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Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest

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Abstract Floristic differentiation and vegetation definition is an important step to recognize biome distribution and for biodiversity conservation. Here, we aim to verify if the distribution of the costal lowland vegetation in Brazilian littoral is congruent with climatic gradient and the previous vegetation definitions. Additionally we discussed the importance of terms for the Atlantic Forest conservation. Our study was based on floristic and geoclimatic data from 58 published surveys. We generate a checklist of 1088 woody species and verified species distribution according to environmental gradient using a Detrended Correspondence Analysis (DCA). We compared DCA's groups with the a priori vegetation definition and generate an a posteriori classification using TWINSPAN. DCA and TWINSPAN resulted in groups determined mainly by rainfall ($r = -0.65$) and soil sandiness ($r = -0.71$). Those groups were not congruent with both the previous vegetation definitions. The coastal lowland vegetation comprises two distinctive floristic groups representing forests and scrubs that occur in wetter climates (Ombrophilous lowland forests) in the Brazilian states of Santa Catarina, Paraná and São Paulo and in drier climates of Espírito Santo, Rio de Janeiro (Restinga-Northern group) and Rio Grande do Sul (Restinga-Southern group) states. The floristic and historical relationships between Ombrophylous lowland forests and Restingas suggest that conservation initiatives should be more conservative and treat collectively all coastal lowland vegetation as a biodiversity hotspot.

Keywords Biogeography · Conservation hotspot · Ombrophilous forest · Restinga · Sandy coastal forest · Tropical rain forest

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Introduction

The Atlantic Forest, the second most widespread tropical forest in Brazil, is better recognized as a complex than as a single vegetation type (Rizzini 1979). Despite its location in the Brazilian east coast and the obvious influence of the Atlantic Ocean, recent studies consider both coastal and hinterland vegetations as part of the Atlantic Forest complex (Morellato and Haddad 2000; Oliveira-Filho and Fontes 2000; Oliveira-Filho et al. 2005). It comprises a range from rain to semi-deciduous forests as well as the marginal vegetation in high altitude and over marine sand deposits (Scudeller et al. 2001; Scarano 2002; Scarano 2009).

Two main centers of endemism are usually recognized in the Atlantic Forest: the northern Atlantic Forest and the southern Atlantic Forest (see Fiaschi and Pirani 2009 for a revision). The northern block shows floristic affinities with the Amazon Forest (Mori et al. 1981; Oliveira-Filho and Ratter 1995; Méio et al. 2003; Oliveira-Filho et al. 2005) and some influence of Caatinga domain and inland forests (*brejos nordestinos* and *Chapada Diamantina*) that boundary the Atlantic Forest by the west (Thomas and Barbosa 2008; Funch et al. 2008; Rodal and Sales 2008). The southern block is influenced by the flora of other regions, such as the Andes and elements of the ancient southern Gondwana (Sanmartin and Ronquist 2004). Altogether, the two regions comprise about 15000 vascular plants and 48% endemic species (Stehmann et al. 2009) that is among the highest in the world (Myers et al. 2000; Martini et al. 2007; Murray-Smith et al. 2009).

The complexity of the Atlantic Forest is derived mainly from the large geographical changes along its area of occurrence associated with climatic variations that cause differences in plant communities. This includes, approximately, latitudes ranging from 5°N to 33°S, longitudes from 35°W to 52°W and altitudes from 0 to 2200 m (IBGE 1992). This wide geographical variation determines a climatic gradient in annual rainfall (approximately, from 800 to 4000 mm) and mean annual temperatures (averages from 15 to 25°C) which influence species distributions (Salis et al. 1995; Scudeller et al. 2001; Ferraz et al. 2004; Oliveira-Filho et al. 2005).

Despite the large variation in vegetation types and climate, the former Brazilian vegetation classification refers to two phyto-ecological regions (excluding mangroves) associated with the Atlantic Ocean (IBGE 1992). The "Ombrophilous Atlantic Forest" comprises high rainfall, high diversity dense forests relatively close to the sea. It is distributed on almost all of the Brazilian coast, from sea level to high altitudes (approximately 1500 m), in the *Serra do Mar* mountains. The "Pioneer Vegetation under marine influence", so called "Restinga", includes a mosaic from herbaceous to woody vegetation that occurs on marine sand plains in the littoral. Since this is a more generic classification, differences in small scales are not detectable and plant communities included in both Ombrophilous forests and Restingas are frequently referred by more specific names (IBGE 1992; Waechter 1990; Araújo 1992; Silva and Britez 2005; Oliveira-Filho 2009). In addition, the spatial proximity and the similar physiognomy among vegetation types make the phytogeographical differentiation unclear, especially for coastal lowland vegetation.

The coastal plains in the Brazilian littoral are formed by deposits of sediments from different ages and sources (Suguio and Martin 1990; Villwock 1994; Cerqueira 2000). The sea level and coastal line have changed dramatically along the Tertiary and Pleistocene resulting in a mosaic of vegetation types, dunes, mangroves and Restinga in these regions (Bigarella 1973). These plains are one of the most populated areas in the country (some of the biggest cities are in this region) and where biodiversity is strongly threatened. The flora of the lowland vegetation in the coastal plains is characterized by high endemism (about

41% of total species) and one of the most susceptible to vanish in with the global warming (Stehmann et al. 2009). Since the description and classification of vegetation is an important step for conservation, the Brazilian government has published laws (Código Florestal 4771/1965, Decreto 750/1993, Lei 11428/2006) and regulatory actions (Resoluções CONAMA 10/1993, 07/1996, 261/1999, 303/2002, 388/2007) to define the vegetation in Atlantic Rain Forest. In some of those documents terms are ambiguous and definitions are based only in physiognomic aspects. These terms and scopes have been used uncritically by researchers and government, but none have investigated their floristic composition.

In the current study we investigated the floristic variation in southern and southeastern coastal lowland vegetation and their relationship with forests in the Brazilian Atlantic Forest complex. We generated a species checklist and a geo-climatic database by consulting literature to address the three main questions: (1) Are the floristic and structural patterns in the coastal lowland vegetation associated with geo-climatic and edaphic gradients? (2) How is the coastal lowland vegetation related in floristics to the neighbouring vegetation of the Atlantic Forest? We discuss these questions considering the current vegetation classification (IBGE 1992) and the importance of terms for the Atlantic Forest conservation.

Methods

Data collection and manipulation

We collected data of tree and shrub species of 58 sites (Fig. 1; Table 1) in the Brazilian littoral from the literature (Electronic supplementary material). We limited the geographical scope to the coasts of the southern and southeastern Brazilian regions (southern block), because it consists of one of the two main biogeographical provinces in the Atlantic Forest (Leitão-Filho 1994; Thomas et al. 1998; Aguiar et al. 2003) and where coastal plains are more common (Joly et al. 1992). Although the Atlantic Forest complex includes an wide spectrum of littoral and inland vegetation, we limited the sample only to Atlantic Ombrophilous Dense Forest and Pioneer Vegetation under marine influence (Restinga) according to Brazilian vegetation classification (IBGE 1992). The Seasonal Semideciduous Forest and Ombrophilous Mixed Forest (Araucaria forest) occurring inland and frequently referred as Atlantic Forest were not considered because climate and species composition are quite distinct from the Atlantic Forest (Oliveira-Filho and Fontes 2000). Survey methods (and sample size) in the studies varied from plot (0.06–1.21 ha) to point centred quarter (30–150 points), line intercept transect (150 to 300 m) and floristic collections. The minimum plant size also varied (1.5 cm > dbh > 10 cm; 0.5 m > height > 2 m). This variation occurs because areas are mainly fragments with limited area and authors used different methods to collect data from scrubs and forests.

We collated geographic (latitude, longitude, altitude, distance from the ocean), climatic (annual rainfall, rainfall in the driest month, average temperature, average temperature in the coldest month), edaphic (soil sandiness, soil pH) and structural (species richness, basal area) data as described in the sources. When the source did not provide all information we obtained data from secondary sources: geographical data from Google™ Earth and climatic data from DNMet (1992) and Rede Nacional de Agrometeorologia (2004).

Species checklists were compiled for the 58 sites and checked for recent synonyms in herbarium collections (UPCB), literature (Flora Neotropica, Flora Ilustrada Catarinense, Flora Fanerogâmica de São Paulo), websites (Instituto Agronômico de Campinas-SP and

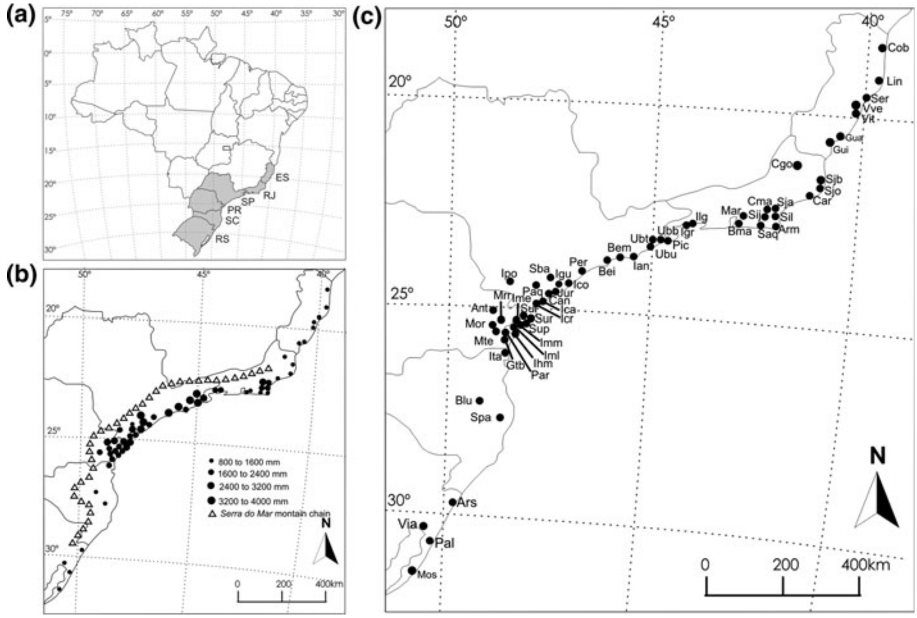

Fig. 1 Map showing the location of sites used in the floristics analysis in the south and southeast Brazil. **a** Brazilian states: ES = Espírito Santo, RJ = Rio de Janeiro, SP = São Paulo; PR = Paraná, SC = Santa Catarina, RS = Rio Grande do Sul; **b** Precipitation (*circles*) and location of the *Serra do Mar* mountain chain (*triangles*); **c** location of the 58 sites (codes as Table 1)

Missouri Botanical Garden), as well as other compilations (Oliveira-Filho et al. 2005). Undetermined species (total 434; average = 6.6 undetermined species per site) were not included in the list. The checklist comprised a total of 1088 tree species.

Floristic differentiation analyses

To lead the analysis of the floristic relationships among sites we constructed two matrices. The main matrix contained the binary data (presence and absence) of the occurrence of 1088 species and the second matrix the geographic, climatic, edaphic and structural data from the 58 sites. We performed a Detrended Correspondence Analysis (DCA) in PC-ORD 5.0. Like other correspondence analyses, DCA ordinates both species and sample units simultaneously. It is suitable where samples are very variable and no assumptions about the distribution of sample units and species in environmental space are necessary (McCune and Grace 2002).

To test if sample size affected the results we performed an additional DCA only for samples with $\leq$100 species ($n = 48$). We compared values generated in DCA for axis 1 and axis 2 in the two situations (before and after data modification) by a Pearson correlation (Zar 1999). We considered that strong correlations indicated no effect caused by sample size.

The correlation coefficients generated by DCA were checked for significance with $\alpha = 0.05$ (Zar 1999). We considered all samples and variables in the analyses except for variables with missing values. In these cases we correlated axis scores with the variable excluding samples with missing values.

Table 1 Characteristics of coastal vegetation studied in 58 sites in south and southeast Brazil

Code	Locality	State	Physiognomy	Altitude (m)
Ant	Antonina	PR	Forest-unflooded	60
Arm	Armação de Búzios	RJ	Forest-unflooded	5
Ars	Arroio do Sal	RS	Forest-unflooded	5
Bei	Bertioga	SP	Forest-flooded	6
Bem	Bertioga	SP	Forest-unflooded	4
Blu	Blumenau	SC	Forest-unflooded	400
Bma	Barra de Maricá	RJ	Scrub-unflooded	5
Can	Cananéia	SP	Forest-unflooded	200
Car	Carapebus	RJ	Scrub-unflooded	5
Cgo	Campos de Goytacazes	RJ	Forest-unflooded	250
Cma	Cachoeira do Macacu	RJ	Forest-unflooded	200
Cob	Conceição da Barra	ES	Forest-unflooded/flooded	5
Gtb	Guaratuba	PR	Forest-unflooded	5
Gua	Guarapari	ES	Forest-unflooded	0.5
Gui	Guarapari	ES	Forest-unflooded	33
Ian	Ilha Anchieta	SP	Forest-flooded	5
Ica	Ilha do Cardoso	SP	Forest-unflooded	9
Ico	Ilha Comprida	SP	Forest-flooded	3
Icr	Ilha do Cardoso	SP	Forest-flooded	7
Igr	Ilha Grande	RJ	Forest-unflooded	5
Igu	Iguape	SP	Forest-unflooded	5
Ihm	Ilha do Mel	PR	Scrub-unflooded	2
Ilg	Ilha Grande	RJ	Forest-unflooded	280
Ime	Ilha do Mel	PR	Forest-flooded	3
Iml	Ilha do Mel	PR	Forest-unflooded	4
Imm	Ilha do Mel	PR	Forest-flooded	3
Ipo	Iporanga	SP	Forest-unflooded	230
Ita	Itapoá	SC	Forest-unflooded	9
Jur	Juréia	SP	Forest-unflooded	7
Lin	Linhares	ES	Forest-unflooded	5
Mar	Marambaia	RJ	Scrub-unflooded	5
Mor	Morretes	PR	Forest-unflooded	400
Mos	Lagoa do Peixe	RS	Forest-unflooded	5
Mrr	Morretes	PR	Forest-unflooded	485
Mte	Morretes	PR	Forest-unflooded	500
Pal	Palmares	RS	Forest-unflooded	5
Paq	Pariquera-Açu	SP	Forest-unflooded	35
Par	Paranaguá	PR	Forest-unflooded	20
Per	Peruíbe	SP	Forest-unflooded	200
Pic	Picinguaba	SP	Forest-unflooded	25
Saq	Saquarema	RJ	Forest-unflooded	5
Sba	Sete Barras	SP	Forest-unflooded	100
Ser	Serra	ES	Forest-unflooded/flooded	2

Table 1 continued

Code	Locality	State	Physiognomy	Altitude (m)
Sij	Silva Jardim	RJ	Forest-unflooded	200
Sil	Silva Jardim	RJ	Forest-flooded	150
Sja	Silva Jardim	RJ	Forest-unflooded	30
Sjb	São João da Barra	RJ	Forest-unflooded	2.5
Sjo	São João da Barra	RJ	Scrub-unflooded	2.5
Spa	São Pedro de Alcântara	SC	Forest-unflooded	300
Sui	Superagui	PR	Forest-unflooded	50
Sup	Superagui	PR	Forest-unflooded	4
Sur	Superagui	PR	Forest-unflooded	7
Ubb	Ubatuba	SP	Scrub-unflooded	2
Ubt	Ubatuba	SP	Forest-unflooded	300
Ubu	Ubatuba	SP	Forest-flooded	3
Via	Viamão	RS	Forest-unflooded	35
Vit	Vitória	ES	Forest-unflooded	5
Vve	Vila Velha	ES	Forest-unflooded	5

Complete dataset available in Electronic supplementary material

The DCA indicated two main floristic groups and we compared the geographic (distance from the sea, altitude), climatic (annual rainfall, rainfall in the driest month) and structural (basal area) characteristics between the groups by Mann–Whitney test (Zar 1999).

Vegetation classification

Once DCA has been performed, we used the same matrices above (binary data for 58 sites and 1088 species) to classify vegetation by Two-Way Indicator Species Analysis (TWINSPAN) in PC-ORD 5.0. Although TWINSPAN has limited application to very complex frameworks (van Groenewoud 1992) it works well with simpler datasets and its hierarchic classification is very helpful, mainly when interpretations are made in comparison with DCA diagrams (McCune and Grace 2002; Tsiripidis et al. 2007; Burnside et al. 2007). It is one of few classification methods that provides a key for the identification of new samples; we propose this as a practical key for future use. We also used TWINSPAN to classify species according to their preference to one vegetation type.

In order to discuss the possible incongruence among vegetation physiognomy, classification and laws for conservation of the Atlantic Forest, we based on descriptions in published papers and allocated sites according three a priori definitions: (a) the vegetation physiognomy, (b) Brazilian Vegetation Classification (IBGE 1992) and (c) regulatory environmental law CONAMA (1999). These definitions were the following:

(a) Physiognomy: based on authors' descriptions, we distinguished forest (tree dominated vegetation) from scrub (shrub dominated vegetation) and flooded vegetation (soil flooded for a period >5 months annually) from unflooded vegetation (dry and well drained soil).
(b) Classification of Brazilian Vegetation (IBGE 1992): it divides the coastal vegetation into:

(b.1) Ombrophilous forest: forests occurring from 5 to 50 m above the sea level (Ombrophilous lowland forest), 50–500 m (Ombrophilous low slope forest), 500–1500 m Ombrophilous montane forest) and >1500 m (Ombrophilous high montane forest).

(b.2) Pioneer vegetation under marine influence (Restinga): herbaceous to woody vegetation occurring in coastal plain sediments next to the sea.

(c) CONAMA (1999): This regulatory document was designed as supplementary material (Resolução 261/1999) of the Brazilian forest law (Código Florestal 4771/1965) to describe the Restinga in Santa Catarina state for conservation proposes, but it has been used for research around the country. It considers as Restinga only the vegetation that occurs on young sediments (late Quaternary). This regulatory document does not mention any other vegetation type and we assumed that all other woody vegetation occurring on older sediments (Pleistocene to Pre-Cambrian) should be considered as Ombrophilous forest.

Results

The DCA showed a homogeneous diagram (Fig. 2). Axis 1 is significantly correlated with 10 variables and axis 2 with 5 variables (Table 2). Rainfall, longitude, altitude and rainfall in the driest month were the strongest correlates of Axis 1. Longitude, latitude and species richness were more strongly related in the axis 2 (Table 1). This analysis was compared with a similar analysis which excluded samples with >100 species: correlation coefficients between axis scores for all samples and axis scores for the reduced set of samples were very high (axis 1: $r = 0.99$; axis 2: $r = 0.85$; both $P < 0.0001$, df $= 46$). Thus, both analyses (before and after manipulation) were very similar and we considered results were not affected by sample size.

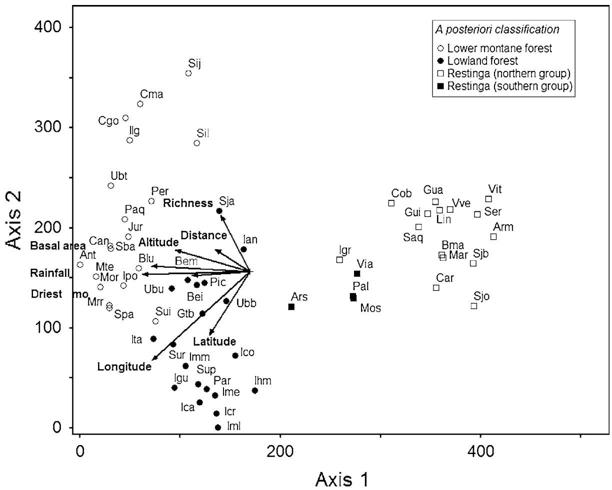

Fig. 2 Axis 1 and 2 of the Detrended Correspondence Analysis (DCA) applied to 58 sites of Atlantic Forest complex in the Brazilian Coast coded for a posteriori classification generated from TWINSPAN. Site codes as in Table 1

Table 2 Correlation coefficients between independent variables and the first two axes of a DCA generated from two matrices of 58 sites in the Atlantic Rain Forest complex

Variable	Axis 1	Axis 2
Geographical		
Latitude	−0.40**	−0.50***
Longitude	−0.62***	−0.59***
Altitude	−0.55***	0.29*
Distance from the ocean	−0.37**	0.30*
Climatic		
Rainfall	−0.65***	−0.10
Rainfall (driest month)	−0.48***	−0.12
Mean annual temperature	−0.20	0.02
Mean temperature (coldest month)	−0.25*	0.09
Edaphic		
Soil pH	−0.07[a]	−0.29[a]
Soil % sand	−0.71***[b]	−0.03[b]
Structural		
Richness	−0.34**	0.48***
Basal area	−0.38**[c]	−0.07[c]
Eigenvalue	0.63	0.32
Length of gradient	3.48	2.68

Significance of correlation coefficients: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Correlations with variables with missing values were calculated with reduced sample sizes

[a] Corrected for 25 sites (df = 23)

[b] Corrected for 21 sites (df = 19)

[c] Corrected for 45 sites (df = 43)

Figure 2 shows a differentiation among sites in two main groups. The first group (axis 1 values >200) includes unflooded forests and scrubs. This group represents communities located in lower (easterly) longitudes and lower (northerly) latitudes and that have low basal area and are located in dry regions. The second group (axis 1 values <200) is bigger and more scattered (on the axis 2) than the first one. This group represents unflooded and flooded forests, as well as scrubs, ranging from high to low diversity and high basal area, occurring in high latitudes, longitudes or altitudes and associated with a wetter and colder climate. The sample distribution in the diagram (Fig. 2) is only weakly related to the a priori definition considering vegetation physiognomy (Fig. 3a), the classification of Brazilian vegetation (Fig. 3b) and the regulatory CONAMA document (Fig. 3c).

The TWINSPAN resulted in an hierarchic classification in two levels (Fig. 4). In the first level the coastal woody vegetation may be divided in two groups that are in agreement with the main DCA groups (Fig. 2). The indicator species *Maytenus obtusifolia*, *Cynophalla flexuosa*, *Byrsonima sericea* and *Ilex theazans* segregate the negative (Ombrophilous forest) and positive (Restinga) groups. The site Ars (Table 1) was a borderline in the analysis, but we considered it as a Restinga since in floristic and geographical location it is closer to that group. In the second level, Ombrophilous forest may be separated into two new groups, depending on five indicator species: *Hyeronima alchorneoides*, *Cariniana estrellensis*, *Calophyllum brasiliense*, *Ocotea pulchella* and *Myrcia multiflora*. The Ombrophilous lowland forest and Ombrophilous lower montane forest are approximately

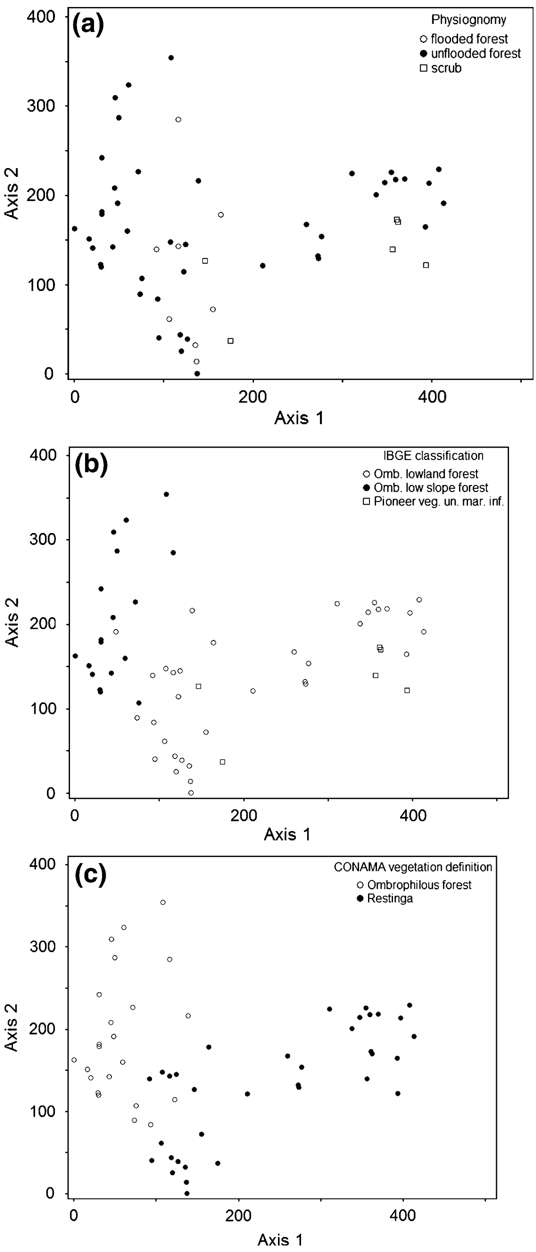

Fig. 3 Axis 1 and 2 of the Detrended Correspondence Analysis (DCA) applied to 58 sites of Atlantic Forest complex in the Brazilian Coast coded for a priori definition: **a** physiognomy; **b** IBGE classification; **c** CONAMA vegetation definition

in agreement with groups in DCA (Fig. 2). In addition, Restinga may be divided in two other groups according to presence of *Erythroxylum argentinum*: the northern and southern Restinga. These groups represent the separations also observed in the DCA (Fig. 2).

Based on the DCA and TWINSPAN we summarized the characteristics of the four groups (three coastal lowland vegetation; Table 3). Restinga and Ombrophilous lowland forest represent vegetation varying in physiognomy (scrub to forest), soil drainage (flooded to unflooded) and sediment age (Holocene to Pleistocene). Ombrophilous lower montane

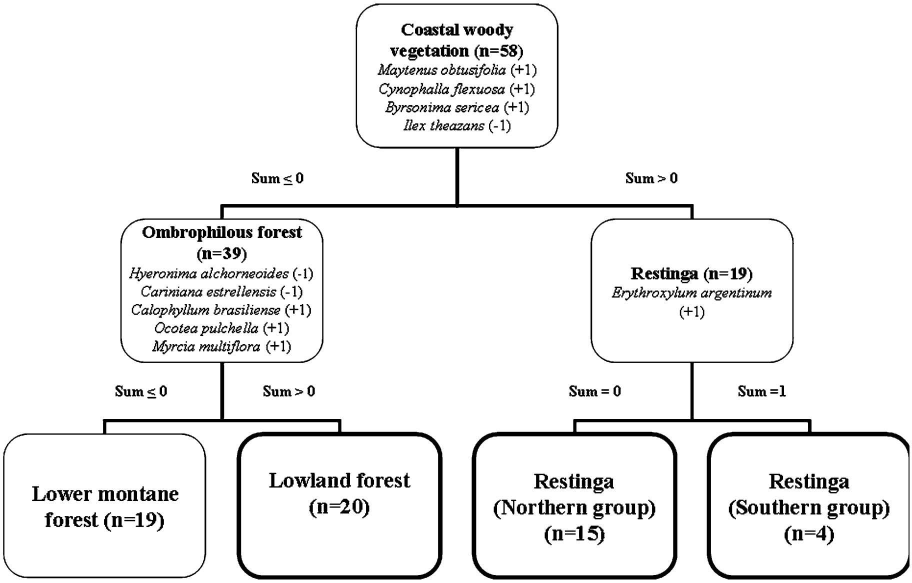

Fig. 4 Key for coastal vegetation classification in the southern and southeastern Brazil generated from TWINSPAN. Indicator species are assigned values (+1 or −1) used to determine allocation of a sample to positive or negative groups. In *bold* is the coastal lowland vegetation

forest is clearly different in the average of species richness, basal area, altitude, and distance from the ocean ($P < 0.05$). The coastal lowland vegetation (Ombrophilous lowland forest, Restinga-Northern group and Restinga-Southern group) is not homogeneous and differ, mainly in annual rainfall (higher in the lowland forest).

According to the TWINSPAN most (75%) of species (total 1088) were indifferent in relation to the vegetation type and can be considered generalist species. Only 25% of the total were considered preferential to one vegetation type in southern and southeastern Brazil. In the Ombrophilous lower montane forest 126 species were preferential to this vegetation, including *Garcinia gardneriana, Miconia cinerascens, Sloanea guianensis, H. alchorneoides, Cabralea canjerana, Quiina glaziovii* and *C. estrellensis*. In the coastal lowland vegetation the number of preferential was also low: 40 species in the Ombrophilous lowland forest (for example *Clusia criuva, I. theazans*, *C. brasiliense, M. multiflora, Andira fraxinifolia* and *Ocotea pulchela*), 100 species in the Restinga-Northern group (*M. obtusifolia, C. flexuosa, Garcinia brasiliensis, B. sericea, Annona acutiflora*, etc.) and 48 species in the Restinga-Southern group (*E. argentinum, Allophyllus edullis, Ficus organensis, Myrrhinium atropurpureum*, etc.).

Discussion

The coastal vegetation in southern and southeastern Brazil is characterized by two distinctive floristic groups representing forests and scrubs that occur in drier climates (Restingas) in the Brazilian states of Espírito Santo, Rio de Janeiro and Rio Grande do Sul, and in wetter climates (Ombrophilous forests) in Santa Catarina, Paraná and São Paulo. Whereas physiognomic-environmental parameters and floristics relationships are two main ways for classifying vegetation (Joly et al. 1999), our results point to a strong influence of

Table 3 Characteristics of coastal lowland vegetation (values are average ± SE) in southern and south-eastern Brazil, after the classification a posteriori

	Ombrophilous forest		Restinga		*Z*
	Lower montane forest	Lowland forest	Northern group	Southern group	
Physiognomy and soil drainage	Forest	Forest to scrub, flooded or unflooded	Scrub to forest, flooded or unflooded	Scrub to forest, flooded or unflooded	
Sediment	Older than Pleistocene	Holocene or Pleistocene	Holocene or Pleistocene	Holocene	
Species richness	97.63 ± 10.13^{a}	50.70 ± 5.51^{b}	63.93 ± 8.00^{b}	38.75 ± 11.51^{b}	16.44*
Basal area (cm)	38.72 ± 3.59^{a}	20.57 ± 3.40^{b}	5.97 ± 2.68^{c}	22.02 ± 11.51^{abc}	25.31*
Altitude (m)	228.80 ± 33.52^{a}	7.80 ± 1.76^{b}	5.03 ± 2.07^{b}	12.50 ± 7.50^{b}	38.63*
Annual rainfall (mm)	2242 ± 161^{a}	2369 ± 130^{a}	1266 ± 88^{b}	1258.75 ± 43^{b}	31.24*
Distance from the ocean (km)	27.50 ± 5.92^{a}	2.69 ± 1.34^{b}	1.04 ± 0.37^{b}	18.71 ± 13.86^{c}	30.45*
Occurrence (Brazilian states)**	SC, PR, SP	SC, PR, SP, RJ (less common)	ES, RJ	RS	
Sites studied**	Ant, Blu, Can, Cgo, Cma, Ilg, Ipo, Jur, Mrr, Mte, Mor, Per, Paq, Sba, Sij, Spa, Sui, Sil, Ubt	Bei, Bem, Gtb, Ime, Ian, Ico, Ihm,Igu, Iml, Imm, Ita, Ica, Icr, Par, Pic, Sup, Sur, Sja, Ubu, Ubb	Arm, Bma, Cob, Car, Gua, Gui, Igr, Lin, Mar, Ser, Sjo, Sjb, Saq, Vve, Vit	Ars, Mos, Pal, Via	

Means followed by the same letter are not different ($P > 0.05$; Mann–Whitney). Coastal lowland vegetation: Lowland forest, Northern group, Southern group

* $P < 0.001$; ** According to Table 1

geo-climatic and edaphic gradients determining floristic distributions in lowland forests. These findings help to understand the complexity of this diverse biome and must to take account to make decisions on the Atlantic Rain forest conservation.

Geo-climatic and edaphic gradients in montane and lowland vegetation

The floristics of Atlantic Rain forest in southern and southeastern littoral is strongly related to the geography and climate. Longitude and latitude are strongly and positively related among themselves due to the littoral shape (see Fig. 1a) and influence floristic differentiation. Variation in Atlantic Rain Forest flora along Brazilian littoral is in accordance to floristic connections with neighbouring vegetation: in the northern block (states of Paraíba, Pernambuco and Alagoas) Atlantic Forest is more related with Caatinga and Amazonian floras (Santos et al. 2007) and is associated with Semideciduous forests and Cerrado floras (states of Bahia and Espírito Santo). In the Southern block (Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul) there is an influence of Subtropical and Semideciduous forests (Oliveira-Filho and Fontes 2000). Thus, differences in the neighbouring flora on the latitudinal gradient probably influenced the floristic differentiation among sites studied here. Besides that, altitude and distance from the ocean are related to species distributions among sites and was important in the differentiation among lower montane forests and coastal lowland vegetation. Differences in temperature and humidity associated with these variables are important factors influencing the occurrence of species in a local scale (Pyke et al. 2001; Ashton 2003; ter Steege et al. 2003; Durigan et al. 2003; Sesnie et al. 2009).

Rainfall and soil sandiness were the most important factors causing floristic differences in vegetation and separating two easily recognized groups in DCA and TWINSPAN. The soil dryness caused by low precipitation and/or fast water drainage (in sandy soils) limit plant growth and only physiologically adapted species survive (Scarano et al. 2001). This occurs in geographically distant, but climatically similar sites in Rio Grande do Sul state (Via, Pal, Mos, Ars, see Table 1) and Espírito Santo and Rio de Janeiro states (Igr, Cob, Gua, Gui, Saq, Lin, Vve, Vit, Ser, Arm, Sjb, Sjo, Car, Mar, Bma, Table 1). Otherwise, wetter (and less sandy) soils are the habitat for hygrophilous species in Santa Catarina, Paraná and São Paulo states. In those regions the *Serra do Mar* mountain chain (Fig. 1b) prevents the wet air masses from the Atlantic Ocean from moving over the continent and causes orographic rains in the littoral. Within this area there are floristic similarities, even in sites varying in altitude and distance from the ocean. Nevertheless, species richness in sites located in higher altitudes (lower montane forests) is higher than in lower altitudes (lowland vegetation), probably due to differences in vegetation age. *Serra do Mar* mountains date from the Early Tertiary period (Almeida and Carneiro 1998) and one can suppose that there was sufficient time for speciation or colonization, resulting in high species. On the other hand, the lowland vegetation is over sediments of Pleistocene to Holocene age, i.e. up 20000 years ago (Suguio and Martin 1990), and species richness tends to be lower.

The coastal lowland vegetation

Neither vegetation physiognomy nor the a priori definitions (IBGE 1992; CONAMA 1999) were fully congruent with the floristic variation among coastal vegetation in the Atlantic Forest complex. The DCA showed that there are two conspicuous groups including areas varying in physiognomy (scrubs to forests and flooded to unflooded sites). The first conclusion that arises from this is that attempts to define coastal vegetation based on physiognomy may be floristically incongruent. The former Brazilian vegetation classification (IBGE 1992) does not distinguish floristic differences along the littoral since was based on large scale information. Consequently, local names are frequently used and more than 30 terms denominate coastal lowland vegetation in the country (see Silva and Britez 2005). Based on our findings, we suggest that in the coastal lowland areas the term Restinga should be used only for scrub to forest vegetation in dry soils as that is found in Espírito Santo, Rio de Janeiro and Rio Grande do Sul states. Although the word Restinga has also other uses (nautical and geological), it is widely used by researches and local population to refer to vegetation. On the other hand there are no floristic reasons to consider forests and scrubs from wetter areas of Santa Catarina, Paraná and São Paulo states to be different from the Ombrophilous lowland forests. Thus we suggest that this term should be used, preserving the name derived from the Brazilian vegetation classification system, but observing that variations in physiognomy (forest to scrub) are possible.

The woody vegetation of coastal plains in the southern and southeastern Brazilian littoral is variable in physiognomy (scrub to forest), in soil water availability (flooded to unflooded) and is established above marine sediment varying in age (Holocene to

Pleistocene). In fact, this variation is observed even in a restricted region (Araújo 1992; Silva and Britez 2005; Nettesheim et al. 2010) and in palynological evidences of the last 5000 years (Scheel-Ybert 2000). Nevertheless, in terms of floristics this vegetation can be said to comprise only two groups (Ombrophilous lowland forest and Restinga) occurring in very different climates (drier in Restinga areas) and distinguished by a small group of species. Our results showed that a large number of species are shared among Ombrophilous lowland forests and Restingas, probably due to the common origin. Previous study showed that Restinga comprises a subgroup of montane and lower montane floras in the southern and southeastern Brazilian littoral (Araújo 2000), denoting their origin from the ancient flora. Thus, the coastal lowland vegetation should be understood as an assemblage of species derived from the inland vegetation, but floristically distinguished according to the soil water availability.

Among species that determine vegetation types (according TWINSPAN) in the coastal plain, *M. obtusifolia*, *B. sericea* and *C. flexuosa* are associated to Restinga and also distributed in the northern and dry vegetation of Cerrado, Caatinga and Seasonal Semideciduous forests (Stehmann et al. 2009; Forzza et al. 2010). *I. theazans*, an indicator species of Ombrophilous forest, is also found in forests in the Amazon, Caatinga and Cerrado (Forzza et al. 2010). In the Restinga, the southern group is determined by *E. argentinum*, a typical tree of the southern Atlantic Forest (São Paulo, Paraná, Santa Catarina and Rio Grande do Sul states, Forzza et al. 2010). On the other hand, in the Ombrophilous forest, the Lowland forests are characterized by the presence of *C. brasiliense* (that occurs also in Amazon, Caatinga and Cerrado), *O. pulchella* (also in Cerrado) and *M. multiflora*, a wide distributed species in Brazil (Forzza et al. 2010). Thus, based on our database, the presence of these species may be used to predict vegetation types and be a tool to understand the floristic differentiation in the coastal vegetation. Nevertheless, the inclusion of a larger dataset comprising also less studied regions (for example, Santa Catarina state) is necessary to confirm this definition.

Vegetation classification and the conservation of the Atlantic Rain Forest

Conservation decisions are usually driven by multiple factors such as politics and economics (Costanza et al. 1997), biological, among others. Regarding to biological and ecological aspects, species distributions and vegetation classification are key factors determining a specific biome. Our results have showed that the Atlantic Rain Forest complex in south-southeast Brazil comprises a large floristic block in with species distribution is affected by geo-climatic features. Thus, every law and regulatory actions that aim to protect the Atlantic Rain Forest must to take the floristic variation in consideration for full conservation of this biome. For example, the specific Atlantic Forest law (Lei 11.428/2006) is sufficiently comprehensive by considering both coastal and hinterland vegetations as part of the Atlantic Forest complex. On the other hand the differentiation among two floristic groups—Restinga and Ombrophylous forest—can not lead to erroneous conservation decision. Several studies have demonstrated that whereas less diverse, the coastal lowland areas are important for maintenance of the Atlantic rain Forest Complex (Joly et al. 1999; Scarano 2002; Scarano 2009) since it has conserved a high endemism for a long time (Carnaval and Moritz 2008). Additionally, both lowland and mountain forests are strongly affected by fragmentation (Liebsch et al. 2008; Lopes et al. 2009). Thus, although floristically distinct, Restinga and Ombrophylous forests are equally vulnerable to the human impact. Conservation initiatives should be more conservative and treat collectively all coastal lowland vegetation as biodiversity hotspot, rather than the specific formation alone. Besides that, the conservation of coastal vegetation as a unique unit, will allow flux of biodiversity in this southern and southeaster costal regions, two of the main biodiversity corridors in the Atlantic Rain Forest biome (Galindo-Leal and Câmara 2005).

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