Acta bot. bras. 24(2): 369-377. 2010.

Influence of environmental variation on Atlantic Forest tree-shrub-layer phytogeography in southeast Brazil

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Recebido em 15/07/2009. Aceito em 22/01/2010

ABSTRACT – (Influence of environmental variation on Atlantic Forest tree-shrub-layer phytogeography in southeast Brazil). This work assessed data from 32 forest sites in Rio de Janeiro and São Paulo, Brazil, using multivariate analysis to answer the question: Are there floristic patterns of the Atlantic Forest tree-shrub layer related to the Serra do Mar and the width of coastal plains in the states of Rio de Janeiro and São Paulo? Three multivariate analyses were performed to investigate the relationship between the tree-shrub flora and environmental variation in these 32 study areas. Our analyses demonstrated the influence of geo-climatic variation on floristic differentiation of tree and shrub species in Atlantic Forest regions generating groups of areas based on similar biotic and abiotic characteristics. These groups support the existence of floristic patterns within the states of São Paulo and Rio de Janeiro and reflect tree-shrub species substitution between the study areas as a consequence of annual rainfall, altitude, and mean annual temperature variation linked to a change in the position of the Serra do Mar and an increase in coastal plain width. Preferential species were cited for each group and should be considered in restoration and conservation programs for the phytoecological regions represented by the groups.
Key words: Atlantic rain forest, floristic composition, multivariate analyses, phytogeography

RESUMO – (Influência da variação ambiental sobre a fitogeografia do estrato arbóreo-arbustivo da Mata Atlântica em dois estados do sudeste brasileiro). O presente trabalho analisou dados de 32 remanescentes florestais nos estados do Rio de Janeiro e São Paulo, através de análises multivariadas para responder a pergunta: Existem padrões floristicos do estrato arbóreo-arbustivo da Floresta Atlântica relacionados a Serra do Mar e alargamento das planícies costeiras nos estados do Rio de Janeiro e São Paulo? Foram utilizadas três análises multivariadas para investigar as relações entre a flora arbóreo-arbustiva e a variação ambiental das 32 áreas. As análises demonstraram influência de alterações geo-climáticas sobre a diferenciação florística das espécies arbóreas e arbustivas da Mata Atlântica. Este fato permitiu gerar grupos com as áreas analisadas baseados em características bióticas e abióticas, sustentando a existência de padrões florísticos nos estados do Rio de Janeiro e São Paulo. Os grupos formados refletem a substituição das espécies arbóreo-arbustivas entre as áreas analisadas como conseqüência de variações da precipitação, altitude e temperatura média anual à medida que modifica o posicionamento da Serra do Mar e cresce a planície costeira. Para cada grupo foram designadas espécies preferenciais que devem ser consideradas em programas de restauração e conservação das regiões fitoecológicas por eles representadas.
Palavras-chave: Análise multivariada, composição florística, fitogeografia, Mata Atlântica

Introduction

Ecosystem fragmentation is one of the major causes of the loss of biodiversity on our planet. The Atlantic forest is the most threatened biome in Brazil, its degradation having been initiated in the 16th century and accelerated with expansion of agriculture and fixation of Europeans and Africans along the Brazilian coast (SOS Atlantic Forest & INPE 2002). Today this forest is one of the planet's 35 biodiversity hotspots, with high species richness and high levels of endemism, although it suffers from rapid reduction of intact habitats (Myers *et al*. 2000). There has been significant recent interest in studies that assess the consequences of forest fragmentation on biodiversity conservation, as many forests have been reduced to disconnected areas (Schellas & Greenberg 1997, Viana *et al*. 1997). These studies have stimulated initiatives for the conservation of remnant areas, as in the case of the Atlantic forest that now occupies only eight percent of its original range (Galindo-Leal & Câmara 2003).

A number of floristic studies in remnant forests on the southeastern Brazilian coast have demonstrated the heterogeneity of the biome as a whole, with greatest similarity between regions of equal forest formation (Peixoto *et al*. 1995, Sanchez *et al*. 1999, Moreno *et al.* 2003, Peixoto *et al.* 2004, Gomes *et al*. 2005, Guedes-Bruni *et al.* 2006b). Studies employing multivariate analyses to facilitate identification of ecological patterns in floristic data (Kent & Coker 1992) have concentrated on phytogeographic relationships and geo-climatic influences in the southeastern part of the country. These studies have revealed important information about the Atlantic forest in that region, such as the floristic differences between ombrophilous and seasonal forests in relation to rainfall; greater similarities between ombrophilous and seasonal forests than with other forest formations; differentiation between ombrophilous and seasonal forests that can be attributed to altitude and temperature; a "gap" in the ombrophilous forest in northern Rio de Janeiro state due to this region's seasonal climate, which cannot be defined as a proper disjunction in distribution of tree species; and the existence of three floristic blocks in Rio de Janeiro state based on tree species of the Fabaceae family (Oliveira-Filho & Fontes 2000, Oliveira-Filho *et al.* 2005, H.C.Lima, unpublished data). Given the value of this kind of information for decision makers and agents involved in planning

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conservation programs in southeastern Brazil, there is a real need for a better understanding of how the environment affects phytogeographic relationships between Atlantic forests remnants in Rio de Janeiro and São Paulo states.

Many of the remnant areas of Atlantic forest in Rio de Janeiro and São Paulo are located in the Serra do Mar and Mantiqueira mountain ranges, which are aligned subparallel to each other (Almeida & Carneiro 1998). The Serra do Mar mountain range crosses these two states in a northeasterly direction, stretching from the southern coast of São Paulo state to northern coastal Rio de Janeiro. In São Paulo the mountain range generally remains close to the coastline and forms a natural barrier capturing orographic rains that fall on the narrow coastal plain and mountain slopes facing the ocean (Barbosa 2007). At Itacuruçá (Rio de Janeiro), the Serra do Mar mountain range advances into the interior of the state, receiving different names as it stretches to northern Rio de Janeiro. The inland orientation of Serra do Mar allows occurrence of a wider coastal plain in Rio de Janeiro than in São Paulo, which is then gradually replaced by tablelands in northern Rio de Janeiro. Changes in the orientation of Serra do Mar mountain range and widening of the coastal plain are attributed to the Guanabara Graben, which was formed by the erosion and retreat of the Atlantic Plateau scarps during the Paleocene era (Almeida & Carneiro 1998).

Considering that the floristic composition of ombrophilous and seasonal forests within the Atlantic forest biome are related to climate variation (Oliveira-Filho & Fontes 2000, Oliveira-Filho *et al.* 2005) and that environmental variation can influence climate (Leuschner 2000), the present study aims to answer the question: Are there floristic patterns of the Atlantic Forest tree-shrub layer related to Serra do Mar and widening of coastal plains in the states of Rio de Janeiro and São Paulo? In order to address to this question we tested the prediction that such floristic patterns do not exist, thus allowing us to accept or reject our null hypothesis.

Material and methods

Atlantic forest data – 32 floristic studies from the states of Rio de Janeiro and São Paulo were selected (Fig. 1) to form two databases. The first consists of a binary matrix (presence/absence) of the tree and shrub species in the 32 areas. The second consists of environmental and geographic information on altitude (a), average annual rainfall (b), average annual temperature (c), average annual temperature variation (d), distance from the ocean (e), latitude - UTM (f), and longitude – UTM (g) of these sites. When these geo-environmental variables were not specified in the original publication, we consulted the authors of the papers, the National Meteorological Institute (2006) or DNMet (1992). The first database was fully revised to eliminate synonyms and errors in the presence/absence of species that could influence the results. In its final form, the matrix contained 1590 species.

Multivariate analysis – canonical correspondence analysis (CCA) was performed (ter Braak 1995) using Canoco for Windows Version 4.5 software program (ter Braak & Smilauer 2002) to investigate the relationship between the tree flora (at the taxonomic level of species) and geo-environmental variables. After preliminary analysis of the data, variation in average annual temperatures (d) and distance from the ocean (e) were discarded from further analysis due to a weak correlation with the four axes ("intra-set" correlation < 0.4) since they poorly explain variation within the data. We opted to maintain species that occurred in at least one of the 32 areas in the database, as their removal greatly reduced the eigenvalues of the axes. However, species considered discrepant with the main cloud of points in the CCA were eliminated during the analysis (Kent & Coker 1992) so that the final principal matrix was composed of 1412 species. A Monte Carlo permutation test was performed to assess the significance of the correlations found by CCA.

We also performed a cluster analysis, using the Jaccard similarity coefficient, through unweighted pair-group method (UPGMA) or group average (McCune & Grace 2002), in order to verify the existence of groups

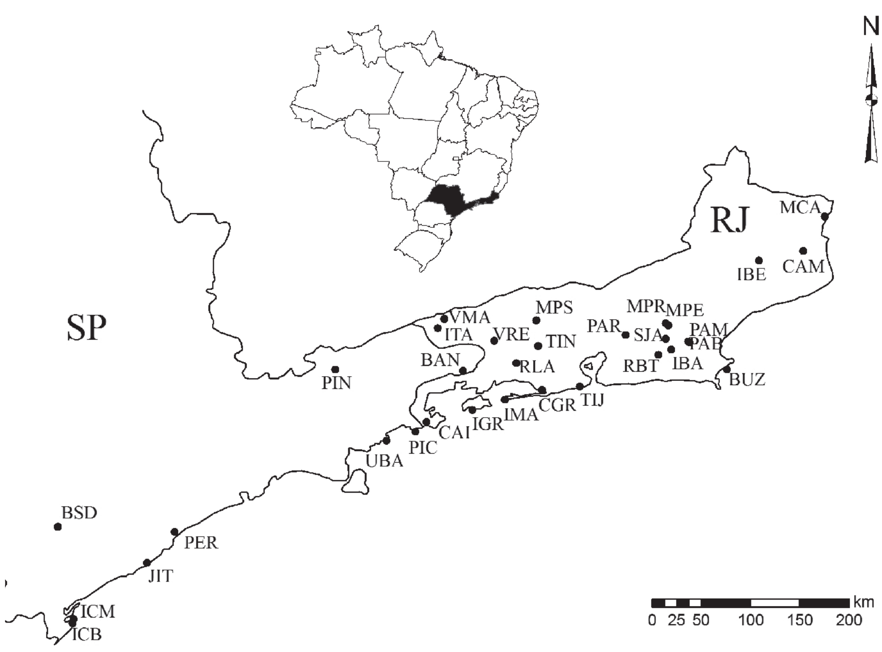

Figure 1. Map indicating the location of the 32 sites analyzed in this study.

based on floristic similarities among the areas analyzed, using MVSP 3.1 – MultiVariate Statistical Package software program (Kovach 2004). TWINSPAN analysis with PC-ORD 4.10 program (McCune & Mefford 1999) allowed us to identify key species among the groups formed by the cluster analysis (Kent & Coker 1992).

Results and discussion

The Atlantic forest sites examined by multivariate analysis are listed in Table 1, and the results of the CCA analyses are shown in Tables 2 and 3. The eigenvalues encountered for the first two axes of the CCA were relatively high (> 0.4), indicating changes in species composition along the gradients synthesized in these ordination axes (ter Braak 1995). The cumulative percentage of variance explained by the axes was low (17.6%), indicating a considerable amount of unexplained "noise". This type of situation is quite common for floristic data and does not diminish the significance of the species-environment relationship (Oliveira-Filho & Fontes 2000). In fact, Pearson's correlations for taxa-environment were consistently high (Table 2) ($r > 0.9$). The Monte-Carlo permutation test indicated high significance (<0.01) of the data expressed in the first canonical axis, as well as for all of the ordination axes considered together (Table 2).

The gradient expressed in the first canonical ordination axis is consistently correlated with longitude (r = 0.65), annual temperature (r = 0.62), and rainfall (r = - 0.63). The second axis showed consistent correlations with latitude (r = 0.83), altitude (r = 0.68), and longitude (r = 0.64). Consistent correlations were also observed between altitude and annual temperature (r = - 0.7); longitude and rainfall (r = - 0.73); and latitude and longitude (r = 0.82) (Table 3). As such, the first ordination axis mainly reflects the change in floristic composition between the states of São Paulo and Rio de Janeiro, indicating a geographic gradient with higher average temperatures and lower altitude and rainfall with increasing longitude in a northeasterly direction. The second axis expresses primarily the gradual alteration of species related to changes in latitude and altitude (latitude diminishing towards the south, and altitude diminishing both towards the coastline and to the northeast). These results are in agreement with patterns observed in southeastern Brazil that indicated the influence of geo-environmental factors on the differentiation of the tree flora in that region (Oliveira-Filho *et al.* 2005).

The relationship between environmental variables and species composition of the 32 sites of Atlantic forest is illustrated by the CCA diagram (Fig. 2). Three distinct groups can be identified: one group of areas (black squares) in the lower left quadrant are all located along (or very near to) the Serra do Mar range near the São Paulo coast, and they are united by a floristic pattern determined by high levels of rainfall, predominantly high temperatures, and low-to-medium altitudes; a group in the upper left quadrant (black triangles) formed by sites in both São Paulo and Rio de Janeiro is associated with high altitudes, low annual temperatures, and intermediate rainfall levels; a large group in the upper and lower right-hand quadrant (white circles) is formed by sites in the Serra do Mar (RJ), Guanabara Graben, coastal mountains, and northern region, all in Rio de Janeiro state, and are associated with low-to-average altitudes, low-to-intermediate rainfall, and high annual temperatures (Fig. 2). These results demonstrate that the floristic differentiation between areas of Atlantic forest in Rio de Janeiro and those in São Paulo are a result of differences in rainfall, altitude, and average annual temperature, and reinforces the role of geo-environmental variables in speciation (Gentry 1982, Huggett 1995, Oliveira-Filho *et al.* 2005).

Among the various environmental factors examined, rainfall plays a significant role in the floristic differentiation between São Paulo and Rio de Janeiro. The importance of rainfall in determining floristic composition has already been confirmed in extensive studies in the Neotropics and in the differentiation of ombrophilous and seasonal forests in the Atlantic forest biome of southeastern Brazil (Gentry 1982, Oliveira-Filho & Fontes 2000). Rainfall decreases from São Paulo to Rio de Janeiro following the Serra do Mar range (which crosses the coastal region of São Paulo in a northeasterly direction) as the slopes become more distant from the coastline, thus causing decreasing influence on orographic rainfall, as the range approaches southern Rio de Janeiro (and northeastern São Paulo state), and allowing widening of the coastal plains known as Guanabara Graben (Almeida & Carneiro 1998). This geographic situation translates into heavier rainfall on the coastal plains (and the slopes of the Serra do Mar range in São Paulo) and lighter rainfall in Rio de Janeiro state (Barbosa 2007). This variation in rainfall imposed by landform changes helps explain the differences observed between the Atlantic forest of São Paulo and Rio de Janeiro (Huggett 1995).

The heterogeneity of the Atlantic forest has been examined in various comparative studies employing cluster analysis (Peixoto *et al.* 2004, Carvalho *et al.* 2006b, Rolim *et al.* 2006). The use of this technique together with TWINSPAN analysis has confirmed and refined information generated by CCA. The interpretation of the dendrogram obtained in the similarity analysis is a subjective task that depends greatly on the researcher who must subdivide groups if there is compelling ecological evidence (Kent & Coker 1992). As such, three consecutive cuts of the dendrogram defined the groups "A", "B", "C", "D", "E", "F", and "G". In the first cut, two principal groups ("A" and "B") were identified; in the second cut, group "B" was subdivided into "C", "D", and "E"; and in the third cut, "E" was subdivided into "F" and "G" (Fig. 3).

Group "A" was separated from the group of dense ombrophilous forests ("B") and is composed mainly of seasonal forests (Fig. 3). According to the CCA, the four sites in this group are related by high temperatures, low rainfall, and low altitude. Although the CGR site is geographically distant from the other sites in this group

Table 1. Code designation, bibliography, and general data concerning 32 areas analyzed in the present study located in the states of Rio de Janeiro and São Paulo, Brazil. Temp. = average annual temperature, Rain = average annual rain (mm), Method = methodology, Total sample = total area (m2) or numbers of points, S = number of species. * Forest formations: FOD = dense ombrophilous forest, FES = semi-deciduous seasonal forest, TB = lowland forests (*Terras Baixas*), SM = submontane, M = Montane. Methodology applied: P = plots, T = transects, PQ = point quadrant, CL = free walks. ** unpublished data.

Códe	Study locality	Forest formation *	Altitude(m)	Temp.(ºC)	Rain	Method*	Inclusion Criteria	Total sample	S	Total nº of individuals
BAN, SP	Bananal**	FODM	1550	17.00	1455.70	PQ	DBH ≥ 5 cm	100	105	400
BSD, SP	Base Saibadela - Zipparro *et al.* (2005).	FODSM	160	23.05	4000.00	CL	Fertile plants	—	241	—
BUZ, RJ	Mata de José Gonçalves**	FESTB	0	28.00	822.00	P	DBH ≥ 5 cm	5000	101	1255
CAI, RJ	Cairuçu, Parati - Marques (1997).	FODSM	700	22.50	2390.00	CL	Fertile plants	—	445	—
CAM, RJ	Campos dos Goytacazes - Carvalho *et al*. (2006a).	FESTB	20	22.70	1023.00	PQ	DBH ≥ 3.2 cm	84	93	336
CGR, RJ	Serra da Capoeira Grande - Peixoto *et al.* (2004).	FODTB	80	23.60	1027.20	PQ	DBH ≥ 4.77 cm	200	64	800
IBA, RJ	Imbaú - Carvalho *et al.* (2006b).	FODSM	250	22.80	1750.00	P	DBH ≥ 5 cm	10000	139	1591
IBE, RJ	Região do Imbé - Moreno *et al.* (2003).	FODSM	150	21.50	1300.00	P	DBH ≥ 10 cm	12000	150	940
ICB, SP	Ilha do Cardoso, baixada**	FODTB	130	22.10	2359.75	P	DBH ≥ 2.5	8000	100	2200
ICM, SP	Ilha do Cardoso, encosta - Melo & Mantovani (1994).	FODSM	400	24.10	2359.75	P	DBH ≥ 2.5	10000	146	2510
IGR, RJ	Praia do Sul, Ilha Grande - Oliveira (2002).	FODSM	165	22.50	1975.00	P	DBH ≥ 2.5 cm	7800	187	2232
IMA, RJ	Ilha da Marambaia - Conde *et al*. (2005).	FODSM	300	23.70	1239.70	T	DBH ≥ 5 cm	4000	239	944
ITA, RJ	Parque Nacional de Itatiaia**	FODM	800	19.00	1765.80	P	DBH ≥ 5 cm	10000	117	569
JIT, SP	Juréia – Itatins - Mamede *et al.* (2004).	FODSM	152	21.40	2000.00	CL	Fertile plants	—	324	—
MCA, RJ	Mata do Carvão - Silva & Nascimento (2001).	FESTB	100	23.00	1084.00	P	DBH ≥ 10 cm	10000	57	564
MPE, RJ	Macaé de Cima secundária - Pessoa *et al.* (1997).	FODM	1000	17.90	2128.00	P	DBH ≥ 5 cm	10000	127	2217
MPR, RJ	Macaé de Cima preservada - Guedes-Bruni *et al.* (1997).	FODM	1100	17.90	2128.00	P	DBH ≥ 5 cm	10000	168	2288
MPS, RJ	Marques de Valença, vale do Paraíba**	FESSM	364	21.00	1285.20	P	DBH ≥ 5 cm	3000	72	395
PAB, RJ	Poço das Antas baixada - Guedes-Bruni *et al*. (2006a).	FODTB	15	24.50	2118.00	P	DBH ≥ 5 cm	10000	83	628
PAM, RJ	Poço das Antas morrote - Guedes-Bruni *et al*. (2006b).	FODSM	115	24.50	2118.00	P	DBH ≥ 5 cm	10000	131	580
PAR, RJ	Cachoeiras de Macacu - Kurtz & Araujo (2000).	FODSM	200	23.00	2558.40	PQ	DBH ≥ 5 cm	150	116	592
PER, SP	Peruíbe - Oliveira *et al.* (2001).	FODSM	250	22.00	2000.00	P	DBH ≥ 5 cm	2875	78	1534
PIC, SP	Picinguaba - Sanchez *et al.* (1999).	FODSM	100	21.90	2448.30	P	DBH ≥ 6.36 cm	4000	115	673
PIN, SP	Pindamonhangaba - Gomes *et al.* (2005).	FODM	875	19.30	2150.00	P	DBH ≥ 5 cm.	2500	74	517
RBT, RJ	Rio Bonito - Carvalho *et al.* (2007).	FODSM	100	26.00	1750.00	P	DBH ≥ 5 cm	4000	94	776
RLA, RJ	Represa de Ribeirão das Lages - Peixoto *et al.* (1995).	FODSM	400	17.50	1717.50	CL	Fertile plants	—	209	—
SJA, RJ	Silva Jardim - Borém & Oliveira-Filho (2002).	FODSM	300	24.20	2188.00	P	DBH ≥ 3.18 cm	3600	146	579
TIJ, RJ	Maciço da Tijuca - Oliveira *et al*. (1995).	FODSM	716	23.80	2300.00	P	DBH ≥ 2.5 cm	2500	175	1207
TIN, RJ	Reserva Biológica Tinguá**	FODM	730	21.60	2099.30	PQ	DBH ≥ 2.5	200	158	800
UBA, SP	Ubatuba - Silva & Leitão Filho (1982).	FODSM	120	22.60	2448.30	PQ	DBH ≥ 10 cm	160	103	640
VMA, RJ	Visconde de Mauá - Pereira *et al.* (2006).	FODM	1250	16.60	2459.00	CL	Fertile plants	—	191	—
VRE, RJ	Floresta da Cicuta, Volta Redonda**	FODSM	360	20.50	1370.00	P	DBH ≥ 2.5 cm	3000	135	969

Table 2. Summary of the results of the canonical correspondence analysis (CCA) and Monte Carlo test with the arboreal flora and environmental variable in 32 areas of Atlantic Forest in the states of Rio de Janeiro and São Paulo.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.465	0.423	0.283	0.261
Species Correlation– environment.	0.976	0.976	0.970	0.943
Variance Accumulation of the species data (%).	5.7	10.9	14.4	17.6
Variance Accumulation of the species relationship – environment (%).	27.6	52.7	69.5	85.0
Monte Carlo Significance Test of the first canonical axis: 0.0006 Monte Carlo Significance Test of the sum of all of the canonical axes: 0.0002				

Table 3. Results of the canonical correspondence analysis (CCA), providing intra-set and inter-set correlations for the first two axes, and the correlations between the environmental variables. Alt. = altitude, Prec. = average annual precipitation, Temp. = average annual temperature, Lat. = latitude; Long. = longitude.

Geo-environmental Variable	Intra-set Correlations		Inter-set Correlations		Geographic and climatic variables				
	Axis 1	Axis 2	Axis 1	Axis 2	Alt.	Prec.	Temp.	Lat.	Long.
Altitude	-0.51	0.68	-0.52	0.70	1.00	---	---	---	---
Precipitation	-0.63	-0.29	-0.65	-0.30	0.01	1.00	---	---	---
Annual temperature	0.62	-0.54	0.63	-0.55	-0.70	-0.02	1.00	---	---
Latitude	0.45	0.83	0.46	0.85	0.30	-0.45	-0.21	1.00	---
Longitude	0.65	0.64	0.66	0.65	0.030	-0.73	0.05	0.82	1.00

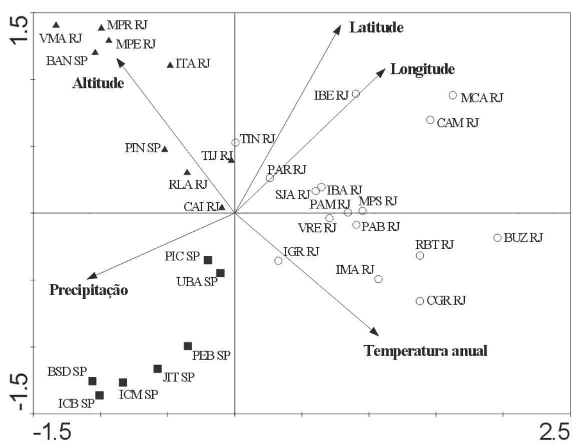

Figure 2. Diagram of canonical correspondence analysis (CCA). The grouping tendencies, demonstrating floristic patterns generated by geo-environmental variation, are denoted by different symbols.

(south-central Rio de Janeiro), and is classified as a dense submontane ombrophilous forest (Veloso *et al.* 1991), it has environmental traits that lend a seasonal character to the site and contribute to differentiating it from other areas in São Paulo and Rio de Janeiro (as has been demonstrated in studies by Oliveira-Filho & Fontes 2000; Moreno *et al.* 2003) – but makes it very similar to the rest of group "A" (Fig. 2). Group "A" has an associated flora composed of species such as *Alseis pickelii* Pilger & Schmale, *Acosmium lentiscifolium* Vogel, *Metrodorea brevifolia* Engl., *Pereskia grandifolia* Haw., and *Trichilia pseudostipularis* (A. Juss.) C. DC., which were identified based on the results of TWINSPAN (Table 4).

Group "B" is composed of dense ombrophilous forests in the states of São Paulo and Rio de Janeiro (Fig. 3) with typical species such as *Alchornea triplinervia* (Spreng.) Müll. Arg., *Cabralea cangerana* Saldanha, *Cariniana estrellensis* (Raddi) Kuntze, *Chrysophyllum flexuosum* Mart., *Euterpe edulis* Mart., and *Licania kunthiana* Hook. f. (Table 4). The inclusion of the MPS site (classified as a semideciduous seasonal forest by Veloso *et al.* 1991) in group "B", as well as its proximity to the dense ombrophilous forests in the CCA diagram (Fig. 2), suggests that the flora is strongly influenced by the surrounding forest formations (Serra do Mar and Serra da Mantiqueira) and helps explain its inclusion in this group. The CCA diagram attributes greater rainfall, intermediate-to-high altitudes, and lower annual temperatures to group "B". It appears that these factors constitute the principal forces of floristic differentiation between the sites in groups "A" and "B".

Dense ombrophilous forest sites are generally grouped together when compared to other physiognomies (Carvalho *et al.* 2006b, Rolim *et al.* 2006), although natural heterogeneity allowed us to separate group "B" into sub-groups "C", "D", and "E" (Fig. 3).

Group "C" comprises areas of dense montane ombrophilous forest – DMOF (Fig. 3) and demonstrated the same tendency in CCA (Fig. 2). The similarities between the high montane forests of São Paulo and Rio de Janeiro draw attention to the relationship between the forests in these two mountain chains (Serra do Mar and Mantiqueira) that are separated by the Paraíba do Sul River valley. This observation was also supported by investigations undertaken

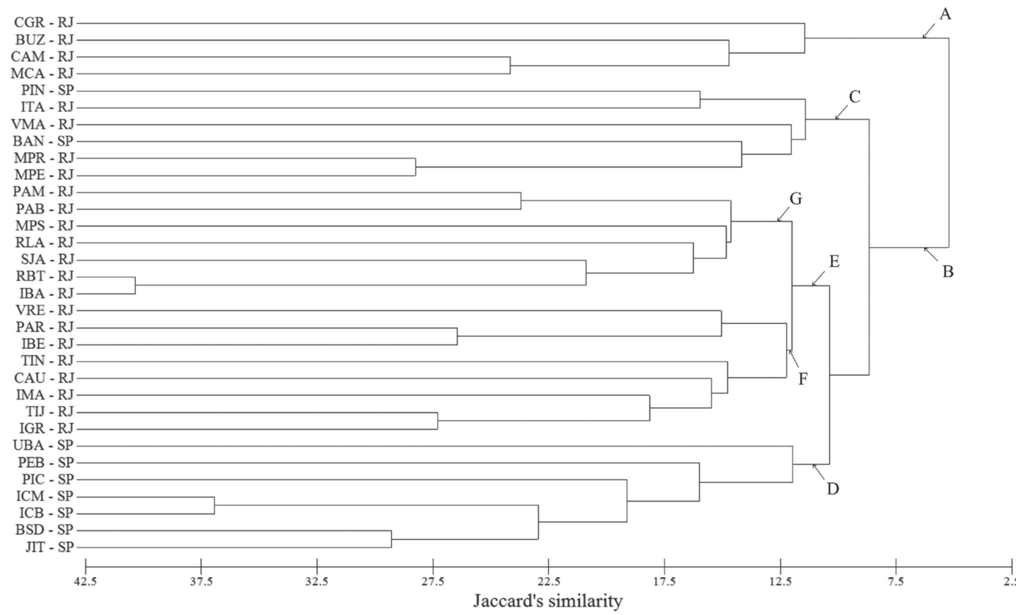

Figure 3. Cluster dendrogram of 32 sites of Atlantic forest in Rio de Janeiro and São Paulo. Associations are generated by group average after calculation of sites Jaccard coefficient similarity matrix. Groups are indicated by letters A, B, C, D, E, F and G. Since there was no dendrogram similarity value smaller than 4% or higher than 42%, axis range is shown from 2,5% to 42,5% to facilitate visualization.

in southeastern Brazil (Oliveira-Filho & Fontes 2000), in the region of Bacias do Leste (Oliveira-Filho *et al.* 2005), and in Rio de Janeiro state (H.C.Lima, unpublished data). As such, our results corroborate the evolution of species in response to limiting factors imposed by high regional altitude and associated temperature variation (Webster 1995). This group comprises characteristic species such as *Cordia ochnacea* DC., *Macropeplus ligustrinus* (Tul.) Perkins, *Ocotea vaccinioides* (Meisn.) Mez, *Vochysia rectiflora* Warm., and *Weinmannia paulliniifolia* Pohl. (Table 4). Although the Tinguá site is classified as a dense montane ombrophilous forest (Veloso *et al.* 1991) it was grouped with forests found at medium-to-low altitudes. This may be the result of sampling in Tinguá, which was concentrated at lower elevations (Rodrigues, unpublished data).

The areas included in group "D" are located along the coast of São Paulo in the Serra do Mar range (with the exception of BSD in the Serra de Paranapiacaba range). These same localities were also grouped by CCA, mainly because of high rainfall, high temperatures, and low-to-medium altitudes (Fig. 2). The formation of group "D", and its distinction from group "E" in the cluster analysis, confirms a floristic differentiation between dense ombrophilous forests in São Paulo and Rio de Janeiro (Fig. 3). This differentiation may be related principally to rainfall, as suggested by the CCA diagram. The separation between the ombrophilous forests in the states of São Paulo and Rio de Janeiro had been detected in earlier studies (Oliveira-Filho & Fontes 2000, Oliveira-Filho *et al.* 2005, Rolim *et al.* 2006). The present study emphasizes the determinant role of landscape in the floristic composition of the Atlantic forest in these states through its influence on regional rainfall patterns (Almeida & Carneiro 1998, Barbosa 2007) that are in turn responsible for the observed difference in species composition. Some of the species indicated as typical for group "D" through TWINSPAN analysis include *Ilex dumosa* Reissek, *Ixora burchelliana* Müll. Arg., *Pseudopiptadenia warmingii* (Benth.) G.P. Lewis & M.P. Lima, and *Roupala paulensis* Sleumer. (Table 4).

Group "E" unites dense ombrophilous forests at low-to-medium altitudes in Rio de Janeiro state having typical species such as *Cordia trichotoma* (Vell.) Arráb. ex Steud., *Guarea kunthiana* A. Juss., *Miconia prasina* (Sw.) DC., *Ocotea schottii* (Meisn.) Mez, *Pradosia kuhlmannii* Toledo, *Sorocea hilarii* Gaudich., and *Xylopia sericea* A. St.-Hil. (Table 4). As was suggested earlier, the floristic differences between groups "E" and "D" appear to result mainly from differences in rainfall between São Paulo and Rio de Janeiro. However, according to the CCA diagram (Fig. 2), it is also possible to detect the influence of higher annual temperatures on the sites in Rio de Janeiro included in group "E", as they are often located on the coastal plain region in the Guanabara Graben. As such, the floristic differences between groups "E" and "D" can be attributed to variation in rainfall and annual temperatures – reinforcing the influence of landscape features on the differentiation of the tree-shrub composition of forests in Rio de Janeiro and São Paulo. Group "E" can be further subdivided into "F" and "G". This subdivision reflects a tendency towards a floristic differentiation between areas in the Guanabara Graben and those on the slopes of the

Table 4. Species associated with the principal groups defined by the grouping analysis, selected on the basis of the TWINSPAN results and based on the species encountered in the 32 areas of Atlantic Forest.

Group	Key Species
A	*Acosmium lentiscifolium, Alseis involuta, Alseis pickelii, Aspidosperma multiflorum, Brasiliopuntia brasiliensis, Caesalpinia ferrea, Trichilia pseudostipularis, Peltogyne discolor, Pereskia grandifolia, Metrodorea brevifolia, Spondias lutea, Parapiptadenia pterosperma, Neoraputia alba, Pterygota brasiliensis, Trigoniodendron spiritusanctense, Rinorea laevigata.*
B	*Aegiphila sellowiana, Alchornea triplinervia, Alseis floribunda, Annona dolabripetala, Aparisthmium cordatum, Cabralea cangerana, Calyptranthes lucida, Cariniana estrellensis, Cecropia glaziovi, Cinnamomum estrellense, Clethra scabra, Chrysophyllum flexuosum, Croton floribundus, Cryptocarya moschata, Cupania oblongifolia, Ecclinusa ramiflora, Endlicheria paniculata, Eriotheca pentaphylla, Euterpe edulis, Garcinia gardneriana, Gomidesia spectabilis, Guarea macrophylla, Handroanthus heptaphylla, Heisteria silvianii, Hirtella hebeclada, Lamanonia ternata, Licania kunthiana, Licaria armeniaca, Machaerium nyctitans, Marlierea obscura, Matayba guianensis, Miconia cinnamomifolia, Micropholis crassipedicellata, Mollinedia schottiana, Myrcia pubipetala, Ocotea dispersa, Ocotea elegans, Pouteria caimito, Psychotria nuda, Quiina glaziovii, Sloanea guianensis, Sloanea monosperma, Tetrorchidium rubrivenium, Trichilia lepidota, Virola oleifera, Xylopia brasiliensis.*
C	*Casearia lasiophylla, Cordia ochnacea, Croton organensis, Daphnopsis fasciculata, Geonoma pohliana, Macropeplus ligustrinus, Meriania claussenii, Miconia brunnea, Miconia octopetala, Myrsine gardneriana, Ocotea vaccinioides, Persea pyrifolia, Siphoneugena kiaerskoviana, Stephanopodium organense, Tibouchina arborea, Tibouchina fissinervia, Trichipteris phalerata, Vochysia rectiflora, Weinmannia paulliniifolia.*
D	*Cordia sylvestris, Chomelia catharinae, Calycorectes acutatus, Erythroxylum ambiguum, Eugenia bocainensis, Eugenia multicostata, Eugenia peruibensis, Gomidesia tijucensis, Geonoma gamiova, Ilex dumosa, Ixora burchelliana, Leandra mosenii, Machaerium scleroxylum, Malouetia cestroides, Marlierea reitzii, Miconia cabussu, Miconia pyrifolia, Mollinedia uleana, Ossaea sanguinea, Ouratea multiflora, Pilocarpus pauciflorus, Piper schenkii, Pouteria grandifolia, Protium kleinii, Pseudopiptadenia warmingii, Psychotria birotula, Roupala paulensis, Rudgea heurchkii, Ruprechtia laxiflora.*
E	*Bauhinia forficata, Cordia trichotoma, Ficus clusiaefolia, Geissospermum laeve, Guapira nítida, Guarea guidonia, Guarea kunthiana, Helicostylis tomentosa, Lacistema pubescens, Lecythis lanceolata, Melanoxylon brauna, Miconia calvescens, Miconia prasina, Mollinedia puberula, Ocotea diospyrifolia, Ocotea schottii, Phyllostemonodaphne geminiflora, Piper arboreum, Plathymenia foliolosa, Pouteria bangii, Pradosia kuhlmannii, Pseudopiptadenia inaequalis, Pseudolmedia hirtula, Rinorea guianensis, Siparuna arianeae, Sorocea hilarii, Tovomitopsis paniculata, Xylopia sericea.*
F	*Aspidosperma ramiflorum, Carapa guianensis, Chrysophyllum gonocarpum, Eugenia mandiocensis, Eugenia microcarpa, Guatteria villosissima, Ixora gardneriana, Licania tomentosa, Maytenus ardisiifolia, Miconia brasiliensis, Mollinedia longifolia, Mollinedia pachysandra, Myrcia laxiflora, Oxandra martiana, Pausandra megalophylla, Picramnia ciliata, Piper rivinoides, Protium warmingiana, Psychotria brasiliensis, Psychotria subspathacea, Qualea glaziovii, Rudgea langsdorfii, Rinorea physiphora, Siparuna apiosyce, Vochysia oppugnata, Zanthoxylum riedelianum.*
G	*Annona laurifolia, Apuleia leiocarpa, Cassia ferruginea, Chamaecrista ensiformis, Dalbergia nigra, Eugenia supraaxilaris, Guatteria ferruginea, Handroanthus chrysotricha, Handroanthus umbellata, Jacaranda bracteata, Mabea fistulifera, Miconia hypoleuca, Ocotea spectabilis, Peltogyne angustiflora, Vismia guianensis.*

Serra do Mar range in Rio de Janeiro state. When studying leguminous tree species in the Atlantic forest of Rio de Janeiro, H.C.Lima (unpublished data) likewise observed differences between sites on the coastal plain and those on slopes at mid altitudes.

Group "F" has key species such as *Carapa guianensis* Aubl., *Ixora gardneriana* Benth., *Vochysia oppugnata* (Vell.) Warm., and *Zanthoxylum riedelianum* Engl.; while *Apuleia leiocarpa* (Vogel) J.F. Macbr., *Dalbergia nigra* (Vell.) Allemao ex Benth., and *Mabea fistulifera* Benth. are examples of species responsible for the formation of group "G" (Table 4). However, a clear distinction between these two groups, as detected by similarity analysis (Fig. 3), cannot be found when observing the CCA diagram (Fig. 2). This may be the result of differences between the types of analyses utilized. The CCA considers species as well as environmental variability, while similarity analysis considers only species. As such, the sites clustered by the dendrogram into groups "F" and "G" may not necessarily be closely aligned in the CCA diagram. Nonetheless, it is possible to perceive a general tendency for the areas composing group "F" to have greater altitudes but colder annual temperatures, while the members of group "G" have a greater tendency to occur at lower altitudes in areas that have higher annual temperatures (Fig. 2).

It is important to note that only qualitative data was used in the present study, and that quantitative data is generally more reliable as it takes both the occurrence and the abundance of species into consideration (Kent & Coker 1992, McCune & Grace 2002). Despite that our results demonstrate the existence of important floristic patterns in the Atlantic Forest tree-shrub layer in Rio de Janeiro and São Paulo states, indicating the substitution of species across these two states, which corroborates many aspects previously published in the scientific literature (Oliveira-Filho & Fontes 2000, Moreno *et al.* 2003, Peixoto *et al.* 2004, Carvalho *et al.* 2006b, Rolim *et al.* 2006). These changes in floristic composition are related to transition of the Serra do Mar Range landscape as it moves further from the coastline (in a northeasterly direction), with consequent widening of the coastal plain (Guanabara Graben). The observed patterns of floristic differentiation were mainly attributed to high rainfall along the coast of São Paulo state, to high and medium average annual temperatures on coastal plain and mountain slopes in Rio de Janeiro, and to influence of altitudinal variation (Gentry 1982, Webster 1995, Oliveira-Filho *et al.*

2005). Because of these patterns we were able to subdivide the 32 areas analyzed into seven different phytoecological regions of Atlantic Forest through the generation of groups, each of which had several preferential species selected on the basis of TWINSPAN results. Therefore, the information provided by this analysis (Table 4) is a valuable guideline for elaborating a list of species to be used in environmental restoration programs in the seven phytoecological regions here applied. This type of data can be very important for orienting conservation efforts in the Atlantic forest, although efforts should be made to address phytogeographical questions using quantitative data, since this information is more accurate and allows the confirmation or rejection of some of the patterns detected in current studies.

Acknowledgments

The authors would like to thank the Botany Department of the Biology Institute at Universidade Federal Rural of Rio de Janeiro for supporting this study; Cyl Farney Catarino de Sá, Miriam Cristina Alvarez Pereira, Jean Louis Valentin, Alexandre Fernandes Bamberg de Araújo, and the anonymous reviewers for their valuable suggestions regarding this work.

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