal Semideciduous Forests (Fig. 5). These floristic groups are sets of

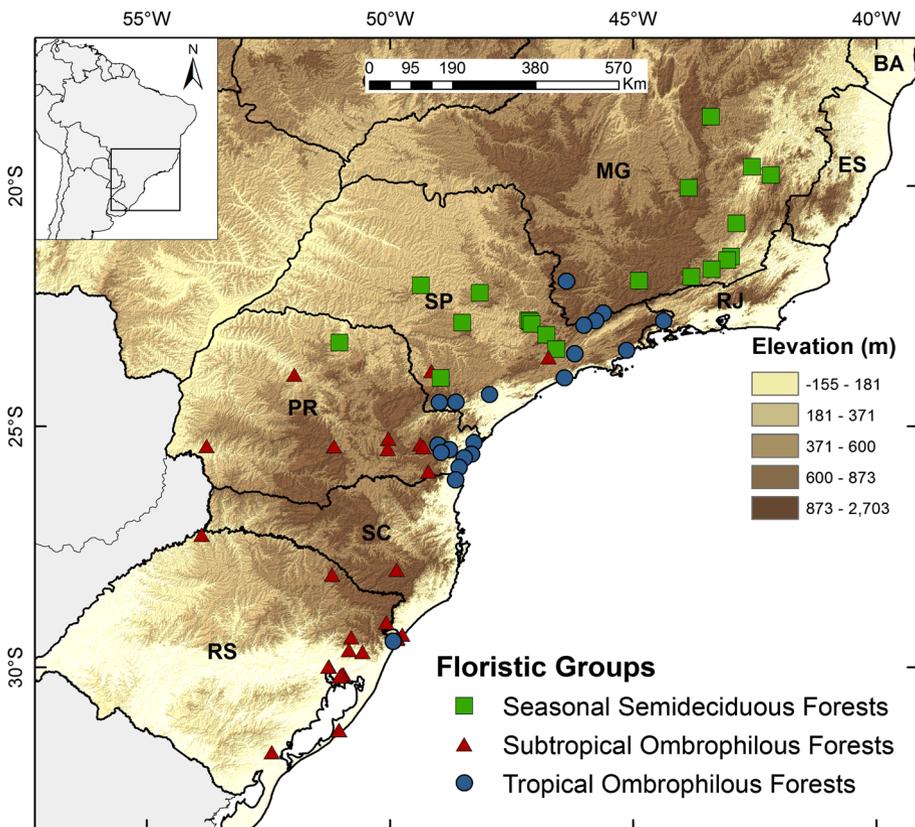


Fig. 5 Final result considering all analyses (UPGMA cluster analysis, CA, and RDA) pooled together. The three floristic groups of herb-layer of southern and southeastern Brazilian Atlantic Forest are shown

Table 1 Indicator species for each floristic group of herb-layer of southern and southeastern Brazilian Atlantic Forest.

Species	A	B	p
Tropical Ombrophilous Forest			
<i>Lindsaea quadrangularis</i>	1.00000	0.22730	0.005**
<i>Alstroemeria cunha</i>	1.00000	0.18180	0.015*
<i>Pleurostachys gaudichaudii</i>	1.00000	0.18180	0.010**
<i>Calathea zebrina</i>	1.00000	0.13640	0.025*
<i>Dictyostega orobanchoides</i>	1.00000	0.13640	0.035*
<i>Lycopodiella cernua</i>	1.00000	0.13640	0.035*
<i>Microchilus arietinus</i>	1.00000	0.13640	0.045*
<i>Phyllanthus rosellus</i>	1.00000	0.13640	0.030*
<i>Schizaea elegans</i>	1.00000	0.13640	0.035*
<i>Stromanthe tonckat</i>	1.00000	0.13640	0.045*
<i>Coccocypselum condalia</i>	0.90790	0.31820	0.005**
<i>Bertonia mosenii</i>	0.81970	0.22730	0.035*
<i>Scleria panicoides</i>	0.73530	0.31820	0.035*
<i>Coccocypselum cordifolium</i>	0.70430	0.27270	0.025*
<i>Blechnum binervatum</i>	0.70140	0.22730	0.040*
<i>Dichorisandra thyrsoflora</i>	0.62370	0.40910	0.035*
Subtropical Ombrophilous Forest			
<i>Spathicarpa hastifolia</i>	1.0000	0.3226	0.005**
<i>Oxalis linearantha</i>	1.0000	0.2903	0.005**
<i>Doryopteris multipartita</i>	1.0000	0.2581	0.005**
<i>Doryopteris pedata</i>	1.0000	0.2581	0.005**
<i>Adiantum raddianum</i>	1.0000	0.1613	0.015*
<i>Centella asiatica</i>	1.0000	0.1613	0.005**
<i>Commelina diffusa</i>	1.0000	0.1613	0.030*
<i>Cyclopogon elatus</i>	1.0000	0.1290	0.020*
<i>Didymochlaena truncatula</i>	1.0000	0.1290	0.035*
<i>Phyllanthus niruri</i>	1.0000	0.1290	0.045*
<i>Tradescantia fluminensis</i>	0.9274	0.5806	0.005**
<i>Carex sellowiana</i>	0.8856	0.3871	0.005**
<i>Homolepis glutinosa</i>	0.8646	0.2903	0.010**
<i>Pharus lappulaceus</i>	0.8187	0.4516	0.005**
<i>Oplismenus hirtellus</i>	0.7107	0.5806	0.005**
<i>Elephantopus mollis</i>	0.5666	0.4516	0.045*
Seasonal Semideciduous Forest			
<i>Asterostigma lombardii</i>	1.0000000	0.2000000	0.005**
<i>Heliconia angusta</i>	1.0000000	0.2000000	0.015*
<i>Lasiacis divaricata</i>	1.0000000	0.2000000	0.010**
<i>Ruellia jussieuoides</i>	1.0000000	0.2000000	0.010**
<i>Begonia digitata</i>	1.0000000	0.1500000	0.010**
<i>Cordia corymbosa</i>	1.0000000	0.1500000	0.015*
<i>Cuphea carthagenensis</i>	1.0000000	0.1500000	0.025*
<i>Cyperus coriifolius</i>	1.0000000	0.1500000	0.020*
<i>Dorstenia artifolia</i>	1.0000000	0.1500000	0.010**

Table 1 continued

Species	A	B	p
<i>Oxalis rhombeo-ovata</i>	1.0000000	0.1500000	0.025*
<i>Scleria mitis</i>	1.0000000	0.1500000	0.030*
<i>Waltheria americana</i>	1.0000000	0.1500000	0.015*
<i>Habenaria petalodes</i>	1.0000000	0.1000000	0.050*
<i>Oxalis hedysarifolia</i>	1.0000000	0.1000000	0.025*
<i>Oeceoclades maculata</i>	0.9156000	0.3500000	0.005**
<i>Rhynchospora exaltata</i>	0.8582000	0.5500000	0.005**
<i>Sacoila lanceolata</i>	0.8230000	0.1500000	0.040*
<i>Ruellia elegans</i>	0.8148000	0.2000000	0.020*
<i>Olyra micrantha</i>	0.7646000	0.4000000	0.005**
<i>Ananas bracteatus</i>	0.7629000	0.2500000	0.030*
<i>Panicum maximum</i>	0.6992000	0.1500000	0.050*
<i>Stachytarpheta cajiennensis</i>	0.6509000	0.3500000	0.020*

The specificity (component A), sensitivity (component B) and *p* value are presented

geographically closer sites that share common species in a much greater proportion than among other sets of sites, i.e., we considered a floristic group as a region with greater coincidence of species distribution with possibly exclusive species. According to MRPP analysis, the mean distance of these three groups was statistically different from that expected under a null hypothesis of no group structure ($\delta = 0.938$, $p = 0.001$).

The Tropical Ombrophilous floristic group (22 sites) extends from the coast of northern São Paulo through central-eastern Paraná and Santa Catarina to northern Rio Grande do Sul. It corresponds to the group C of UPGMA (Fig. 2) and is reinforced by the results of the CA (Fig. 3) and the RDA analyses (Fig. 4). This floristic group was particularly influenced by high annual precipitation and annual mean temperature. Some non-lowland ombrophilous forests were included in this group, but these sites were very close to the coastline, on the low windward slopes.

The Subtropical Ombrophilous floristic group (31 sites) extends from the slopes of the Serra do Mar in central-northern São Paulo to central Paraná until southern Rio Grande do Sul (Fig. 5), in montane and upper-montane forests from lower latitudes and sub-montane and lowland forests from higher latitudes. The Subtropical Ombrophilous floristic group corresponds to the group F from UPGMA (Fig. 2) and is reinforced by CA (top-left quarter) and RDA (right quarters; Figs. 3, 4, respectively). This floristic group is associated with high precipitation in the coldest quarter, lower mean temperature, and high temperature seasonality. Almost all mixed ombrophilous forests (with *Araucaria angustifolia*) were included in this floristic group.

The Seasonal Semideciduous floristic group (20 sites) occurs in the hinterland from southern Minas Gerais to central-north Paraná. This group is a consensus of groups E and G of the UPGMA along with the results of CA (bottom quarters) and RDA analyses (top-left quarter, Figs. 3, 4, respectively). All analyses grouped the seasonal semideciduous forests into a concise cluster associated with high precipitation seasonality and high isothermality and annual mean temperature.

The species assemblage

In spite of the distribution in gradients among the floristic groups, 54 of the 368 species used in our multivariate analyses were significantly associated with one of the three

floristic groups: 16 species with Tropical Ombrophilous Forests, 16 with Subtropical Ombrophilous Forests and 22 species with Seasonal Semideciduous Forests (Table 1). Most species had high specificity (component A), indicating that they were unique to a particular floristic group. However, the sensitivity (component B) was low in most species, indicating low frequency of occurrence within a particular group.

Discussion

The flora and the floristic groups

The number of 803 resident native species of the herb-layer in only 80 surveys reinforces the great diversity of the Brazilian Atlantic Forest. Oliveira-Filho and Fontes (2000) counted 2532 tree species in 125 surveys in the southeastern Atlantic Forest *s.l.*, and Scudeller et al. (2001) 2410 tree species in 210 floristic surveys in the entire Atlantic Forest. In spite of difference of methods and sampling efforts among surveys and databank gathering, the richness of terrestrial herbs of the Brazilian Atlantic Forest emphasizes the statement by Gentry and Dodson (1987) regarding the important contribution of herbaceous species to total diversity of tropical forests. Almost 50 % of the 803 herbs species were sampled in a single site, indicating a high level of rarity. For tree species, Bertonecello et al. (2011) showed that 20 % of them occur in ten or more localities in the same geographical area of our study. For herbaceous species, only 3.9 % of the total species number occurred in ten or more localities, indicating a much more restricted geographical distribution of the herb-layer species of the Brazilian Atlantic Forest.

Our results seem to be a trustworthy answer to whether the herb-layer flora is distributed in a fuzzy gradient or in distinct floristic groups. The analyses we used were complementary to each other and produced similar results, giving us a good background to state that the herb-layer flora is distributed in three major floristic groups: Tropical Ombrophilous Forests, Subtropical Ombrophilous Forests and Seasonal Semideciduous Forests. We also found that the ecotones among these floristic groups occur as gradients presided mainly by climate.

The distribution of the herb-layer flora into three floristic groups agrees with the broad divisions of the Brazilian Atlantic Forest into Ombrophilous Forest and Seasonal Semideciduous Forest (IBGE 2012). Although this division was highly supported by our data, the distribution pattern of the herb-layer flora did not support the distinction of mixed ombrophilous forests as a separate phytoecological region. Studying the tree flora of the mixed ombrophilous forests in the State of São Paulo, Souza (2009) and Ribeiro et al. (2013) found that the recognition of this forest sub-type is maintained for its physiognomic aspect (occurrence of *A. angustifolia*) rather than the floristic composition itself.

Further analyses of each floristic group are needed to better clarify the distribution patterns of the herb-layer flora in the Brazilian Atlantic Forest. As indicated by the very high proportion of restricted species (50 %), more surveys on the herb layer in Brazilian Atlantic Forest are needed. Reliable species identification in the inventories is also needed to be improved. To overcome these issues in our analyses, we considered only species that were identified by taxonomic authorities (specialists) and that were recorded in more than one site.

Herbs versus tree species

The three herb-layer floristic groups would be the outcome of present environmental conditions and evolutionary processes, which we suggest to be partially different from the ones that have acted upon the tree flora. During the Quaternary the southern/southeastern Brazilian Atlantic was dominated by grasslands in glacial times (Behling and Lichte 1997), whereas in interglacial times the trees expanded and dispersed from residual gallery forests (Behling et al. 2005). However, both the tree and the herb-layer species have been submitted to the same physical events described in the literature. Why would the resulting geographical pattern be non-identical between these two species sets? We propose that at least partly the answer could rely on differences in evolutionary strategies between their growth habits. Different evolutionary strategies between trees and herbs have been demonstrated by many authors considering different features such as the rate of genome-wide recombination (Jaramillo-Correa et al. 2010), the rates of evolution through time (Levin and Wilson 1976), the age at maturity (Verdú 2002), the breeding system, and the seed dispersal mechanism (Hamrick and Godt 1996). For example, Smith and Donoghue (2008) found a 2.5 times faster average rate of evolution in herbs than in trees or shrubs, thus reaching a maximum rate difference of 4.75 times between the herb *Dorstenia* (Moraceae) and its tree/shrub sister clade.

Petit and Hampe (2006) reviewed the general evolutionary strategies of trees in relation to other growth habits, especially herbaceous plants, and highlighted that (a) trees have higher levels of genetic diversity within their populations than herbaceous plants and shrubs, but smaller differentiation among populations; (b) trees seem to be capable of rapid adaptation to new conditions; (c) trees could experience comparatively more gene flow than herbs with the same mating system; (d) frequent long-distance pollen movements should buffer tree populations against diversity loss resulting from fragmentation; (e) trees should accumulate less mutations per unit of time compared to short-lived plants such as herbs; (f) trees experience markedly slower mutation, nucleotide substitution and speciation rates than other plant forms; (g) trees are able to persist under difficult conditions, thereby reducing extinction risks arising from demographic stochasticity; and (h) local adaptation, despite low evolutionary rates, seems to be the key to the success of tree species from an evolutionary standpoint.

Thus, during glacial times, the herb-layer species may have been confined in gallery forests along the rivers, such as some tree species (Behling 1998, 2002; Behling et al. 2005). In this hypothetical scenario, the distances between isolated patches of gallery forests might have been very strong physical barrier limiting gene flow among populations of herb species. Considering the different evolutionary strategies between trees and herbs and the much faster evolutionary rates of herbs, the climatic oscillations in the Quaternary period in southern/southeastern Atlantic Forest may have acted as much stronger vicariant events for the herb-layer species than for the tree flora. Tree species should be distributed in gradient patterns without sharp limits coinciding with different climates because they would suffer weaker habitat selectivity due to long-distance pollen movements, higher gene flow and rapid adaptation traits. On the other hand, due to their higher level of specialization and lower gene flow (Petit and Hampe 2006), herb-layer species should have been more strongly selected by local conditions, such as high precipitation seasonality and low temperature seasonality (Seasonal Semideciduous Forest group), high temperature and precipitation (Tropical Ombrophilous Forest group), and lower temperatures and high precipitation seasonality (Subtropical Ombrophilous Forest group). We encourage these

hypotheses about differences in pattern and processes among tree and herbaceous species to be tested by several other methods.

Conservation goals

The differences in distribution patterns between herbs and trees that we found are very important for conservation strategies. Our findings suggest that tree and herb-layer species have not completely coincident distribution patterns, implying that the same conservation units do not manage to conserve both species sets. Given that natural reserves should conserve the biodiversity of the region in which they are (Margules et al. 2002), the herb-layer must be included in the assessment of the Brazilian Atlantic Forest protection actions.

Also, Margules and Pressey (2000) stated that the basic role of reserves is to separate elements of biodiversity from processes that threaten their existence in the wild. For instance, global warming can affect the distribution of plant communities by shifting species ranges and changing species composition and risk of extinction (Walther et al. 2002; Schaich and Milad 2013). So, what can we expect for the future distribution of herbaceous species, considering that similar ecological conditions and changes through time may produce different distribution patterns between trees and herbs? We suggest that the indicator species of each floristic group would be interesting objects for modeling studies that could forecast potential distribution ranges for different future climate scenarios.

We highlighted the importance of creating more reserves in each one of the three main floristic groups of herb-layer species in the Brazilian Atlantic Forest, especially in the Seasonal Semideciduous Forest, which includes the most threatened forests considering the small area of the remaining fragments and the high level of isolation between fragments (Ribeiro et al. 2009). Since the greatest challenge of conservation units is to encompass the highest diversity, the criteria to select reserve areas must consider not only the trees, but also the herbaceous species distribution patterns.

Acknowledgments We thank CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for the Doctorate and Master scholarships granted to the first and second authors. The authors are grateful to the São Paulo Research Foundations (FAPESP Grant #2001/05146-6) and Brazilian Council for Research and Technologic Development (CNPq Grant #479084/2007-6) for financial support. We also thank Pedro V. Eisenlohr and Ary Teixeira de Oliveira-Filho for the invitation to this special issue.

References

- APG III (2009) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants. *Bot J Linn Soc* 161:105–121
- Behling H (1998) Late Quaternary vegetational and climatic changes in Brazil. *Rev Palaeobot Palynol* 99:143–156. doi:10.1016/s0034-6667(97)00044-4
- Behling H (2002) South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeogr Palaeoclimatol Palaeoecol* 177:19–27
- Behling H, Lichte M (1997) Evidence of dry and cold climatic conditions at glacial times in tropical SE Brazil. *Quat Res* 48:348–358
- Behling H, Pillar V, Bauermann S (2005) Late Quaternary grassland (Campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in western Rio Grande do Sul (southern Brazil). *Rev Palaeobot Palynol* 133:235–248. doi:10.1016/j.revpalbo.2004.10.004
- Bertoncello R, Yamamoto K, Meireles LD, Shepherd GJ (2011) A phytogeographic analysis of cloud forests and other forest subtypes amidst the Atlantic forests in south and southeast Brazil. *Biodivers Conserv* 20:3413–3433. doi:10.1007/s10531-011-0129-6

- Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Use R! Series. Springer, New York
- Cáceres MD, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574. doi:[10.1890/08-1823.1](https://doi.org/10.1890/08-1823.1)
- Caiafa AN, Martins FR (2007) Taxonomic identification, sampling methods, and minimum size of the tree sampled: implications and perspectives for studies in the Brazilian Atlantic Rainforest. *Funct Ecosyst Commun* 1:95–104
- Carvalho GH, Cianciaruso MV, Batalha MA (2010) Plantminer: a web tool for checking and gathering plant species taxonomic information. *Environ Model Softw* 25:815–816. doi:[10.1016/j.envsoft.2009.11.014](https://doi.org/10.1016/j.envsoft.2009.11.014)
- Cestaro LA, Waechter JL, Baptista LRM (1986) Fitossociologia do estrato herbáceo da mata de Araucária da Estação Ecológica de Aracuri. *Esmeralda, Rio Grande do Sul Hoehnea* 13:59–72
- Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants. *Bioscience* 41:760–766
- Chazdon R, Pearcy R, Lee D, Fetcher N (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey S, Chazdon R, Smith A (eds) Tropical forest plant ecology. Springer, New York, pp 5–55. doi:[10.1007/978-1-4613-1163-8_1](https://doi.org/10.1007/978-1-4613-1163-8_1)
- De Cáceres M, Legendre P, Wiser SK, Brotons L, O'Hara RB (2012) Using species combinations in indicator value analyses. *Methods Ecol Evol* 3:973–982. doi:[10.1111/j.2041-210X.2012.00246.x](https://doi.org/10.1111/j.2041-210X.2012.00246.x)
- Dormann CF et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46. doi:[10.1111/j.1600-0587.2012.07348.x](https://doi.org/10.1111/j.1600-0587.2012.07348.x)
- Dufrene M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Eisenlohr PV (2014) Persisting challenges in multiple models: a note on commonly unnoticed issues regarding collinearity and spatial structure of ecological data Brazilian. *J Bot* 37:365–371. doi:[10.1007/s40415-014-0064-3](https://doi.org/10.1007/s40415-014-0064-3)
- ESRI (2010) ArcGIS 10.0. Environmental Systems Research Institute Inc, Redlands
- Falkenberg DB (2003) Matinhas nebulares e vegetação rupícola dos Aparados da Serra Geral (SCRS), sul do Brasil. PhD, University of Campinas
- Felfili JM, Eisenlohr PV, Melo MMRF, Andrade IA, Meira-Neto JAA (2011) Fitossociologia no Brasil: Métodos e Estudos de Casos, vol 1. Editora UFV, Viçosa
- Forzza RC et al (2010) Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro, Rio de Janeiro
- Gauch HG Jr (1982) Multivariate analysis in community ecology. Cambridge University Press, Cambridge
- Gentry AH, Dodson C (1987) Contribution of non-trees to species richness of a tropical rain forest. *Biotropica* 19:149–156
- Gonzaga APD, Oliveira-Filho AT, Machado ELM, Hargreaves P, Machado JNM (2008) Diagnóstico florístico-estrutural do componente arbóreo da floresta da Serra de São José, Tiradentes, MG, Brasil. *Acta Bot Bras* 22:505–520
- Hamrick JL, Godt MJW (1996) Effects of life history traits on genetic diversity in plant species. *Philos Trans R Soc Lond B Biol Sci* 351:1291–1298
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. doi:[10.1002/joc.1276](https://doi.org/10.1002/joc.1276)
- Hill MO (1973) Reciprocal averaging: an eigenvector method or ordination. *J Ecol* 61:237–249
- IBGE (2012) Manual técnico da vegetação brasileira, 2ª edn. Fundação Instituto Brasileiro de Geografia e Estatística - IBGE, Rio de Janeiro
- Ivanauskas NM, Monteiro R, Rodrigues RR (2000) Similaridade florística entre áreas de floresta atlântica no estado de São Paulo Brazilian. *J Ecol* 1–2:71–81
- Jaramillo-Correa JP, Verdu M, Gonzalez-Martinez SC (2010) The contribution of recombination to heterozygosity differs among plant evolutionary lineages and life-forms. *BMC Evol Biol* 10:22. doi:[10.1186/1471-2148-10-22](https://doi.org/10.1186/1471-2148-10-22)
- Legendre P, Gallagher E (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280. doi:[10.1007/s004420100716](https://doi.org/10.1007/s004420100716)
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Levin DA, Wilson AC (1976) Rates of evolution in seed plants: net increase in diversity of chromosome numbers and species numbers through time. *Proc Natl Acad Sci USA* 73:2086–2090
- Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405:243–253
- Margules C, Pressey R, Williams P (2002) Representing biodiversity: data and procedures for identifying priority areas for conservation. *J Biosci* 27:309–326. doi:[10.1007/bf02704962](https://doi.org/10.1007/bf02704962)
- McCune B (1997) Influence of noisy environmental data on canonical correspondence analysis. *Ecology* 78:2617–2623
- Mulkey SS, Smith AP, Wright SJ (1991) Comparative life history and physiology of two understory neotropical herbs. *Oecologia* 88:263–273

- Oksanen J et al. (2014) vegan: Community Ecology Package. R package version 2.0-10, edn. <http://CRAN.R-project.org/package=vegan>. Accessed 12 Sept 2014
- Oliveira RJ (2006) Variação da composição florística e da diversidade alfa das florestas atlânticas no estado de São Paulo. University of Campinas, Campinas
- Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. *Biotropica* 32:793–810. doi:10.1111/j.1744-7429.2000.tb00619.x
- Oliveira-Filho AT et al (2005) Análise florística do compartimento arbóreo de áreas de Floresta Atlântica sensu lato na região das bacias do leste (Bahia, Minas Gerais, Espírito Santo e Rio de Janeiro). *Rodriguésia* 56:185–235
- Oliveira-Filho AT, Jarenkow JA, Rodal MJN (2006) Floristic relationships of seasonally dry forests of eastern South America based on tree species distribution patterns. In: Pennington RT, Lewis GP, Ratter JA (eds) Neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation. CRC Press, New York, pp 159–192
- Palmer MW (1993) Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74:2215–2230
- Pearcy RW (1983) The light environment and growth of C3 and C4 tree species in the understory of a Hawaiian forest. *Oecologia* 58:19–25. doi:10.1007/bf00384537
- Petit RJ, Hampe A (2006) Some evolutionary consequences of being a tree. *Annu Rev Ecol Syst* 37:187–214. doi:10.1146/annurev.ecolsys.37.091305.110215
- R Development Core Team (2014) R: a language and environment for statistical computing, 3.1.1 edn. R Foundation for Statistical Computing, Vienna
- Raich JW (1989) Seasonal and spatial variation in the light environment in a tropical dipterocarp forest and gaps. *Biotropica* 21:299–302
- Rao CR (1964) The use and interpretation of principal component analysis in applied research *Sankhya*. *Indian J Stat Ser A* 26:329–358
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biol Conserv* 142:1141–1153
- Ribeiro TM, Iwanauskas NM, Martins SV, Polisel RT, Santos RLRd, Miranda Neto A (2013) Mixed rain forest in southeastern Brazil: tree species regeneration and floristic relationships in a remaining stretch of forest near the city of Itaberá. *Brazil Acta Bot Bras* 27:71–86
- Richards PW (1996) The tropical rain forest: an ecological study. Cambridge University Press, Cambridge
- Salis SM, Shepherd GJ, Joly CA (1995) Floristic comparison of mesophytic semideciduous forests of the interior of the state of São Paulo. *Southeast Brazil Vegetatio* 119:155–164
- Schaich H, Milad M (2013) Forest biodiversity in a changing climate: which logic for conservation strategies? *Biodivers Conserv* 22:1107–1114. doi:10.1007/s10531-013-0491-7
- Scudeller VV, Martins FR, Shepherd GJ (2001) Distribution and abundance of arboreal species in the Atlantic ombrophilous dense forest in southeastern Brazil. *Plant Ecol* 152:185–199
- Smith SA, Donoghue MJ (2008) Rates of molecular evolution are linked to life history in flowering plants. *Science* 322:86–89. doi:10.1126/science.1163197
- Smith AR, Pryer KM, Schuettpelz E, Korall P, Schneider H, Wolf PG (2006) A classification for extant ferns *Taxon* 55:705–731
- Souza RPM (2009) Estrutura da comunidade arbórea de trechos de florestas de Araucaria no estado de São Paulo, Brasil. Escola Superior de Agricultura Luiz de Queiroz - ESALQ/USP
- ter Braak CJF (1995) Ordination. In: Jongmann RHG, ter Braak CJF, van Tangeeren ORF (eds) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, pp 91–173
- Torres RB, Martins FR, Kinoshita LS (1997) Climate, soil and tree flora relationships in forests in the state of São Paulo, southeastern Brazil. *Rev Bras Bot* 20:41–49
- Tropicos.org (2011) Missouri Botanical Garden <http://www.tropicos.org/>. Accessed 2010–2011
- Verdú M (2002) Age at maturity and diversification in woody angiosperms. *Evolution* 56:1352–1361. doi:10.1111/j.0014-3820.2002.tb01449.x
- Walther G-R et al (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Wartenberg D, Ferson S, Rohlf FJ (1987) Putting things in order: a critique of detrended correspondence analysis. *Am Nat* 129:434–448
- Yamamoto LF, Kinoshita LS, Martins FR (2005) Florística dos componentes arbóreo e arbustivo de um trecho da Floresta Estacional Semidecídica Montana, município de Pedreira, estado de São Paulo. *Rev Bras Bot* 28:191–202
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14. doi:10.1111/j.2041-210X.2009.00001.x