

# The role of climate on floristic composition in a latitudinal gradient in the Brazilian Atlantic Forest

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**Background and aims** – Latitudinal gradients have an important influence on species distribution reflecting the effects of environmental factors such as temperature, rainfall, soil, and geographical distance. In the southeastern Brazilian Atlantic Forest, the role of climatic variables in the floristic composition is better known for altitudinal gradients of the *Serra do Mar* Mountains rather than for the latitudinal gradient. Here, we investigated the effects of mean annual temperature and rainfall on tree species distribution and composition in a latitudinal gradient in the Atlantic forest.

**Methods** – We calculated each species frequency of occurrence and the latitudinal range. We used multivariate analyses (direct ordination, Hierarchical Clustering followed by Indicator Species analysis and NMDS) to investigate variation in floristic composition, and regression analyses to evaluate mean annual temperatures and rainfall effects on tree species composition along the latitudinal gradient (21°S to 28°S).

**Key results** – A total of 789 species were registered, of which a majority (646 species) were present in less than 20% of the sampled areas, and only four species (0.5%) were present in more than 80% of the sampled areas. Only ten species (1.3%) reached the maximum latitudinal range (~6°). We found a strong correlation between variation in floristic composition and the spatial position in the latitudinal gradient. The cluster analyses detected two main floristic groups, one composed by the forests from Rio de Janeiro (21°S to 23°S) and the second by the forests from São Paulo, Paraná and Santa Catarina States (23°S to 28°S). The multiple regression analysis revealed a strong effect of the climatic variables on the variation of the floristic composition along the latitudinal gradient ( $r^2 = 0.81$ ,  $P < 0.001$ ), where 62.82% of the variation were explained by mean annual temperature, 8.27% by annual rainfall and 10.45% by both variables together.

**Conclusions** – The restricted distribution of most species may be explained by variations in mean annual temperature and annual rainfall along the latitudinal gradient. For instance, the decreasing mean annual temperature along the coast and the occurrence of frosts at higher latitudes may limit the southward distribution of some species while the lower annual rainfall (with marked seasonality) in the north of the gradient may limit the northward distribution of other species. Although mean annual temperature explained most of the variation in species composition along the latitudinal gradient, the abrupt variation in annual rainfall may explain the high floristic dissimilarity detected in the north of the gradient.

**Key words** – Atlantic Rain Forest, climatic gradient, *Mata Atlântica*, ombrophilous dense forest, *Serra do Mar*, species distribution.

## INTRODUCTION

The Brazilian Atlantic Rain Forest (AF) was originally distributed over large extensions of the Brazilian coast and continental inland under the influence of heterogeneous envi-

ronmental conditions (Rizzini 1979, Daly & Mitchell 2000, Oliveira-Filho & Fontes 2000, Oliveira-Filho et al. 2005, Fiaschi & Pirani 2009). From sea level to 2700 m a.s.l. and from approximately 3° to 30°S under different climates, the AF encompasses many different vegetation types, from open

and low vegetation to dense and tall forests over sandy, clayish or rocky soils (Eisenlohr et al. 2013, Fiaschi & Pirani 2009, Joly et al. 2014) across altitudinal and latitudinal gradients. In the last decades, some studies have revealed the role of climate on floristic differentiation between different physiognomies (ombrophilous dense forest and semideciduous forest), along altitudinal gradients (*Serra do Mar* Mountains), and between geographic regions (northeastern and southeastern Brazilian coast) in the AF (e.g. Oliveira-Filho & Fontes 2000, Ivanauskas et al. 2000, Scudeller et al. 2001, Joly et al. 2012, Eisenlohr et al. 2013).

The AF is classified in two main forest formations: the ombrophilous dense forest (ODF), or Atlantic Forest *sensu stricto*, distributed across lowlands and mountains of the humid coast; and the semideciduous forest, found in part of the coast and widely distributed inland, usually associated with drier climates (Oliveira-Filho & Fontes 2000). The occurrence of semideciduous forests in the coastal region between 20° and 21°S separates the ODF in two regions (Cracraft 1985, Joly et al. 1999, Oliveira-Filho & Fontes 2000, Fiaschi & Pirani 2009): the warmer northeastern AF, which has some influence of the Amazonian flora due to historical connections (Rizzini 1963, Mori et al. 1981, Costa 2003), and the southeastern AF, usually subjected to lower temperatures (especially at higher latitudes and altitudes), and with some influence of the flora from the Andean region (Fiaschi & Pirani 2009). Nonetheless, the interruption of the ODF by semideciduous forests in this part of the coastal region represents a floristic gradient rather than a floristic break between northeastern and southeastern AF (Oliveira-Filho et al. 2005).

In the southeastern AF, it is expected that the temperature has a strong effect on species distribution because of the decreasing temperatures toward higher latitudes and altitudes along the coast (Oliveira-Filho et al. 2015). Variations in temperature have been reported as one of the most important factors affecting species turnover along latitudinal gradients (Qian et al. 2003, Zhang et al. 2009). In the southeastern AF, both temperature and rainfall are well known to affect floristic variation along altitudinal gradients of the *Serra do Mar* Mountains (Ivanauskas et al. 2000, Oliveira-Filho & Fontes 2000, Scudeller et al. 2001) but little is known about the role of these climatic variables on species composition along the latitudinal gradient on this stretch of the coast (Oliveira-Filho & Fontes 2000, Scudeller et al. 2001).

Besides current climatic conditions, historical factors may also explain species distribution along latitudinal gradients (Whittaker et al. 2001, Leigh et al. 2004). Climatic changes in the past are supposed to have promoted forest expansion and retraction, speciation and species extinction (Haffer 1969, Prance 1982, Haffer & Prance 1998). For instance, the southeastern AF experienced colder and drier climates followed by forest retraction in the end of the Pleistocene, especially at higher latitudes (Behling & Negrelle 2001, Carnaval & Moritz 2008). Thus, many species not adapted to lower temperatures and drier climates may have had their geographic distribution restricted to forest refugia at lower latitudes (Carnaval & Moritz 2008), posteriorly migrating to higher latitudes after the reestablishment of current climatic conditions.

Here, we investigated the influence of climatic variables (mean annual temperature and annual rainfall) on floristic composition in the southeastern AF to answer the following questions: How are species distributed along the latitudinal gradient in the southeastern AF? How does floristic composition vary along this latitudinal gradient? What is the role of mean annual temperature and annual rainfall on species distribution and floristic composition along the gradient? First, we calculated species latitudinal range and frequency of occurrence along the gradient. Then, we showed how variation on species composition is correlated with the latitudinal gradient. Finally, we described the floristic variation along the latitudinal gradient and tested how mean annual temperature and annual rainfall explain this variation.

## METHODS

### Data preparation

The studied area included most of the latitudinal extent of the southeastern AF, corresponding to the coastal region of Rio de Janeiro, São Paulo, Paraná and Santa Catarina States (fig. 1), from 21°S to 28°S. This extension is almost coincidental with the limits of the *Serra do Mar*, a set of scalloped escarpments of the Atlantic Plateau that stretches over more than a thousand kilometers from Rio de Janeiro to Santa Catarina (Almeida & Carneiro 1998, Tessler & Goya 2005), following most part of the southeastern AF limits as proposed by Oliveira-Filho & Fontes (2000) and the official classification of the Brazilian vegetation (Veloso et al. 1991, IBGE 2004). Altitude was controlled by limiting the sample sites to altitudes between 5 and 500 m a.s.l., encompassing the lowland forests (between 5 and 50 m a.s.l. from 16°S to 24°S and between 5 and 100 m a.s.l. from 24°S to 32°S) and lower montane forests (between 50 and 500 m a.s.l. from 16°S to 24°S and between 30 and 400 m a.s.l. from 24°S to 32°S) according to the official classification of the Brazilian vegetation (Veloso et al. 1991, IBGE 2004). Besides the altitudinal classification, these forests types are usually floristically distinct from the montane forests (> 1000 m a.s.l.) according to previous investigations (Ivanauskas et al. 2000, Scudeller et al. 2001, Joly et al. 2012, Eisenlohr et al. 2013). We did not include the *restinga* forests, a distinct type of vegetation distributed over sandy soils between 0 and 5 m a.s.l. in the Brazilian coast (Marques et al. 2011, Assis et al. 2011, Eisenlohr et al. 2013).

We selected from the literature 19 floristic surveys of trees (including arborescent palms and ferns) in areas of ODF distributed along the southeastern coastal AF (table 1). Because some of these studies included plots at different altitudes, here we considered each plot an independent sampling area, totalizing 27 sampled areas in our dataset. Only the samples located in São Pedro de Alcântara, Peruíbe and Cubatão were defined as secondary forests by the authors of the studies. For the other areas, we assumed some level of human disturbance, but not relevant to our analysis. Synonymy and spelling of species names were verified according to The International Plant Names Index (IPNI 2012) and the List of species of the Brazilian Flora (Forzza et al. 2010). Taxa not identified at species level were removed from the analysis. Finally, we set up a presence/absence matrix of 790 species

approach proposed by Scudeller et al. (2001) in which:  $FR_i = (N_i/N) * 100$ , where  $N_i$  is the number of sample areas where the species 'i' occurred and  $N$  is the total number of sample areas; LR is the difference (in degrees) between the maximum and minimum latitude where the species occurred. Species were categorized as very frequent ( $Fr \geq 80\%$ ), intermediate ( $20 \leq Fr < 80\%$ ) or infrequent ( $Fr < 20\%$ ). We evaluated the pattern of species substitution in the latitudinal gradient by applying a direct species ordination by the latitudinal gradient for the 139 species with intermediate frequencies. We excluded from this analysis the very frequent and the infrequent species since they would not add information about species substitution in the gradient.

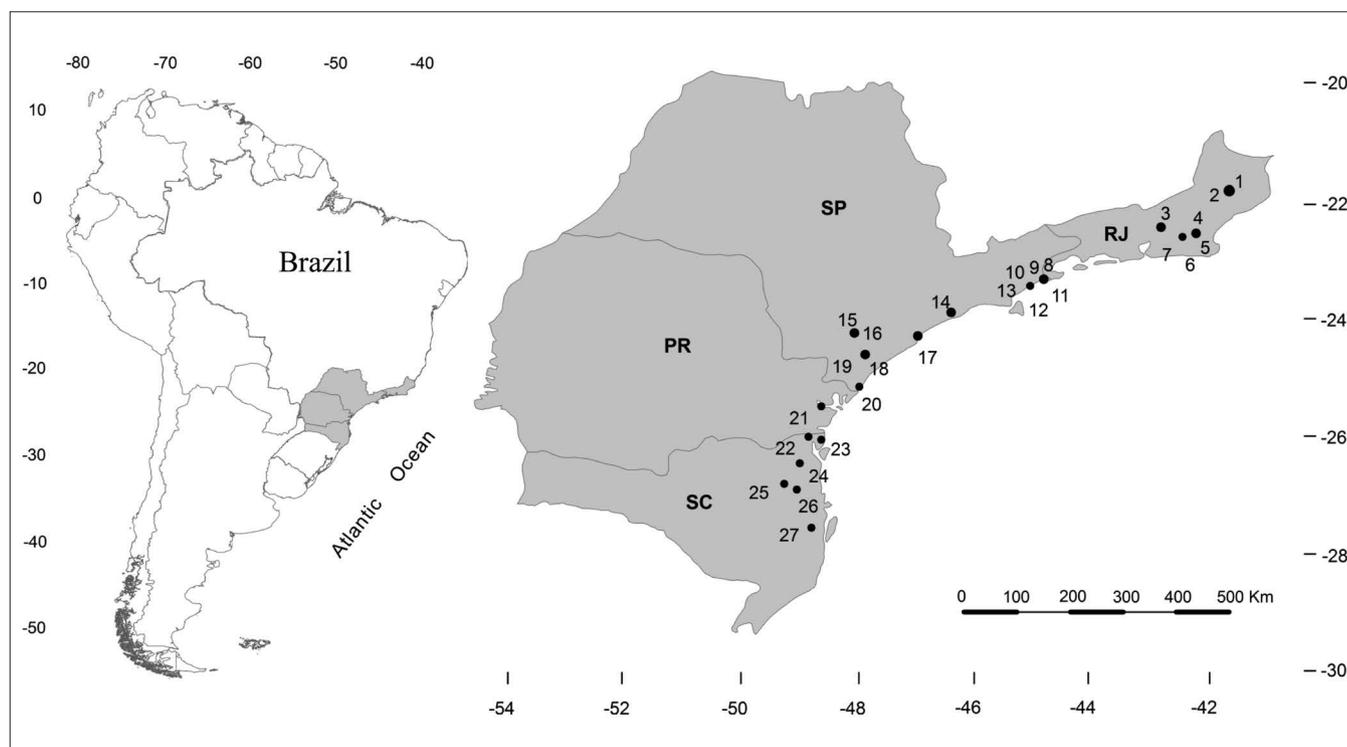
In order to reduce the floristic variation to one dimension, we applied a Non-metric Multidimensional Scaling Analysis (NMDS; Kruskal & Wish 1978) over a matrix of species dissimilarity between sample areas (calculated using the Jaccard dissimilarity index), with the function 'metaMDS'. To estimate how much of the floristic variation was retained by the NMDS axis, we first generated a pairwise dissimilarity matrix (using the Euclidian distance) from the scores of the NMDS axis. Then, we correlated this dissimilarity matrix with the Jaccard dissimilarity matrix (calculated from the matrix of species composition per sample area) by applying a Mantel Test ( $P < 0.05$ ), using the function 'mantel'. We applied a linear regression model followed by an Analysis of Variance (ANOVA,  $P < 0.05$ ) to evaluate the relation between variation in species composition (dependent variable, represented by the NMDS axis) and the latitudinal position (independent variable) of the sample areas along the gradient, using the function 'lm'. We conducted a Hierarchical Clus-

tering analysis followed by an Indicator Species analysis in order to investigate how sample areas are grouped and which are the indicator species of each group, using the functions 'dist', 'hclust' and 'indval'. Finally, we investigated the role of the variables mean annual temperature and annual rainfall (independent variables) on species composition (dependent variable, represented by the NMDS axis) by applying a multiple regression analysis followed by an Analysis of Variance (ANOVA,  $P < 0.05$ ), with the function 'lm'. We calculated the percentage of variation explained by each variable separately, the percentage shared between variables, and the unexplained variation. All analyses were performed in the software R (R Development Core Team 2016), using the packages 'stats', 'vegan' (Oksanen et al. 2018) and 'labdsv' (Roberts 2016).

## RESULTS

### Frequency, amplitude and species ordination in the latitudinal gradient

Out of the 789 species, only four (0.5%) were classified as very frequent ( $> 80\%$  of samples): *Hieronyma alchorneoides* Allemão, *Garcinia gardneriana* (Planch. & Triana) Zappi, *Sloanea guianensis* (Aubl.) Benth. and *Euterpe edulis* Mart. A total of 139 species (17.6%) occurred at intermediate frequencies (between 20 and 80%) and most of them (646 or 81.9%) were infrequent (less than 20% of the areas). A large proportion of the species (310 or 39.3%) was observed in only one sample area. The number of species (10) that reached the maximum latitudinal range ( $\sim 6^\circ$ ) was low (1.3%). They are: *Cabralea canjerana* (Vell.) Mart., *Euterpe edulis* Mart., *Guapira opposita* (Vell.) Reitz, *Heiste-*



**Figure 1** – Map showing the distribution of the sample areas (1 to 27) along the coastal region of the southeastern Atlantic Forest. RJ = Rio de Janeiro State, SP = São Paulo, PR = Paraná and SC = Santa Catarina.

**Table 1 – Floristic surveys conducted in the Atlantic Ombrophilous Dense Forest and used in our analysis.**

Geographical coordinates are shown in decimal degrees, altitude in meters, Mean Annual Temperature (MT) in degrees Celsius, Annual Rainfall (AR) in millimeters, Methods used in the survey (P – plots; Q – Point-Centered Quarter method) / sampled area in hectare for plots (ha) or number of points (np) for Point-Centered Quarter method, Inclusion criteria (Dbh – diameter at breast high), Total number of species in the area (Tsp), Total number of species used in the analyses (Tspa) and respective authors. \* unpublished data presented in Lacerda (2001).

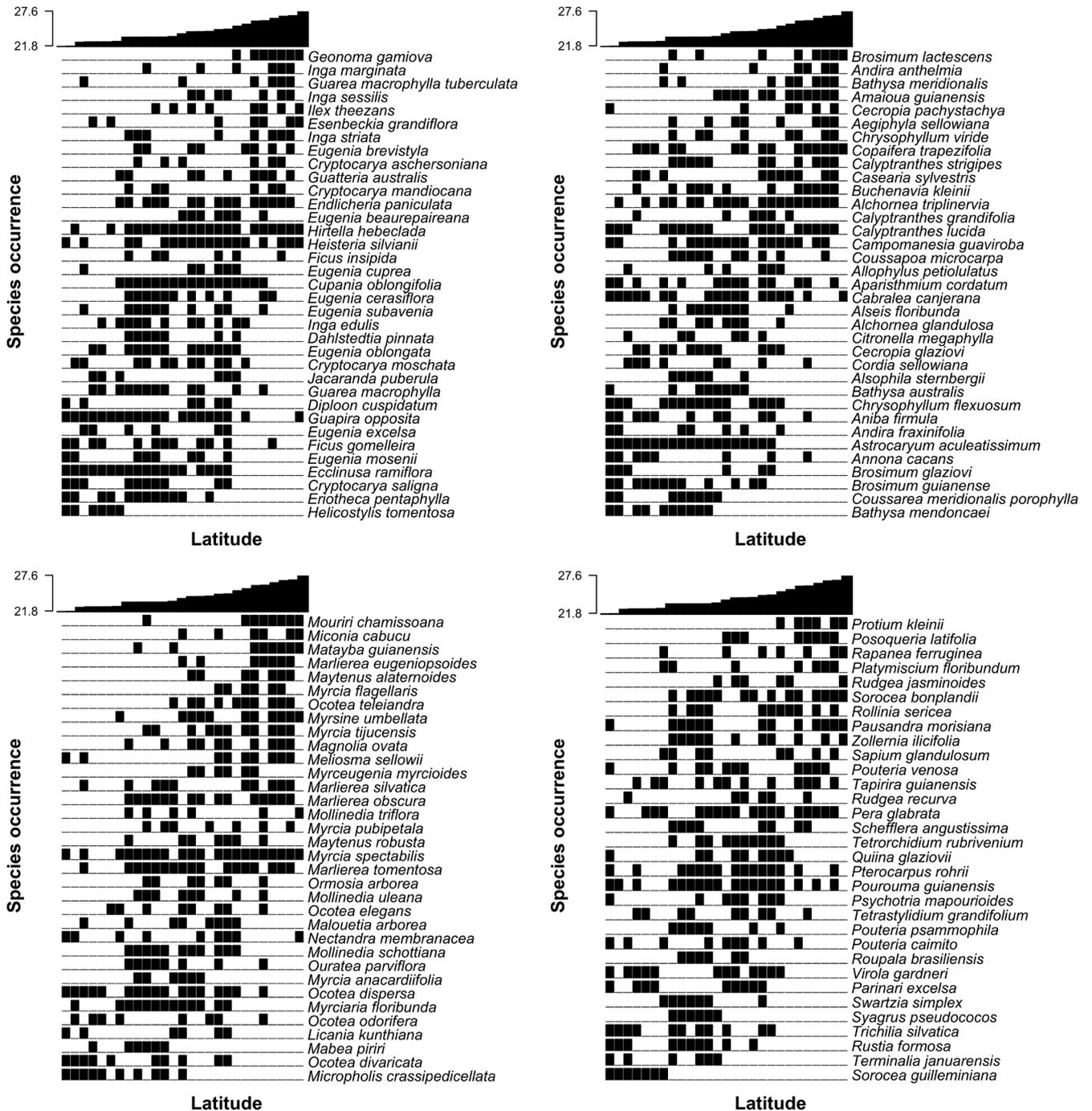
Locality	Lat(S)/Lon(W)	Altitude (m)	MT (°C)	AR (mm)	Method/ ha or np	Dbh (cm)	Tsp	Tspa	References
1.Campos dos Goytacazes-RJ	21.800/41.667	50	22.7	1137	P/0.6	3.2	126	87	Moreno et al. 2003
2.Campos dos Goytacazes-RJ	21.833/41.667	250	22.7	1137	P/0.6	3.2	145	112	Moreno et al. 2003
3.Cachoeiras do Macacu-RJ	22.480/42.917	200	22.8	1595	Q/150	5	138	114	Kurtz & Araújo 2000
4.Rebio Poço das Antas-RJ	22.553/42.233	5–200	23.2	1097	P/0.225	5	64	51	Pessoa & Oliveira 2006
5.Rebio Poço das Antas-RJ	22.555/42.233	5–200	23.2	1097	P/0.575	5	107	74	Pessoa & Oliveira 2006
6.Rebio Poço das Antas-RJ	22.558/42.233	5–200	23.2	1097	P/0.65	5	151	104	Pessoa & Oliveira 2006
7.Silva Jardim-RJ	22.617/42.467	5–200	22.6	1198	P/1	5	161	138	Carvalho et al. 2006
8.Picinguaba-SP	23.330/44.822	100	22.2	2320	P/0.4	4.8	98	91	Gianotti unpubl. data*
9.Picinguaba-SP	23.334/44.832	70–90	22.2	2320	P/1	4.8	142	130	Campos 2008
10.Picinguaba-SP	23.337/44.831	100	22.2	2320	P/0.4	6.4	120	107	Sanchez et al. 1999
11.Picinguaba-SP	23.338/44.834	40–70	22.2	2320	P/1	4.8	156	135	Prata et al. 2011
12.Picinguaba-SP	23.340/44.837	35–55	22.2	2320	P/1	4.8	137	122	Assis et al. 2011
13.Ubatuba-SP	23.450/45.067	20–190	22.5	2525	Q/160	10	123	100	Silva & Leitão Filho 1982
14.Cubatão-SP	23.900/46.417	5–100	22.1	2610	P/0.4	6.4	145	125	Leitão Filho 1993
15.Saibadela-SP	24.218/48.067	92	21.5	1602	P/0.99	5	135	129	Guilherme 2003
16.Saibadela-SP	24.233/48.083	120	21.5	1602	P/0.99	5	140	132	Guilherme 2003
17.Peruíbe-SP	24.300/46.987	50	22.6	2063	P/0.2	5	63	60	Oliveira et al. 2001
18.Pariquera-Açú-SP	24.600/47.883	30–40	22.1	1612	P/0.61	4.8	128	121	Ivanauskas et al. 2000
19.Pariquera-Açú-SP	24.667/47.867	30–40	22.1	1612	P/0.6	4.8	162	145	Ivanauskas et al. 2000
20.Ilha do Cardoso-SP	25.167/47.983	5–100	19.9	2294	P/0.8	2.5	109	92	Pinto 1998
21.Morretes-PR	25.500/48.633	485	20.9	2082	Q/80	4.8	70	56	Silva 1994
22.Itapoá-SC	26.017/48.850	9	20.5	1789	P/1	5	128	127	Negrelle 2006
23.Garuva-SC	26.067/48.633	25	21.1	1884	P/0.32	1	115	105	Veloso & Klein 1968
24.Guaramirim-SC	26.467/49.000	30	20.7	1618	P/0.16	1	82	79	Veloso & Klein 1968
25.Timbó-SC	26.817/49.267	68	20.6	1676	P/0.16	1	86	85	Veloso & Klein 1968
26.Blumenau-SC	26.917/49.050	21	20.2	1552	P/0.16	1	95	92	Veloso & Klein 1968
27.São Pedro de Alcântara-SC	27.567/48.800	300	18.6	1623	P/0.06	0.3	63	41	Siminski et al. 2004

and 27 sample areas. For each area, we extracted latitude and longitude data from the original study or, when absent, we used the coordinates of the municipality in which the sample area was located. We used WorldClim 1.4 version (Hijmans et al. 2005) to extract mean annual temperature and rainfall values for each sample area (30 arc-seconds resolution, ~1 km). WorldClim provides data of 50-year means for each month, and here we calculated the mean annual temperature from the mean monthly values and the annual rainfall from the sum of the monthly rainfall values. Although not directly used in our analysis, we checked the records of minimum dai-

ly temperatures available for some localities along the latitudinal gradient (downloaded from: <http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep>). The occurrence of minimum daily temperatures close to 0°C are expected to be more frequent from 25°S southward, where frosts are more likely to occur (Leitão Filho 1987).

**Data analysis**

To determine the frequency of occurrence (Fr) and the latitudinal range (LR) of species distribution, we used the same



**Figure 2** – Pattern of species substitution revealed by the analysis of species ordination along the latitudinal gradient (21°S to 27°S).

**Table 2 – List of families and species of the Ombrophilous Dense Forest that reached the distribution range of 5° along the latitudinal gradient (excluding the area of secondary forest sampled in São Pedro de Alcântara, SC).**

\* species that occurred throughout the gradient (range of 6°), considering all sample areas.

Families	Species
Annonaceae	<i>Annona cacans</i> Warm.
Areaceae	<i>Euterpe edulis</i> Mart.*
Chrysobalanaceae	<i>Hirtella hebeclada</i> Moric. ex DC.*
Elaeocarpaceae	<i>Sloanea guianensis</i> (Aubl.) Benth.*
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Mull.Arg.
	<i>Aparisthium cordatum</i> (A.Juss.) Baill.
	<i>Pausandra morisiana</i> (Klotzsch) Baill.*
	<i>Pera glabrata</i> (Schott) Poepp. ex Baill.
Lauraceae	<i>Aniba firmula</i> (Nees & Mart.) Mez
	<i>Nectandra grandiflora</i> Ness
	<i>Nectandra leucothyrsus</i> Meisn.*
	<i>Ocotea aciphylla</i> (Nees & Mart.) Mez
Lecythidaceae	<i>Ocotea dispersa</i> (Nees & Mart.) Mez
	<i>Cariniana estrellensis</i> (Raddi) Kuntze
	<i>Cabralea canjerana</i> (Vell.) Mart.*
Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.*
Moraceae	<i>Ficus gomelleira</i> Kunth & C.D.Bouché
	<i>Calyptanthes lucida</i> Mart. ex DC.
Myrtaceae	<i>Calyptanthes concinna</i> DC.
	<i>Myrcia spectabilis</i> DC.*
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz*
Olacaceae	<i>Heisteria silvianii</i> Schwacke*
Phyllanthaceae	<i>Hieronima alchorneoides</i> Allemão*
Sabiaceae	<i>Meliosma sellowii</i> Urb.
Sapotaceae	<i>Pouteria venosa</i> (Mart.) Baehni

*ria silvianii* Schwacke, *Hieronima alchorneoides* Allemão, *Hirtella hebeclada* Moric. ex DC., *Myrcia spectabilis* DC., *Nectandra membranacea* (Sw.) Griseb., *Pausandra morisiana* (Casar.) Radlk. and *Sloanea guianensis* (Aubl.) Benth. This number increased to 24 (3%) when we excluded from the analysis the secondary forest areas located in São Pedro de Alcântara (27°S) (table 2).

The direct species ordination analysis along the latitudinal gradient revealed a strong pattern of species substitution among the 27 sampled areas (fig. 2). For instance, the species *Actinostemon verticillatus* Baill., *Helicostylis tomentosa* (Poepp. & Endl.) Rusby and *Sorocea guilleminiana* Gaudich. were restricted to the gradient's northern forests, while *Mollinedia schottiana* (Spreng.) Perkins and *Tetrorchidium rubrivenium* Poepp. & Endl. were found in the central part and *Geonoma gamiova* Barb.Rodr. and *Protium kleinii* Cuatrec. were more frequent in the south region of the latitudinal gradient (fig. 2).

## Multivariate, indicator species and regression analyses

The NMDS axis retained 67% of the information contained in the Jaccard dissimilarity matrix calculated from the species composition data (Mantel,  $r = 0.67$ ,  $P < 0.0001$ ). A strong correlation between the NMDS axis and the latitudinal position was detected by the linear regression analysis. ( $r^2 = 0.74$ ,  $P < 0.001$ ) (fig. 3). The clustering analysis revealed a first floristic separation around 23°S, with one group composed by the sample areas of Rio de Janeiro State (areas 1 to 7, north of the gradient) and a second group subdivided in two subgroups around latitude 25°S: one composed by the forests of São Paulo (8 to 20, middle of the gradient) and the other by forests of Paraná and Santa Catarina States (21 to 27, south of the gradient) (fig. 4). It is worth noting that the northern forests (8 to 12) and southern forests (15, 16 and 18 to 20) of São Paulo tended to be separated, although three areas remained unplaced (13, 14 and 17) in the cluster analysis. The indicator species analysis detected *Actinostemon verticillatus*, *Helicostylis tomentosa* and *Sorocea guilleminiana* as indicative of the first group (1 to 7), while *Mollinedia schottiana* and *Tetrorchidium rubrivenium* were indicative of the second group (8 to 27), within which *Geonoma gamiova* and *Protium kleinii* were indicative of the second subgroup (21 to 27) ( $P < 0.005$  for all these species).

Our multiple regression analysis revealed a strong effect of both mean annual temperature and annual rainfall on the variation of the floristic composition along the latitudinal gradient ( $r^2 = 0.81$ ,  $P < 0.001$ ). The variance partition showed that 62.82% of the total floristic variation was explained by mean annual temperature, 8.27% by annual rainfall and 10.45% by both variables together, while 18.46% remained unexplained.

## DISCUSSION

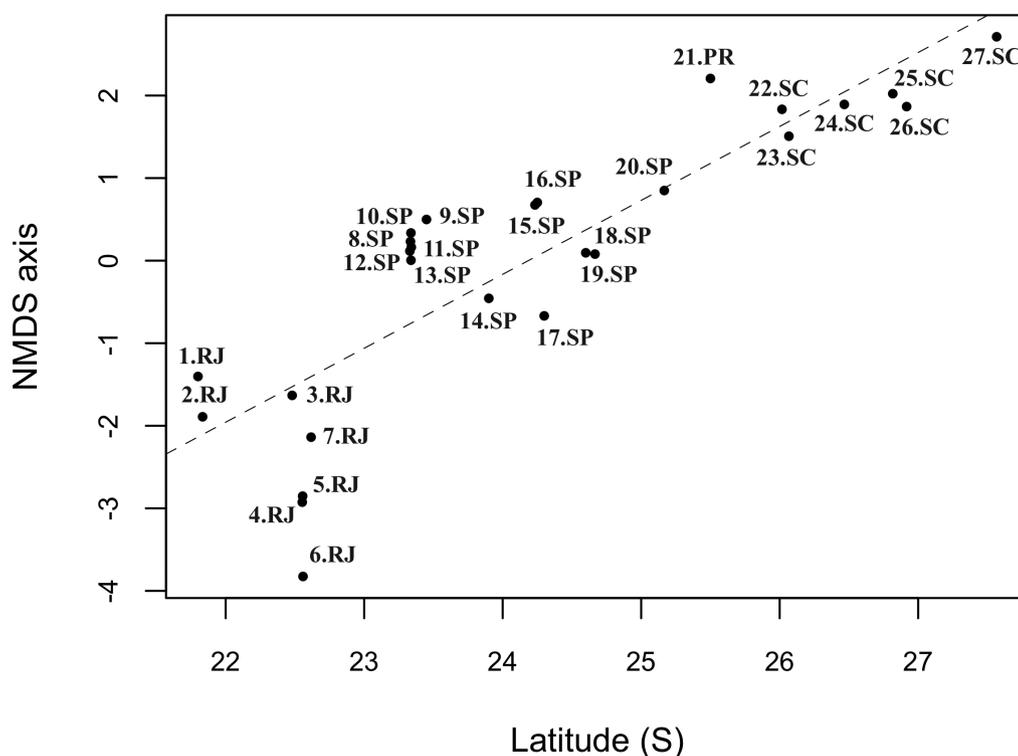
The number of tree species here registered (789) was high given that we sampled only part of the altitudinal gradient within the latitudinal gradient and that taxa not identified at species level were excluded from the analysis. This result reflects the high species richness expected for the AF, one of the richest among the Neotropical forests (Leitão-Filho 1987, Fiaschi & Pirani 2009, Stehmann et al. 2009, Raedig et al. 2010). We found that most species occurred with low frequency and that few species reached the maximum latitudinal range, resulting in a strong pattern of species substitution as evidenced by the species ordination against the latitudinal gradient. Thus, our results suggest that the AF is characterized by the occurrence of species with low frequency and restricted distribution (Scudeller et al. 2001), what probably help to explain the high local and regional species diversity of this hotspot (Myers et al. 2000, Eisenlohr et al. 2013, Joly et al. 2014).

The strong correlation between latitude and the NMDS axis revealed that variation in floristic composition in the southeastern AF is dependent on the spatial position along the latitudinal gradient. The high floristic dissimilarity detected between the forests from Rio de Janeiro and the forests from São Paulo, Paraná and Santa Catarina States suggests a high species turnover around 23°S, differently of the hypoth-

esized by Leitão Filho (1982, 1987), who proposed a floristic break in the southern coast of São Paulo or northern coast of Paraná (around 25°S) due to reoccurring frosts (minimum daily temperatures around 0°C) southward from this region. Here, we found that the forests from the north of São Paulo, despite geographically closer to Rio de Janeiro (c. 250 km apart), are floristically more similar to the southern forests even though geographically more distant (up to c. 650 km apart), as evidenced by the cluster and species indicator analyses. However, we agree that frosts may affect species composition along the coast, probably restricting the southward distribution of some species to around 25°S, such as *Micropholis crassipedicellata* (Mart. & Eichler) Pierre, *Bathysa mendoncae* K.Schum., *Brosimum guianense* (Aubl.) Huber and *Eriotheca pentaphylla* (Vell. & K.Schum.) A.Robyns. This would in part explain the floristic dissimilarity between the forests from São Paulo and those from Paraná and Santa Catarina, where frosts are more common. Finally, although no differentiation was detected between the floras from the northern and the southern coast of São Paulo in previous studies (Ivanauskas et al. 2000, Scudeller et al. 2001), here we found some degree of floristic dissimilarity between these two regions. The floristic dissimilarity of the sample areas 'Cubatão' (14) and 'Peruibe' (17) in relation to the northern and southern forests of São Paulo is probably related to the successional status of these vegetations, characterized as secondary forests by Leitão Filho (1993) and Oliveira et al. (2001), respectively.

Our regression models revealed that most of the floristic variation along the southern AF was explained by the decreasing mean annual temperatures toward higher latitudes. However, annual rainfall may play an important role in the north region of the latitudinal gradient: from approximately 20.5°S to 23°S, the climate is characterized by the occurrence of up to five months of drought per year (IBGE 2002) as consequence of the cold Brazilian oceanic upwelling current (Araújo 1997). At this stretch of the coast, semi-deciduous forests substitute most part of the ODF and approximately half of the species present in the ODF are shared between both forest types (Oliveira-Filho & Fontes 2000), which means that the ODF is in part composed by species tolerant to drier climates. Thus, the effect of the abrupt decreasing in annual rainfall from northern São Paulo (23°S) to northern Rio de Janeiro (20.5°S), from 2,310 to 1,137 mm, may restrict the northward distribution of species associated to more humid climate, such as *Tetrorchidium rubrivenium* and *Protium kleinii*. Moreover, the high variation in floristic composition in the north of the gradient is also related to the occurrence of species shared with the northeastern AF and with the Amazon forest, with southward distribution limited to approximately 23°S, as some of the indicator species in the north of the gradient (e.g. *Actinostemon verticillatus*, *Helicostylis tomentosa* and *Sorocea guilleminiana*).

The strong relation between climate and species composition along the latitudinal gradient in the AF may be explained by species tolerance to lower or higher temperatures and annual rainfall. For instance, intolerance to colder climates



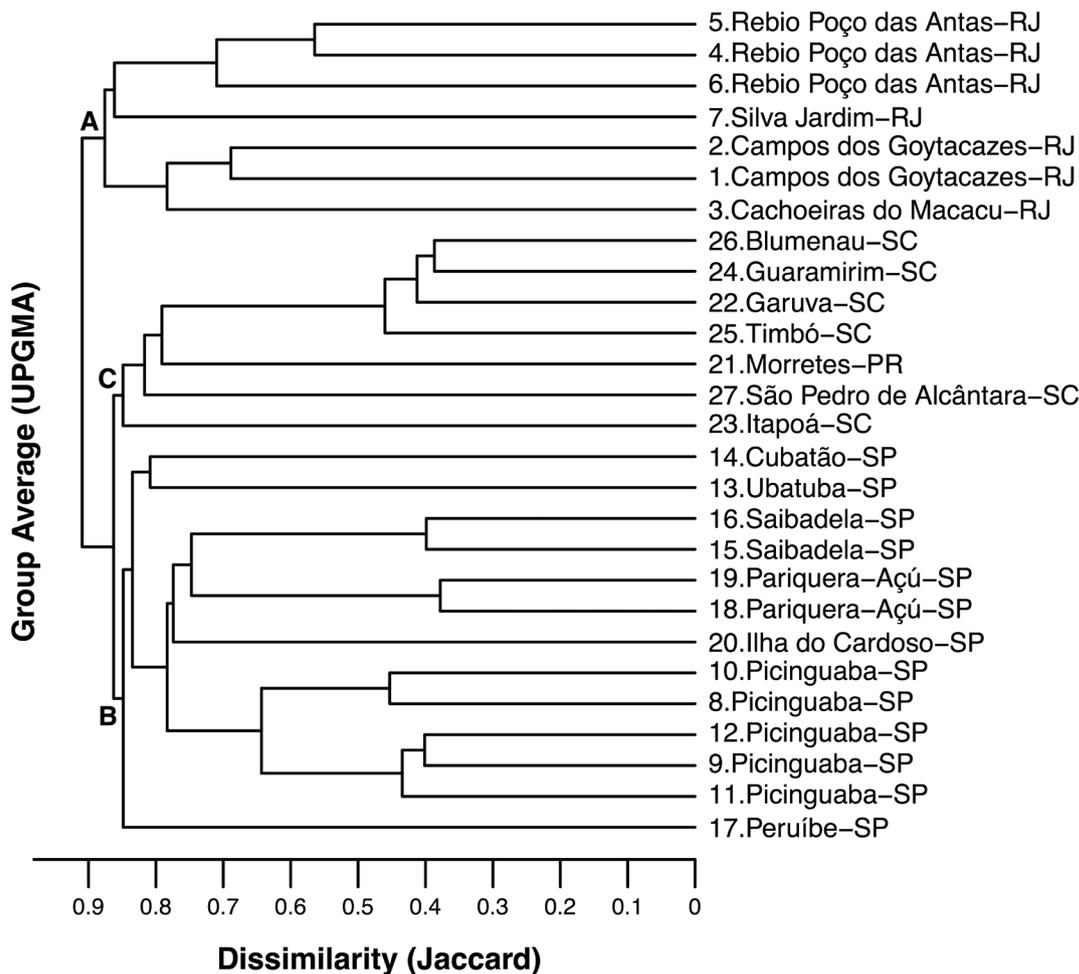
**Figure 3** – Linear regression analysis between the NMDS axis (representing the variation in floristic composition) and the latitudinal position of the 27 sample areas distributed along the coastal region of the southeastern Atlantic Forest ( $r^2 = 0.74$ ,  $P < 0.001$ ). RJ = Rio de Janeiro State, SP = São Paulo, PR = Paraná and SC = Santa Catarina.

may restrict the occurrence of some species to warm regions while sensitivity to drought may restrict the occurrence of some species to humid regions (Currie et al. 2004). According to this hypothesis, a larger pool of species can potentially persist in warm and humid climates when compared to dry or cold climates (Currie et al. 2004). In fact, the region around 23°S combines high values of mean annual temperature and annual rainfall (table 1) and concentrates one of the highest species richness along the latitudinal gradient (Raedig et al. 2010). Interestingly, this is the region with highest narrow endemism in the southern AF (Mori et al. 1981, Prance 1982, Raedig et al. 2010) and it also coincides with one of the few small-sized potential area of historical climatic stability (forest refugia in the Pleistocene) in the southern AF (Carnaval & Moritz 2008).

Historically, the AF had been under the influence of drier and colder climates during the Quaternary (Behling & Negrelle 2001, Mori et al. 1981, Prance 1982, Carnaval & Moritz 2008). For instance, palynological evidence suggests the predominance of grasses and patches of cold-adapted forests in the southern part of the gradient in the late Pleisto-

cene (Behling & Negrelle 2001), with the re-establishment of the ODF around 12500 yr BP. In the northern part of the gradient, the ODF and the semideciduous forests were re-established around 8000 yr BP after a long period of drought in the late Pleistocene (Martin et al. 1993, Barth 2003). The effects of dry and cold climates on species composition in the past were more intense at higher latitudes, while forest refugia were more likely to have occurred in the north region of the southern AF (but mainly in the northeastern AF) (Carnaval & Moritz 2008). Thus, many of the tree species adapted to warmer climates currently distributed along the southern AF may have had their distributions restricted to these forest refugia in the past with posterior migration southward following forest expansions (Oliveira-Filho et al. 2015).

Here, we demonstrated that variation in tree species composition in the southern AF is strongly correlated to climate along the latitudinal gradient. While the variation in mean annual temperature explains most of the variation in floristic composition, variation in annual rainfall may affect species composition mainly in the northern region of the latitudinal gradient. This region (21°S to 23°S) is climatically



**Figure 4** – Cluster analysis showing the floristic dissimilarity between the 27 sample areas distributed along the coastal region of the southeastern Atlantic Forest. A, group composed by the forests of Rio de Janeiro State (sample areas 1 to 7), in the north of the gradient; B, group composed by the forests of São Paulo (8 to 20), in the middle of the gradient; C, group composed by the forests of Paraná and Santa Catarina States (21 to 27), in the south of the gradient.

more similar to the northeastern AF and the Amazon forest than with the southward region of the gradient (IBGE 2002), which probably explains the occurrence of shared species between these forests. The strong association between variation in tree species composition and climate in the southern AF indicates that future climatic changes will directly impact floristic composition along the latitudinal gradient. However, the future of the AF will depend not only on natural climatic dynamics but also on its urgent effective conservation.

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