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Article

Leguminosae tree species diversity in coastal forests of Rio de Janeiro, Brazil

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Abstract: This study investigated the current Leguminosae tree species composition in coastal forests over lithosoil soil or sandy plains in the eastern and central portion of Rio de Janeiro state, Brazil. A comparative study between the Atlantic Forest areas of the Southeast Region of Brazil was conducted to evaluate the influence of environmental variables on floristic differentiation. A total of 34 areas of the Southeast Region was selected from the NeoTropTree platform and the Leguminosae species in these areas were the basis for a similarity analysis. The Jaccard Similarity Index and the UPGMA method were applied for grouping analysis. The relationships between the Leguminosae species composition and the environmental variables were investigated via Cannonical Correspondance Analysis (CCA). The cluster analysis showed that the Leguminosae tree species group of this portion of Rio de Janeiro coastline share floristic affinity with seasonal forests, a result confirmed by CCA. This floristic differentiation is sustained by an exclusive group of Leguminosae species established over lithosoils or sandy plains, and signals that the extent of dry forests in Rio de Janeiro state might be larger than currently stated. The results justify distinct conservation actions in view of the floristic singularities of these areas.
Keywords: *Diversity; dry forest; endemism; Fabaceae; floristic similarity.*

Diversidade de espécies de Leguminosae arbóreas nas florestas costeiras do Rio de Janeiro, Brasil

Resumo: O presente trabalho investigou a composição de espécies arbóreas de Leguminosae presentes em florestas litorâneas, estabelecidas sobre solos litólicos ou planície arenosa, na porção Central e Leste do estado do Rio de Janeiro, Brasil. Foi realizado um estudo comparativo entre áreas de Floresta Atlântica no Sudeste brasileiro para avaliar a influência de variáveis ambientais nas diferenciações florísticas. Foram elencadas 34 áreas da Região Sudeste na plataforma NeoTropTree e tabuladas as espécies de Leguminosae dessas áreas para análise de similaridade. Foi utilizado o índice de similaridade de Jaccard e o método UPGMA para as análises de agrupamento. As relações entre a composição de espécies de Leguminosae e as variáveis ambientais foram investigadas através da análise de Correspondência Canônica (CCA). A análise de agrupamento mostrou que o conjunto de espécies de Leguminosae arbóreas dessa porção do litoral fluminense possui afinidade florística com as florestas estacionais, resultado igualmente corroborado pela CCA. Essa diferenciação florística é sustentada por um conjunto exclusivo de espécies de Leguminosae, estabelecidas nessas florestas sobre solos litólicos ou planície arenosa e sinaliza que a extensão de matas secas no estado do Rio de Janeiro pode ser maior que o apresentado atualmente. Este resultado justifica ações diferenciadas em termos de conservação, tendo em vista a singularidade florística apresentada por estas áreas.
Palavras-chave: *Diversidade; Fabaceae; endemismo; matas secas; similaridade florística.*

Introduction

The Atlantic Domain is well known for its great heterogeneity, notably its latitudinal extent and topographic variation (Oliveira-Filho & Fontes, 2000; Joly et al., 2014). The rainfall distribution and temperature fluctuations are the main differentiating factors between seasonal and ombrophilous forests, and strongly control the floristic composition of these different forest types (Oliveira-Filho & Fontes, 2000; Oliveira-Filho et al., 2005; Nettesheim et al., 2010). The overall differentiation between these two floristic blocks is more apparent in the East-West distribution related to gradients in seasonal rainfall according to the distance from the ocean (Salis et al., 1995; Scudeller et al., 2001; Joly et al., 2014), with seasonal forests extending into the Domain's inner boundaries. The climate in the Brazilian Southeastern Region at the central portion of the Atlantic Coast varies drastically, with seasonal forests reaching as far as the Rio de Janeiro northern coastal zone (Oliveira-Filho & Fontes, 2000). This drier coastal climate is caused by the cold oceanic resurgence phenomena in the Região dos Lagos (Araujo, 1997), which spreads in both north and south directions along the Rio de Janeiro coastline (Barbiére, 1984; Oliveira-Filho et al., 2005). In addition, precipitation decreases gradually with the distancing from top of Serra do Mar towards the coast and in the west-east direction, due to less orographic control (Bohrer et al., 2009).

The seasonal forests are currently acknowledged as part of a singular global biome denominated Seasonally Dry Tropical Forests (SDTF), and, in Rio de Janeiro, only 10% of the areas originally covered by these forests remains, most of them (50%) highly fragmented, composed by patches smaller than 100 ha (Fidalgo et al., 2009; Pennington et al., 2009). SDTFs show rainfall of less than 1600mm per year and with periods of at least 5 to 6 months of 100mm. The vegetation is mainly deciduous, the degree of deciduality increases with decreasing rainfall (Mooney et al., 1995; Pennington et al., 2000; 2009). Scarano et al. (2009) point out that these areas are little known regarding their floristic and structural composition, with studies having been centered in the North and Northwestern regions (e.g. Silva & Nascimento 2001; Carvalho et al., 2006; Nascimento & Lima 2008; Dan et al., 2010; Mauad 2010; Abreu et al., 2014; Souza 2015; Fortes et al., 2020); in the Southern Paraiba river basin region (e.g. Peixoto et al., 1995; Bloomfield 1997; Spolidoro 2001; Souza et al., 2007; Fernandes et al., 2012; Freitas & Magalhães 2014; Medeiros et al., 2020); and in the Cabo Frio Plant Diversity Center (CDVCF) (e.g. Sá 1992, 2002, 2006; Araujo et al., 2009; Kurtz et al., 2009; Ribeiro & Lima 2009; Sá & Araujo 2009; Carvalho et al., 2018).

Among the lesser known forest formations in Rio de Janeiro State, the coastal forests mainly stand out for their co-occurrence on lithosoil or over sandy plains (restinga). Although located at the edge of the Dense Ombrophilous Forest (IBGE 2012), they can be distinguished by their microclimate characteristics which feature a brief dry season which is intensified by the soil conditions, since sandy soils generally have low water retention capacity (Scarano 2009). These areas are considered the Atlantic Rain Forest's marginal habitats, upon which environmental factors act and limit species distributions (Scarano 2009; Neves et al., 2017).

This study aimed to compare the Leguminosae tree composition of these forests with other Atlantic Rain Forests in the Southeast Region and to evaluate the influence of environmental variables on floristic differentiation among the forest areas. The hypothesis raised in this study is that the Leguminosae tree composition of coastal forests presents greater floristic affinity with Semi-Deciduous Seasonal Forests due to the occurrence of similar environmental filters. This hypothesis will be tested using the Leguminosae as an indicator for richness and composition evaluation, since it is featured among the five richest in species in Rio de Janeiro state, and is well represented in floristic and phytosociological inventories of different phytophysiognomies (Araujo 2000; Lima 2000; Barros 2008; Ribeiro & Lima 2009; BFG 2015; Coelho et al., 2017; Fortes et al., 2020). Leguminosae is the plant family with the greatest species richness and abundance in the SDTF (DRYFLOR 2016), been used a model family for biogeographic studies of this biome before in South America (e.g. Särkinen et al., 2012).

Although there is already a relatively robust set of floristic data on the SDTF, currently compiled in databases such as NeoTropTree (Oliveira-Filho 2017), the low representativeness of inventories, particularly in the southeastern Atlantic coastal strip, has hampered more comprehensive biogeographic analyzes. Filling this gap is urgent to advance global and local conservation strategies of this biome, which is extremely threatened by its disjunct distribution, high level of threat and low representation in protected areas. In addition, it is expected that the results of this study can support conservation actions of those remaining in the region. The strongholds of Seasonal Forests in the state of Rio de Janeiro are still poorly studied when compared to Ombrophilous Forests and poorly represented in conservation units, especially those of Integral Protection. Improving the knowledge of the distribution of family species on the coast of Rio de Janeiro, understanding issues of diversity and turnover are points that can help in the conservation of dry forests and lead to the improvement of conservation strategies for these remnants.

Material and Methods

A total of 34 areas corresponding to ombrophilous forests, seasonal forests and restinga forests in the Southeast Brazilian Atlantic Rain Forest in the NeoTropTree database were analyzed, of which 21 are in Rio de Janeiro state, six in Minas Gerais, four in Espírito Santo and three in São Paulo (Table 1; Figure 1). The NeoTropTree database (Oliveira-Filho 2017) provides arboreal species lists and environmental variables obtained in sites with a single phytophysiognomy. Thus, a single area can encompass several sites, provided that those sites correspond to different phytophysiognomies (Eisenlohr & Oliveira-Filho 2015).

There are coastal forests encountered in the central and eastern portions of Rio de Janeiro state, including in the areas of Niterói and Maricá (RJnite), Ilha de Marambaia (RJmrbm), Maciço do Itaoca (RJitaoc), Cabo Frio (RJcabo) and Saquarema (RJsaqu). The Leguminosae list for Niterói and Maricá solely gathers species occurring in coastal slopes and lithosoil areas within three Conservation Units in Niterói (Área de Proteção Ambiental do Morro do Morcego, da Fortaleza de Santa Cruz e dos Fortes do Pico e do Rio Branco, Parque Natural Municipal de Niterói and Parque Estadual da Serra da Tiririca) and in four localities of the Refúgio de Vida Silvestre de Maricá (Pedra de Inoã, Pedra de Itaocaia, Pedra do Macaco and Serra do Camburi). Only species in Saquarema with occurrence at the Núcleo Massambaba of the Parque Estadual da Costa do Sol encompassing only Restinga formation were collected.

The Leguminosae species were organized into a binary matrix, revised and complemented by additional data. This complement was based on consulting the collections of FCAB, GUA, HB, HRJ, HUENF, NIT, R, RB, RBR, RFA and RFFP herbaria (acronyms in accordance

Table 1. Environmental variables of the 34 areas of the Southeast Region used in the Canonical Correspondence analysis. Alt (Altitude); DOcean (Distance from Ocean); Soil Salinity; TBS (Soil fertility based on average TBS - % of total base saturation); WDD (Average dry season duration). Phy (phytophysiognomy: Dense Ombrophilous Forest – DOF/Seasonal Semideciduous Forest - SSF/Restinga - RES).

Study area	Phy	Code	Coordinates		Environmental Variables				
			Latitude	Longitude	Alt (m)	DOcean (Km)	Soil Salinity (dS/m)	TBS (%)	WDD (days)
Cabo Frio	SSF	RJcabo	-228.644	-420.342	15	2	20	37	70
C. de Macacu, E. Paraíso	DOF	RJcach	-224.772	-426.761	337	55	0	17	60
Cachoeiro de Itapemirim	SSF	ESitpm	-207.422	-413.011	133	56	0	37	110
Campos, Terras Baixas	SSF	RJcamp	-216.529	-414.708	60	47	0	17	115
Carangola	SSF	MGcarg	-206.742	-419.997	890	118	0	17	85
Castelo	SSF	EScast	-20.61	-411.714	133	54	0	37	100
Descoberto	SSF	MGdesc	-214.236	-429.531	752	156	0	17	105
Desengano, Imbé	DOF	RJimb	-218.475	-416.772	314	48	0	17	65
Ilha de Marambaia	RES	RJmrbm	-230.483	-438.694	13	2	15	17	0
Ilha Grande	DOF	RJilha	-231.514	-442.011	825	25	0	17	0
Itatiaia	DOF	RJitat	-224.261	-44.62	1218	65	0	37	45
Juiz de Fora	SSF	MGjuiz	-217.483	-433.181	893	146	0	17	95
Lima Duarte	SSF	MGlima	-218.567	-438.661	768	131	0	17	105
Linhares	SSF	Esrvrd	-191.586	-400.217	50	40	0	17	25
Macaé de Cima	DOF	RJcima	-224.408	-425.694	1424	52	0	37	0
Maciço do Itaoca, Campos	SSF	RJitaoc	-217.936	-414.481	391	45	0	17	85
Maciço da Pedra Branca	DOF	RJpdbc	-229.406	-434.481	456	9	0	17	0
Maciço da Tijuca	DOF	RJtiju	-229.636	-433.014	730	6	0	17	0
Maciço do Tinguá	DOF	RJting	-225.511	-434.131	749	52	0	17	0
Mimoso do Sul	SSF	ESmimo	-210.131	-413.856	348	36	0	17	95
Miraí	SSF	MGmira	-212.447	-426.147	514	158	0	17	115
Muriaé	SSF	MGmrae	-210.803	-424.286	336	151	0	17	120
Natividade	SSF	RJnatv	-210.356	-419.275	470	102	0	17	115
Niterói/Maricá	DOF	RJnite	-229.294	-429.794	123	3	15	17	0
Paraty	DOF	RJpara	-232.972	-447.919	820	3	0	17	0
Petrópolis	DOF	RJpetr	-225.347	-431.581	1203	58	0	17	0
Picinguaba	DOF	SPpic	-233.181	-448.097	305	8	0	17	0
Poço das Antas	DOF	RJpoco	-225.414	-422.867	143	27	0	17	30
S. Francisco de Itabapoana	SSF	RJsaof	-213.933	-410.958	24	10	15	17	90
São José do Barreiro	SSF	SPjjbr	-226.347	-446.569	550	43	0	17	95
Saquarema	RES	RJsaqu	-229.072	-424.914	38	3	15	17	0
Teresópolis	DOF	RJtere	-224.544	-429.503	1180	62	0	37	0
Ubatuba	DOF	SPuba	-233.692	-450.203	525	1	0	17	0
Valença	SSF	RJvale	-223.333	-437.067	638	73	0	17	90

with Thiers 2020). All evaluated materials were identified or revised at species level. A nomenclatural revision was performed based on Flora do Brasil (2020a). The binary matrix gathered a total of 250 species.

The cluster analysis was performed, adopting Unweighted Pair Group Method with Arithmetic Mean (UPGMA) and the Jaccard index (Mueller-Dombois & Ellemberg 1974) as a similarity measure between formations, using the PAST v.2.10 program (Hammer et al., 2001). Venn diagrams were made to visualize legume species shared between distinct groups (Gotelli & Ellison 2016).

A Canonical Correspondence Analysis (CCA) was applied to analyze the correlation between species distribution and environmental variables. A total of 50 environmental variables acquired via the NeoTropTree (Eisenlohr & Oliveira-Filho 2015) database were initially considered. After preliminary CCA, 45 of those slightly correlated or highly redundant variables with high inflation factors in the analysis (ter Braak 1987) were discarded. The final CCA has five variables: altitude (m); DOcean – distance from the ocean (km); Soil Salinity (dS/m); TBS – soil fertility based on the average percentage of Total Base Saturation; WDD – dry season average

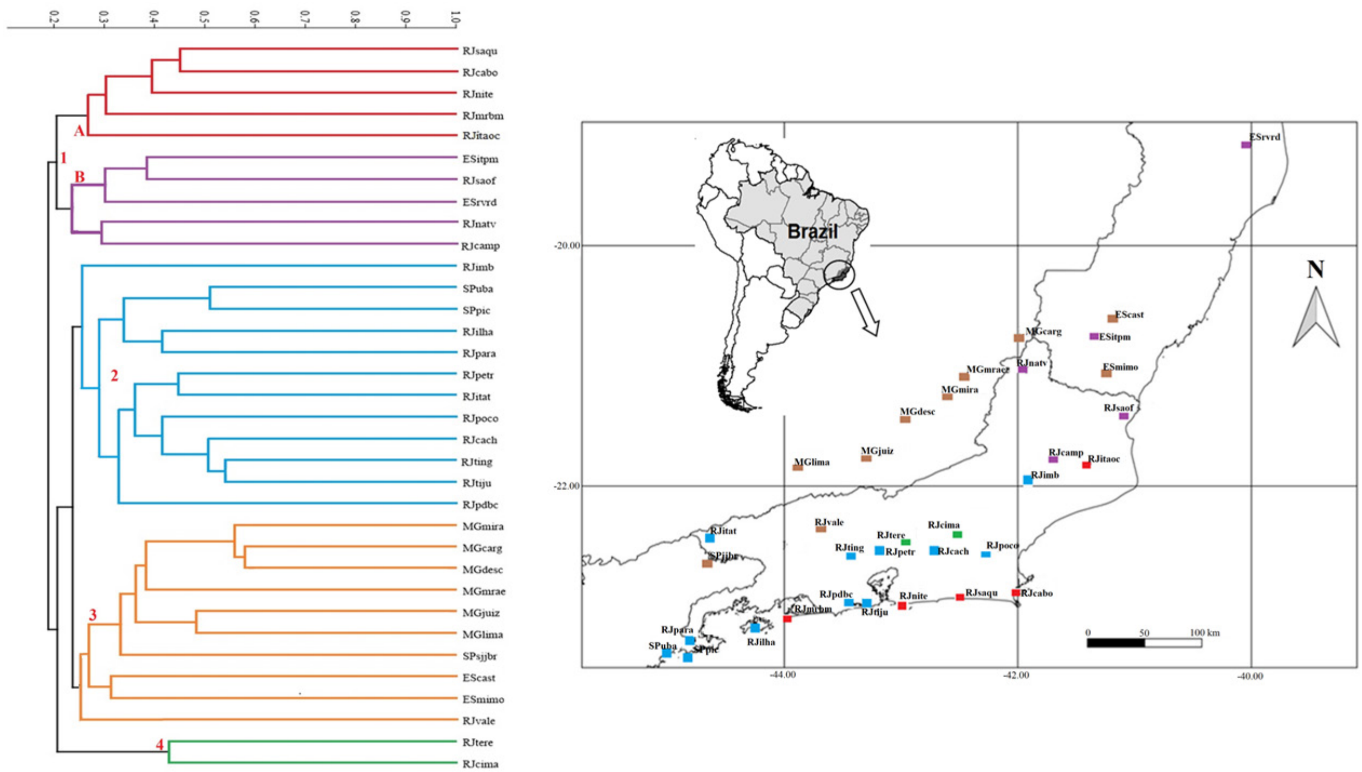

Figure 1. Stretch from the Southeastern Region of Brazil with the 34 areas grouped in the similarity analysis (Cophenetic Correlation Coefficient = 0.7442). Group 1: Seasonal Forests RJ / ES and Coastal Forests inserted in the central and eastern portion / RJ; Group 2: Ombrophilous Forests RJ / SP; Group 3: Seasonal Forests RJ / ES / MG; Group 4: Ombrophilous Forests / RJ. Areas: EScast = Castelo, ESitpm = Itapemirim, ESmimo = Mimoso do Sul, ESrvrd = Linhares/C. Vale do Rio Doce, MGcarg = Carangola, MGdesc = Descoberto, MGjuiz = Juiz de Fora, MGlima = Lima Duarte, MGmira = Miraí, MGmrae = Muriaé, RJcabo = Cabo Frio, RJcach = Cachoeiras de Macacu/Paraíso, RJcamp = Campos dos Goytacazes, RJcima = Macaé de Cima, RJilha = Ilha Grande, RJimb = Desengano/Imbé, RJitaoc = Maciço do Itaoca/Campos, RJitat = Itatiaia, RJmrbm = Ilha de Marambaia, RJnatv = Natividade, RJnite = Niterói/Maricá, RJpara = Paraty, RJpdbc = Maciço da Pedra Branca, RJpetr = Petrópolis, RJpoco = Poço das Antas, RJsaof = São Francisco do Itabapoana/Carvão, RJsaqu = Saquarema, RJtere = Teresópolis, RJtiju = Maciço da Tijuca, RJting = Maciço da Tinguá, RJvale = Valença, SPjjbr = São José do Barreiro, SPpic = Picinguaba, SPuba = Ubatuba.

duration, expressed by the number of days with water deficit (Table 1). The Monte Carlo Permutation Test was applied with 999 permutations in order to evaluate the canonical correlation significance, adopting a 95% significance level ($P<0.05$) (ter Braak 1987; Palmer 1993). The PAST v.2.10 software program was also used for this analysis.

Results

1. *Similarity analysis*

The cluster analyses revealed four well supported (approximately 0.75 of Cophenetic Correlation Coeficient - CCC) groups (Figure 1). The Centre-East Coastal Forests were included in Group 1, together with Rio de Janeiro and Espírito Santo seasonal forests. It was possible to distinguish two subgroups in the similarity variation summarized in the dendrogram for this group (Jaccard index between 0.2 and 0.5), which gathered the coastal forests inserted in Rio de Janeiro's central and eastern (RJsaqu, RJcabo, RJnite, RJmrbm and RJitaoc – Subgrup A) and the forests of the Rio de Janeiro's northern and northwestern regions, as well as the northern and southern regions of Espírito Santo (RJsaof, RJnatv and RJcamp, ESitpm and ESrvrd – Subgroup B).

Another three groups were highlighted in the dendrogram, grouping Dense Submontane Ombrophilous Forest (Group 2), Montane and High Montane forest of Rio de Janeiro state (Group 4) and Seasonal forests of Middle Paraíba in Rio de Janeiro, Minas Gerais and São Paulo States (Group 3). However, the differentiation shown by coastal forests of the central and eastern portions of Rio de Janeiro is highlighted, which have greater Leguminosae species similarity with Seasonal Forests in Rio de Janeiro and Espírito Santo.

2. *Condensed analysis of species sharing*

Of the 250 species selected, 170 were found in the Ombrophilous Forests and 180 in Semi-Deciduous Seasonal Forests. These numbers imply 113 common species, with 57 being species exclusive to Ombrophilous Forests and 67 exclusive to Semi-Deciduous Seasonal Forests (Figure 2). Proportionally, these numbers correspond to 45.2%, 22.8% and 26.8% species in total. Comparing the Leguminosae species composition in Seasonal Forests (n=180) with the central and eastern portion areas of Rio de Janeiro Coastal Forests (n=108) (Figure 2), there are 80 common species, with 100 species exclusive to Semi-Deciduous Seasonal Forests and 28 to Coastal Forests. It appears that few species are shared between these areas when the geographic substitution patterns of Leguminosae species are observed among the five stretches of coastal forests (Figure 3), even among the closest ones.

3. *Environmental variables and species composition*

The CCA results (Table 2) gave eigenvalues of 0.28 (axis 1), 0.22 (axis 2) and 0.14 (axis 3), which were considered low, indicating the existence of short gradients, where only the first axis eigenvalue

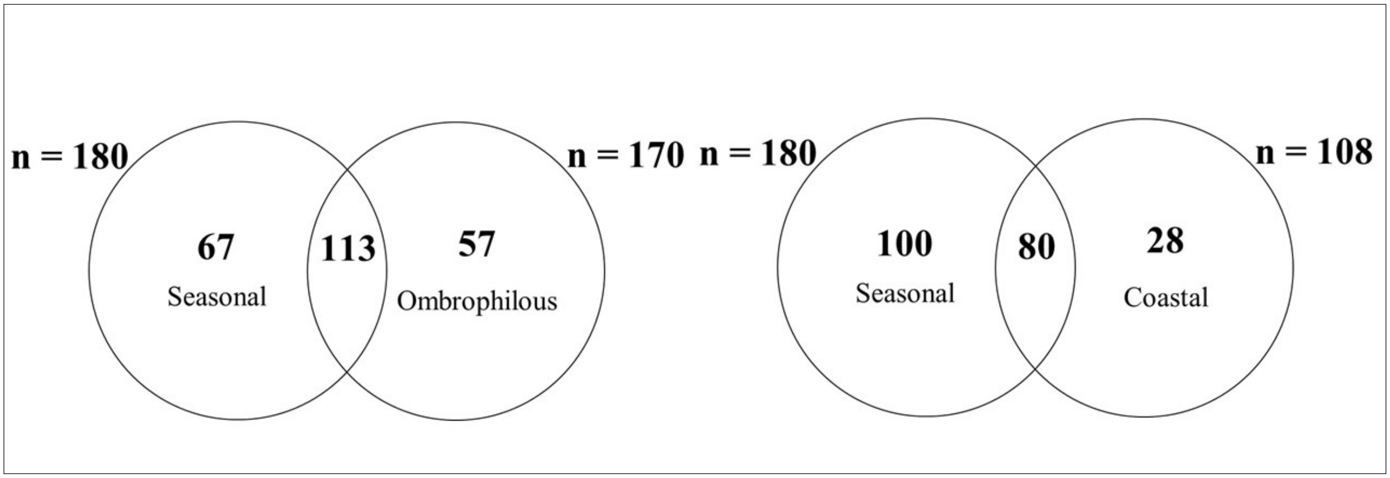

Figure 2. Leguminosae sharing between seasonal and ombrophilous forests and between seasonal and coastal forests inserted in the central and eastern portion of the state of Rio de Janeiro.

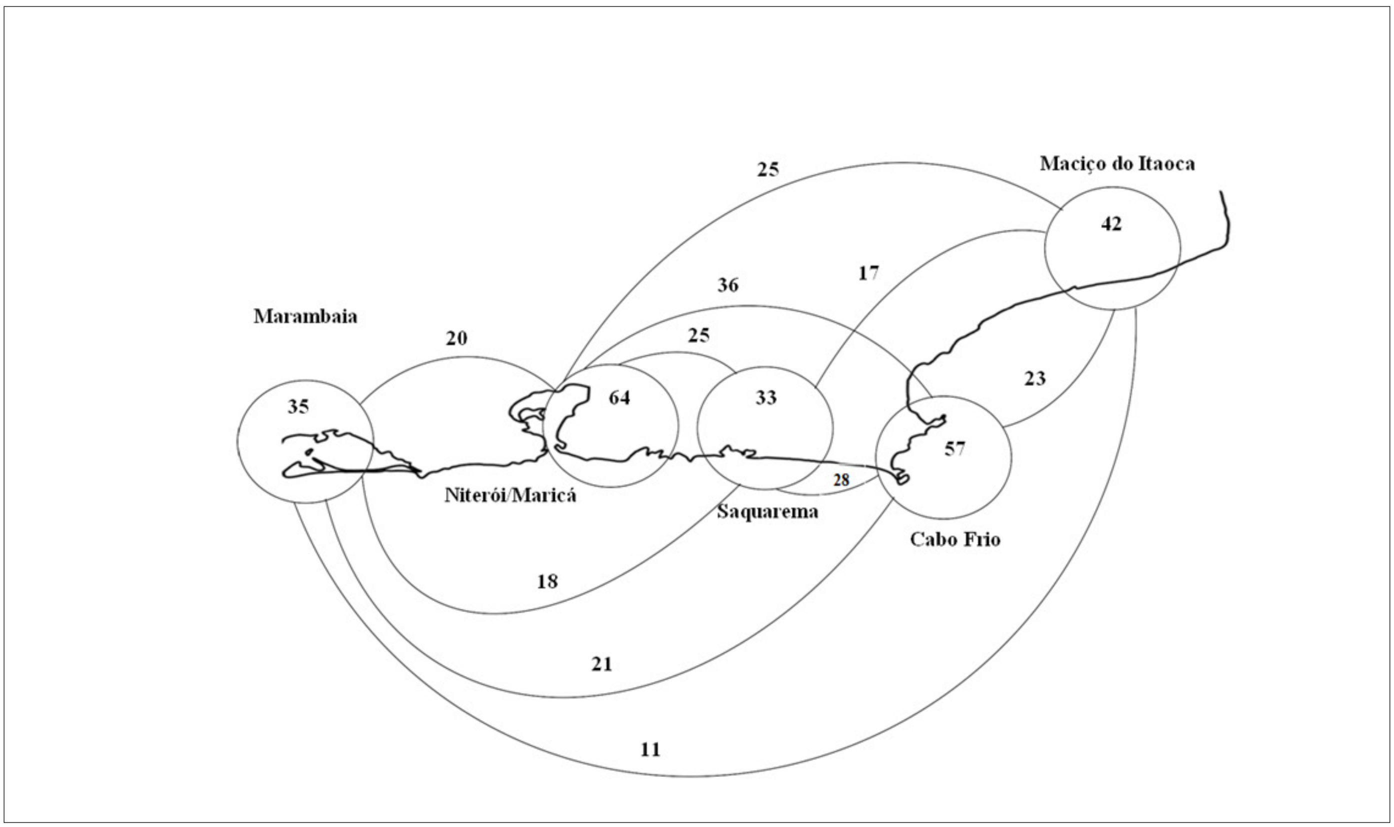

Figure 3. Geographic patterns of Leguminosae species substitution (turnover) among the five coastal forests inserted in the central and eastern portion of the state of Rio de Janeiro grouped in the similarity and CCA analyses. Circles (Leguminosae richness in each area); curves (richness shared between each area).

approaches the limit value (0.3) (ter Braak 1995, Felfili et al., 2011). The three axes explained 85.8% of the total variance, in which the first axis accounted for 37.3%, the second axis accounted for 29.9%, and the third axis 18.6%. The test was effective with P=0.001 and F=1.75, implying significant gradients for the three axes and significant correlations between environmental variables and species distribution. Those with stronger correlation (r > 0.7) with the first CCA axis were soil salinity (r = 0.81) and altitude (r = - 0.79). The strongly correlated variables for the second axis were the dry season duration (r = -0.84) and DOcean (r = -0.57) (Table 3). The CCA clearly shows a five group division (Figure 4), with central and eastern coastal forests included in a distinct group (Group 5), and the RJitaoc and RJsaof areas in an intermediate position between groups 4 and 5 (Interior Seasonal Forests).

Discussion

1. *Leguminosae tree composition in coastal forests in the state of Rio de Janeiro*

Table 2. Estimators of the canonical order axes (CCA analysis) among the 34 analyzed areas and the main environmental variables.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.280	0.224	0.140
Variance (%)	37.32	29.86	18.61
Monte Carlo test	0.001	0.001	0.001

Table 3. Correlation of the main environmental variables in the two axes of canonical ordering (CCA analysis) among the 34 analyzed areas.

Environmental Variables	Axis 1	Axis 2
Distance from Ocean	-0.519696	-0.565544
Altitude	-0.786054	0.385223
Average dry season duration	0.022908	-0.843088
Soil fertility based on mean TBS (% of total base saturation)	-0.0316089	0.285007
Soil Salinity	0.812388	0.30686

The similarity pattern found in the Leguminosae tree species' composition among different forest sites of Rio de Janeiro, São Paulo, Minas Gerais and Espírito Santo states (Figures 1 and 4) shows great resemblance to previous studies (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al., 2005; Nettesheim et al., 2010), suggesting that floristic differentiation is correlated to altitude and average duration of the dry season. However, coastal forests showed greater correlation with soil salinity in addition to these variables.

The groupings in the present study point to a distinguished aspect from the current Rio de Janeiro Ombrophilous and Seasonal forest formation distribution proposal (Ururahy et al., 1983). The Brazilian Southeastern Ombrophilous Forests in this mapping (IBGE 2012), are associated with the mountain ranges (Serras do Mar and Mantiqueira) and surrounding oceanic slopes and coastal plains, while Seasonal Forests are found inland, yet reach the coastline through the northern stretch of Rio de Janeiro state (Silva & Nascimento 2001; Nascimento & Lima 2008), reaching as far as the Cabo Frio Vegetal Diversity Center (Sá 2006). The lack of Ombrophilous Forests in this region mainly occurs due to the distance from the mountain ranges of the Atlantic coast. This biogeographic discontinuity is known as the "Campos de Goytacazes gap", in which a considerable reduction in humidity through southern São Paulo to northern Rio de Janeiro occurs. The Ombrophilous Forests from this region reappear in Espírito Santo in accordance with an increase in the average annual rainfall and declining seasonality, reaching as far as southern Bahia (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al., 2005).

There is a gradual decrease in rainfall western portion of the study area (Araujo et al., 2009). The climate between Rio de Janeiro city and the Serra do Mato Grosso (border between the municipalities of Maricá and Saquarema) is classified as *Aw* according to the Köppen-Geiger system, being warm and humid with a rainy season in summer and dry in winter (Barbiéri 1984; Araujo et al., 2009). The mountain range and coastal massifs in Rio de Janeiro city approach the coast, forming a natural screen and influence the climate, with increased rainfall to values which can exceed 2,000 mm per annum, as seen in the Tijuca National Park (Costa 1986). Niterói and Maricá are part of the pluviometric transition between the coastal plain and the coastal massif (Barros 2008), with average precipitation values between 1,000 and 1,500 mm.year^{-1} being recorded (Barbiére & Coe-Neto 1999). The precipitation between Saquarema and Cabo Frio drastically decreases to around 800 mm/year with five months of drought (Ribeiro & Lima 2009). The climate in this stretch is classified as *BSh*, a variation of the Köppen-Geiger hot semi-arid climate, and factors such as the relief (distance from the Serra do Mar towards the coast and towards the West-East) and the coastal upwelling of Cabo Frio lead to a decrease in the rainfall in this zone (Araujo et al., 2009; Bohrer et al., 2009).

The State of Rio de Janeiro Bioclimatic Map (Cronemberger et al., 2011) characterized Niterói and Maricá in the Pre-Region of the Lakes with a Tropical Sub-humid to Humid climate based on the Thornthwaite classification, and its vegetation as transitional. This categorization is related to the fact that Niterói and Maricá are inserted in a transitional area of two climatic zones which makes it less rainy than in the capital of Rio de Janeiro, but is also not characterized by the marked water deficit between Cabo Frio and Saquarema (Barros 2008). Nevertheless, part of these forests are on lithosols, with a shallow horizon and part of the crystalline massif, which can generate a "local seasonality" intensified by low water retention, especially in periods of high temperatures, and thereby cause the deciduousness seen in SDTF.

However, the analysis showed that the presence of Seasonal Forests may extend along the coastline beyond the Região dos Lagos and reach the municipalities of Maricá and Niterói, as well as other areas such as Ilha de Marambaia (Figure 1 - subgroup 1a). As highlighted by Scarano (2009), these areas have a transitional nature, sharing a flora derived from the surrounding areas with characteristic elements of rocky environments or outcrops, which are considered peripheral in the Atlantic Forest.

The results also highlighted the group of seasonal forests in the states of Rio de Janeiro and Espírito Santo (Figure 1 - group 1b), and a floristic pattern which has already been pointed out by Rizzini (1963, 1979), Oliveira-Filho & Fontes (2000), Oliveira -Filho et al. (2005), Nascimento & Lima (2008) and Saiter et al. (2016). This high floristic differentiation is often overlooked due to vegetation gradients, but is a very important aspect in the Atlantic Forest's biogeographic history, as some Angiosperm clades are confined to or concentrated in SDTF of the South American tropics (Pennington et al., 2009). This draws attention to this composition of tree species from these coastal forests as relictual elements of dry forests present in these environments. This irradiation is associated with profound changes in temperature and precipitation during the Quaternary period, with possible implications for the current distribution of forest formations (Ledru et al., 1998; Oliveira-Filho & Fontes 2000).

Although grouped with the seasonal formations, the forests on sandy plains and coastal outcrops (Figure 1 - subgroup 1a) showed a high level of dissimilarity (Jaccard Index $\leq$ 0.4), highlighting the heterogeneity in the composition of Leguminosae species in seasonal environments in the Atlantic Forest of the state of Rio de Janeiro. The coastal vegetation of the Lakes Region has been considered distinct, initially as a vegetative enclave with links to the Caatinga (Ab´Saber 1973, 1977; Ururahy 1987).

Although the forests growing on lithosoils are considered as part of the ombrophilous formations due to the frequent incidence of marine winds and shallow soils, their low physiognomy was classified as a "woody thicket" by Rizzini (1979). The floristic affinity between these coastal formations with the state's forests on Baixada Campista tablelands (Lima 2000; Nascimento

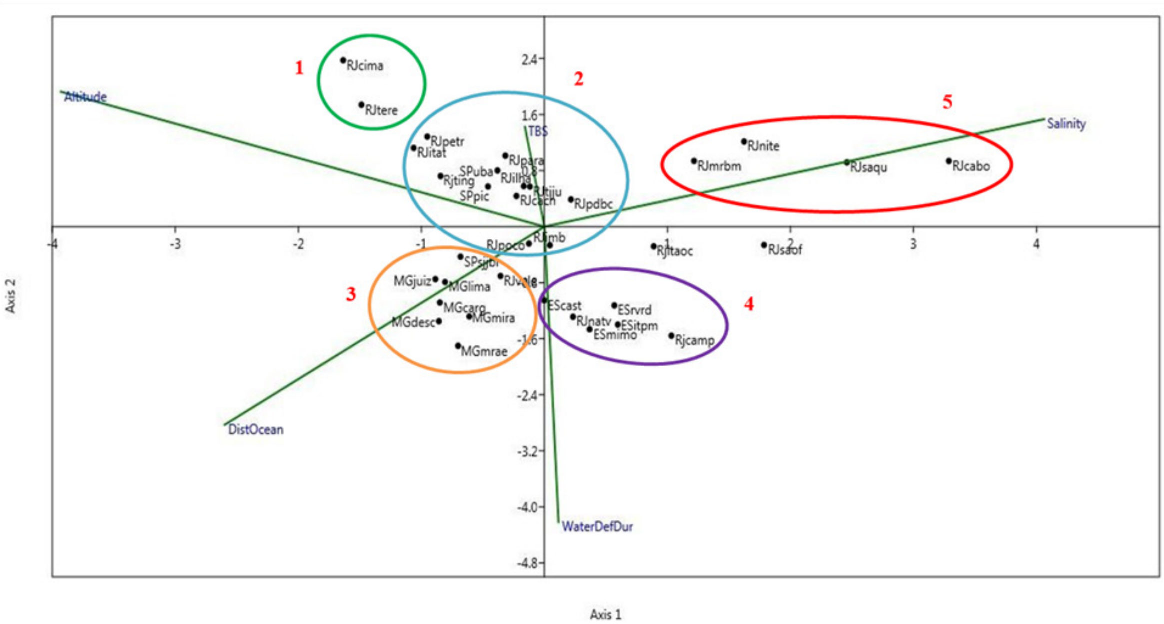

Figure 4. Biplot ordering diagram resulting from the analysis of canonical correspondence with the 34 Atlantic Forest areas of the Southeast analyzed regarding their arboreal Leguminosae composition and the correlated environmental variables. Group 1: Ombrophilous Forests / RJ; Group 2: Ombrophilous Forests RJ / SP; Group 3: Seasonal Forests RJ / ES / MG; Group 4: Seasonal Forests RJ / ES; Group 5: Coastal Forests inserted in the central and eastern portion / RJ. Areas:EScast = Castelo, ESitpm = Itapemirim, ES mimo = Mimoso do Sul, Esrvrd = Linhares/C. Vale do Rio Doce, MGcarg = Carangola, MGdesc = Descoberto, MGjuiz = Juiz de Fora, MGlima = Lima Duarte, MGmira = Miraí, MGmrae = Muriaé, RJcabo = Cabo Frio, RJcach = Cachoeiras de Macacu/Paraíso, RJcamp = Campos dos Goytacazes, RJcima = Macaé de Cima, RJilha = Ilha Grande, RJimb = Desengano/Imbé, RJitaoc = Maciço do Itaoca/Campos, RJitat = Itatiaia, RJmrbm = Ilha de Marambaia, RJnatv = Natividade, RJnite = Niterói/Maricá, RJpara = Paraty, RJpdbc = Maciço da Pedra Branca, RJpetr = Petrópolis, RJpoco = Poço das Antas, RJsaof = São Francisco do Itabapoana/Carvão, RJsaqu = Saquarema, RJtere = Teresópolis, RJtiju = Maciço da Tijuca, RJting = Maciço do Tinguá, RJvale = Valença, SPjjbr = São José do Barreiro, SPpic = Picinguaba, SPuba = Ubatuba.

& Lima 2008; Ribeiro & Lima 2009) was only recently suggested. The variation in Leguminosae species composition in these coastal forest stretches suggests a different floristic pattern than those presented by Barros (2008) and Conde et al. (2005), showing an even greater similarity with Cabo Frio and Saquarema, which are areas highlighted by Sá (2006), Dantas et al. (2009) and Ribeiro & Lima (2009) as having marked seasonality and whose arboreal component is characteristic of these dry forests. This analysis carried out with Leguminosae is a first approach to this discussion, about a floristic differentiation pattern which is more related to seasonal forests.

Although the coastal group is supported by Jaccard values (Figure 1), there is great variation within this group. An exclusive group of Leguminosae species for each of the coastal areas (Figure 3) supports the floristic differentiation which is sometimes established on lithosols, and sometimes grows on a stretch of sandy plains. Although Ilha de Marambaia and Maciço do Itaoca belong to this same coastal group, they showed greater dissimilarity. This result may be related to the geographical distance between these areas and mainly to the effect of the surrounding forest formations, as highlighted by Scarano (2009). In the case of Ilha de Marambaia there is a contribution of species from Ombrophilous Forest and in the case of Maciço do Itaoca from the Semi-Deciduous Seasonal Forest (Conde et al., 2005; Souza 2015). In contrast, Cabo Frio and Saquarema were the most similar areas, which might be related to their greater geographical proximity and to the effects of the soil and salinity.

The presence of these 108 Leguminosae species (Figure 2, Table 4) in Cabo Frio, Maciço do Itaoca, Ilha de Marambaia, Maricá/Niterói and Saquarema highlights the differentiation of coastal forests located in the central and eastern portion of the state of Rio de Janeiro, and shows that they would better be considered seasonal forests among marginal rain forest strongholds. Therefore, the Semi-Deciduous Seasonal Forest area in the state of Rio de Janeiro may be much larger than that referred by to IBGE (2012) and other literature (Sá 2006; Nascimento & Lima 2008; Ribeiro & Lima 2009; Abreu et al., 2014), and reach the south of the state. Lima (2000) argued in his analysis that although there are strong indications of Leguminosae floristic differentiation (coinciding with different altitudinal bands), a continuous pattern was detected along this gradient, which sometimes leads to difficulty in distinguishing the limits of the different forest types adopted in the different Brazilian vegetation classification systems.

Thus, our results suggest that the debate regarding the forests relationships of the of the Atlantic Domain will be resolved as new data on floristic structure and composition are collected, as we have done by filling the gaps in the Rio de Janeiro state inventories.

2. *Richness and sharing of Leguminosae tree species in the coastal forests in the state of Rio de Janeiro*

The listing of 250 Leguminosae tree species in the selected areas (Table 4) confirmed the high representativeness of the family in the forests which was already revealed in several studies about the Atlantic Rain Forest (Leitão-Filho 1986; Oliveira-Filho & Fontes 2000; Lima 2000). The family is virtually found in every plant formation throughout the planet, although the family's endemic center is currently in the Neotropics (Lavin et al., 2004; LPWG 2017). They compose significant elements in species diversity and abundance, ranging from humid tropical forests to dry forests and savannas all over the tropics (LPWG 2017). It is represented by 795 genera and almost 20,000 species, of

Table 4. Brazil Geographic distribution, phytophysiognomy (Dense Ombrophilous Forest - DOF/Seasonal Semideciduous Forest - SSF) and endemism of the Leguminosae tree species of the coastal stretch of Rio de Janeiro. Occurrence in the coastal stretch (IMAR – Ilha de Marambaia; NIT – Niterói and Maricá; SAQ – Saquarema; CBF – Cabo Frio; ITA – Maciço do Itaoca); Distribution in Brazil, State acronyms: Acre – AC; Alagoas – AL; Amapá – AP; Amazonas – AM; Bahia – BA; Ceará – CE; Espírito Santo – ES; Goiás – GO; Maranhão – MA; Mato Grosso – MT; Mato Grosso do Sul – MS; Minas Gerais – MG; Pará – PA; Paraíba – PB; Paraná – PR; Pernambuco – PE; Piauí – PI; Rio de Janeiro – RJ; Rio Grande do Norte – RN; Rio Grande do Sul – RS; Rondônia – RO; Roraima – RR; Santa Catarina – SC; São Paulo – SP; Sergipe – SE; Tocantins – TO). Data (Flora do Brasil 2020a; Lima 2000). *endemic species of Brazil. ** occurrence restricted to the coastal stretch of RJ.

Species	IMAR	NIT	SAQ	CBF	ITA	Distribution (Brazil)	Phytophysiognomy
Abarema cochliacarpos (Gomes) Barneby & J.W. Grimes*	X	X	X	X		Northeast and Southeast (except MA and PI)	DOF, SSF
Abarema langsdorffii (Benth.) Barneby & J.W. Grimes*				X		Southern and Southeastern Regions and BA	DOF, SSF
Acosmium lentiscifolium Schott*		X	X	X	X	BA, ES, MG, RJ	DOF, SSF
Albizia pedicellaris (DC.) L. Rico	X					All Regions (except CE, GO, PI, RS and SC)	DOF, SSF
Albizia polycephala (Benth.) Killip ex Record*	X	X	X	X	X	Midwestern, Northeastern, Southern and Southeastern Regions (except MA)	DOF, SSF
Anadenanthera colubrina (Vell.) Brenan		X		X		Midwestern, Northeastern, Southeastern, Southern (except AL, ES, MA, RS and SC)	DOF, SSF
Anadenanthera peregrina (L.) Speg.					X	Midwestern, AC, AM, BA, MG, PA, PB, PR, RJ, RR and SP	DOF, SSF
Andira anthelmia (Vell.) Benth.*	X			X		Northeastern, Southern and Southeastern Regions (except CE, MA, PI and RS)	DOF
Andira fraxinifolia Benth.*	X	X	X	X		Midwestern, Northeastern, Southern and Southeastern (except MA and MT)	DOF, SSF
Andira legalis (Vell.) Toledo*	X		X	X		BA, ES, MG, PE and RJ	SSF
Apuleia leiocarpa (Vogel) J.F. Macbr.		X		X		All Regions, except AP	DOF, SSF
Barnebydendron riedelii (Tul.) J.H.Kirkbr.					X	AC, BA, ES, RJ and SP	DOF, SSF
Bauhinia albicans Vogel*, **		X		X		RJ	SSF
Bauhinia forficata Link		X			X	Southern, Southeastern and AL, BA and PE	DOF, SSF
Bauhinia longifolia (Bong.) Steud.		X			X	Midwestern and Southeastern Regions, BA, PA, PR and RO	DOF, SSF
Bowdichia virgilioides Kunth				X		All Regions (except AC, SC and RS)	SSF
Calliandra harrisii (Lindl.) Benth.	X			X		RJ and BA	DOF, SSF
Calliandra tweedii Benth.		X				Southern and Southeastern Regions	DOF, SSF
Cassia ferruginea (Schrad.) Schrad. ex DC.		X				All Regions (except AC, AM, AP, MS, RN, RR, SC)	DOF, SSF
Cenostigma pluviosum var. *peltophoroides* (DC.) Gagnon & G.P.Lewis*				X		ES, RJ and BA	SSF
Centrolobium tomentosum Guillem. ex Benth.*		X				Southeastern Region, BA, GO, MT and PR	DOF, SSF
Chamaecrista ensiformis (Vell.) H.S. Irwin & Barneby	X	X		X		Northeastern, Southeastern, GO, PA and TO	DOF, SSF
Chloroleucon tortum (Mart.) Pittier*	X		X	X		Southeastern, BA, MS, GO and TO	SSF
Copaifera langsdorffii Desf.					X	Midwestern, Northeastern, Southeastern Regions, PR, RO, RS and TO	DOF, SSF

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Copaifera lucens Dwyer *	X	X	X	X		Southeastern Region and BA	DOF, SSF
Copaifera trapezifolia Hayne		X	X	X	X	BA, MG, PR, PE, RJ, SC and SP	DOF, SSF
Dahlstedtia grandiflora (A.M.G. Azevedo) M.J. Silva & Azevedo*					X	RJ	DOF, SSF
Erythrina speciosa Andrews*		X				BA, MG, MS, GO, PB, PR, RJ, SC and SP	DOF
Exostyles venusta Schott*		X	X	X	X	BA, ES, RJ and SP	DOF, SSF
Grazielodendron rio-docensis H.C. Lima*				X		BA, ES and RJ	SSF
*Hymenaea aure*a Y.T.Lee & Langenh.*					X	BA, ES and RJ	DOF, SSF
Hymenaea courbaril L.					X	All Regions (except RS and SC)	DOF, SSF
Inga capitata Desv.	X	X	X	X	X	Northeastern, Northern and Southeastern Regions (except AL, CE, PI, RN and TO)	DOF, SSF
Inga congesta T.D. Penn.*		X				BA, ES and RJ	DOF, SSF
Inga cordistipula Mart.*		X		X		Southeastern Region	DOF, SSF
Inga edulis Mart.	X					Northern and Southeastern Regions, BA, MT, PB, PE, PR and SC	DOF, SSF
Inga flagelliformis (Vell.) Mart.		X				AC, AM, AP, BA, ES, MG, PA and RJ	DOF, SSF
Inga lanceifolia Benth.*	X	X				ES, RJ and SP	DOF, SSF
Inga laurina (Sw.) Willd.	X	X	X	X	X	All Regions (except AL, AP, PI, RO, RN, RR, RS, SC, SE and TO)	DOF, SSF
Inga lenticellata Benth.*		X				MG, RJ and SP	DOF, SSF
Inga marginata Willd.		X				All Regions (except RN, RR and SE)	DOF, SSF
Inga maritima Benth.*	X		X	X		RJ	SSF
Inga subnuda subsp. *luschnathiana* (Benth.) T.D.Penn.*	X	X	X	X	X	Southern, Southeastern (except ES and RS)	DOF, SSF
*Inga tenui*s (Vell.) Mart.*					X	BA, ES and RJ	DOF
Inga vera subsp. *affinis* (DC.) T.D.Penn.		X				All Regions (except AL, RN and SE)	DOF, SSF
Libidibia ferrea (Mart. ex Tul.) L.P. Queiroz		X	X	X		All Regions (except MT)	SSF
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima			X			Southern and Southeastern Regions, AC, AL, AM, BA, GO, MS, PE, RN, RO and SE	DOF, SSF
Machaerium brasiliense Vogel				X	X	Southeastern Region, AL, AM, BA, GO, MA, MT, PE and PR	DOF, SSF
Machaerium firmum (Vell.) Benth.*, **		X		X		RJ	DOF, SSF
Machaerium hirtum (Vell.) Stellfeld	X	X	X	X	X	All Regions	DOF, SSF
Machaerium incorruptibile (Vell.) Benth.*		X		X	X	BA, ES, RJ and SP	DOF, SSF
Machaerium leucopterum Vogel*				X		BA, MG, PE and RJ	SSF
Machaerium nyctitans (Vell.) Benth.					X	Southern and Southeastern Regions and BA	DOF, SSF
Machaerium obovatum Kuhlm. & Hoehne*, **		X		X		RJ	SSF
Machaerium pedicellatum Vogel*		X	X	X		BA, ES, MG and RJ	DOF, SSF
Machaerium robsonnianum Filardi & H.C. Lima*		X		X	X	ES, MG and RJ	SSF
Machaerium stipitatum Vogel				X	X	Southern and Southeastern Regions, BA, GO and MS	DOF, SSF

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Martiodendron mediterraneum (Mart. ex Benth.) R.C.Koeppen*						MG, RJ, PA, PE, MA, PI and TO	DOF, SSF
Mimosa arenosa (Willd.) Poir. var. *arenosa*		X		X		Northeastern and Southeastern (except ES)	SSF
Mimosa bimucronata (DC.) Kuntze var. *bimucronata*	X	X	X	X		Midwestern, Northeastern, Southern and Southeastern (except MT, PI, PB and RN)	DOF, SSF
Mimosa schomburgkii Benth.		X				AC, AM, BA, ES, MG, PA, PE,RJ and RR	DOF, SSF
Muellera filipes (Benth.) M.J. Silva & A.M.G. Azevedo*	X					RJ and SP	DOF
Muellera virgilioides (Vogel) M.J. Silva & A.M.G. Azevedo*		X	X	X		BA, MG and RJ	SSF
Myrocarpus fastigiatus Allemão*		X		X		AL, BA, ES, MG, PE and RJ	DOF, SSF
Myrocarpus frondosus Allemão	X					Southern and Southeastern Region and BA	DOF, SSF
Ormosia arborea (Vell.) Harms*	X	X	X	X	X	RJ and ES	DOF, SSF
Parapiptadenia pterosperma (Benth.) Brenan*		X	X	X	X	BA, ES, MG and RJ	SSF
Parapiptadenia rigida (Benth.) Brenan					X	Southern Region, MT, MS, RJ and SP	SSF
Paubrasilia echinata (Lam.) Gagnon, H.C. Lima & G.P. Lewis*		X	X	X		AL, BA, ES, PB, PE, RJ, RN and SE	SSF
Peltogyne discolor Vogel*		X		X	X	RJ	SSF
Peltophorum dubium (Spreng.) Taub.		X				Midwestern, Northeastern, Southern, Southeastern (except MA and PI)	DOF, SSF
Piptadenia gonoacantha (Mart.) J.F. Macbr.	X	X			X	All Regions (except AP, MA, PI and RR)	DOF, SSF
Piptadenia paniculata Benth.*		X			X	Southeastern, BA, PR and SC	DOF, SSF
Plathymenia reticulata Benth.					X	Midwestern, Southeastern, BA, CE, MA, PA, PI and PR	DOF, SSF
Platycyamus regnellii Benth.*		X				Southeastern Region, BA, GO and PR	DOF, SSF
Platymiscium floribundum Vogel var. *floribundum**		X	X			BA, CE, MG, PE, PR, RJ and SC	DOF, SSF
Platymiscium floribundum var. *nitens* (Vogel) Klitg.*				X		BA, CE, ES, GO, MG, RJ, PE and PI	SSF
Poecilanthe falcata (Vell.) Heringer*			X	X	X	BA, ES and RJ	SSF
Pseudopiptadenia contorta (DC.) G.P. Lewis & M.P. Lima*	X	X	X	X	X	Northeast and Southeastern Regions (except CE, PI, MA)	DOF, SSF
Pseudopiptadenia inaequalis (Benth.) Rauschert*	X	X	X			RJ	DOF, SSF
Pseudopiptadenia leptostachya (Benth.) Rauschert*	X	X				MG, RJ and SP	DOF, SSF
Pseudopiptadenia schumanniana (Taub.) G.P. Lewis & M.P. Lima*		X			X	ES and RJ	DOF, SSF
Pterocarpus violaceus Vogel	X	X	X	X	X	MS, PR, SC, Southeastern and Northeast Regions (except MA)	DOF, SSF
Pterogyne nitens Tulasne		X				Midwestern, Northeast, Southern, Southeastern and AM	DOF, SSF
Schizolobium parahyba (Vell.) S.F. Blake	X					All Regions (except AP, MA, PB, RN, RR, SE, TO)	DOF, SSF

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Senegalia duartei Seigler & Ebinger*		X		X	X	BA, MG and RJ	SSF
Senegalia grandistipula (Benth.) Seigler & Ebinger*		X				Southeastern Region, AL, BA, GO, PA, PE, PR and SC	DOF, SSF
Senegalia langsdorffii (Benth.) Seigler & Ebinger*			X			BA, CE, ES, GO, MG, MS, PB, PI, RJ and RN	DOF, SSF
Senegalia polyphylla (DC.) Britton & Rose		X	X			All Regions (except AP, PI, RS, SC and SE)	DOF, SSF
Senegalia riparia (Kunth) Britton & Rose ex Britton & Killip		X				Southeastern Region, AM, BA, CE, MT,RN, RR, RS and SC	DOF, SSF
Senna affinis (Benth.) H.S. Irwin & R.C. Barneby*		X		X		Southeastern Region and BA	DOF, SSF
Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	X	X				Midwestern, Northeastern, Southern, Southeastern and TO	DOF, SSF
Senna pendula (Humb.& Bonpl. ex Willd.) H.S. Irwin & Barneby	X	X	X	X	X	All Regions	DOF, SSF
Senna silvestris (Vell.) H.S. Irwin & Barneby	X			X		All Regions (except AL, PB, PE, RN, RS and SE)	DOF, SSF
Swartzia apetala Raddi var. apetala*		X	X	X	X	BA, ES, MG and RJ	DOF, SSF
Swartzia apetala var. glabra (Vogel) R.S.Cowan*				X	X	BA, ES, MG, RJ and SE	SSF
Swartzia flaemingii Raddi*			X	X	X	Southeastern Region and AL, BA, CE, MA, PA, PE, PI, SE and TO	DOF, SSF
Swartzia glazioviana (Taub.) Glaz.* , **				X		RJ	SSF
Swartzia langsdorffii Raddi*	X					MG, RJ and SP	DOF, SSF
Swartzia myrtifolia var. *elegans* (Schott) R.S. Cowan*				X		BA, ES, MG and RJ	DOF, SSF
Swartzia simplex var. *grandiflora* (Raddi) R.S. Cowan		X			X	BA, ES, RJ and SP	DOF, SSF
Sweetia fruticosa Spreng.				X		Southeastern Region and BA, MA, MS, MT and PR	SSF
Tachigali denudata (Vogel) Oliveira-Filho*	X					RJ, PR, SC and SP	DOF, SSF
Tachigali paratyensis (Vell.) H.C.Lima*	X					Southeastern Region,BA, PE and PR	DOF, SSF
Tachigali pilgeriana (Harms) Oliveira-Filho*					X	BA, ES, MG and RJ	DOF, SSF
Zollernia glabra (Spreng.) Yakovlev	X	X	X	X	X	BA, ES, RJ and SP	DOF, SSF
Zollernia ilicifolia (Brongn.) Vogel	X					Southeastern, AL, BA, PB, PE, PR, RN, RO, SC and SE	DOF, SSF
Zygia latifolia (L.) Fawc. & Rendle					X	Southeastern Regions, AC, AM, AP, BA, GO, MT, PA, PE, PR, RO and RR	DOF, SSF

which 253 genera and 3033 species occur in Brazil. Of the latter, it is estimated that around 50% are endemic to Brazil (Flora do Brasil 2020b).

The family is morphologically, physiologically and ecologically diverse, representing one of the most spectacular examples of evolutionary diversification in plants (LPWG 2017). The pantropical intercontinental disjunction, observed along the geological scale, is an interesting biogeographic pattern that helps to understand Leguminosae diversification in Angiosperms. It can be explained by the Boreotropic Hypothesis, which postulates an exchange between North America and Eurasia tropical biotic during the beginning of the Tertiary (Schrire et al., 2005). Many taxa (e.g. *Bauhinia*) resulted from the boreotropical flora rupture per climatic cooling after the Paleocene-Eocene Thermal Maximum (PETM) (Lavin & Luckow 1993; Meng et al., 2014). Furthermore, the family's origin was dated via fossil records found in North America, Europe, Africa and Asia up to 60 million years AP in the Eocene at least, with subsequent rapid diversification around the world (Herendeen et al., 1992; Schrire et al., 2005). In the Neotropics, this diversification of Leguminosae can also be understood by historical climate changes, which drove the diversification of SDTF in the Tertiary and Quaternary periods (Pennington et al., 2004; 2009). Other issues contribute to this understanding, such as historical (e.g. rising of the Andes and the Panama's Isthmus) (Fiaschi et al., 2016) and punctual factors involving local climatic and edaphic variations or on a microscale with endemism and species with reduced area of occurrence (e.g. Mansano & Tozzi 2001; Morim 2006; Ribeiro & Lima 2009).

The floristic sharing analysis (Figure 2) also showed that although the number of common species between the Ombrophilous and Seasonal Forests is higher (45.2% - 113 species), the species exclusive to the seasonal formations is also relatively high (26.8% - 67 species). This number also stands out when comparing interior and coastal seasonal forests (Figure 2), indicating that there is a distinctive component in these forests. Oliveira-Filho & Fontes (2000) and Oliveira- Filho et al. (2005) argue that a good part of the seasonal forests' arboreal flora is solely composed by the fraction of rain forest flora which is capable of resisting and competing under water stress. However, in testing the limiting characteristics as a function of the floristic component of the Atlantic Forest, Neves et al. (2017) showed that about 45% of all endemic species only occur in areas experiencing more extreme environmental conditions. Although extremely neglected in terms of conservation, they contribute significantly to the richness and diversity of the Atlantic Forest.

The coastal forests on sandy plains and lithosoil showed a high level of floristic heterogeneity as already highlighted in the similarity analysis (Figure 1). Changes in the composition are evident, indicating floristic differentiation even in geographically proximal areas (Figure 3). The connection between Niterói/Maricá and the areas of Cabo Frio and Saquarema is relatively high and supported by sharing of 36 and 25 species respectively, which further supports that the Seasonal Forests' nucleus in the Região dos Lagos extends along the coast to the Guanabara Bay vicinity (Lima 2000).

The species distribution in the group of coastal forest areas showed variations between the amount of exclusive Seasonal Forest floristic components and those shared with Ombrophilous Forests. Although preliminary, the data support the proposal that the distribution of Ombrophilous Forests in the Atlantic Forest is limited by extreme environmental conditions and is replaced by Seasonal Forests (Scarano 2002) where there is a fraction of the flora capable of resisting and competing under water stress (Oliveira-Filho & Fontes 2000; Oliveira-Filho et al., 2005). Recent molecular phylogenetic studies have shown a strong PNC pattern in SDTF plant genealogy (Särkinen et al., 2011), highlighting the importance of old, niche conserved lineages confined to these plant formations. It is likely that this SDTF pattern also explains the floristic differentiation in coastal seasonal forest shelters in southeastern Brazil, but future studies are needed to infer the origin and biogeographic history of plant lineages with a preference for rocky outcrops and sandy coastal plains in the Atlantic Forest.

3. *Anthropic activity and implications for the conservation of coastal seasonal forest remnants in Rio de Janeiro*

The different economic activities developed throughout the state of Rio de Janeiro have resulted in profound environmental changes which have led to a drastic reduction in forest remnants, as well as marked changes in their composition and vegetation structure, which have consequences for the fauna and the environment. Such changes have happened since the arrival of Portuguese settlers with the removal of brazil wood (*Paubrasilia echinata* (Lam.) Gagnon, H.C. Lima & G.P. Lewis) to extract tree`s red dye. Other tree species were intensively logged between the 16th and 19th centuries with the expansion of the naval and timber industry, and are currently categorized under different threat of extinction levels (Fernandez et al., 2018). The planting of sugar cane (*Saccharum officinarum* L.) and coffee (*Coffea arabica* L.) monocultures in several stretches of Dense Ombrophilous Forest and mainly in the Semi-Deciduous Seasonal Forests of the Paraíba River Valley in those same centuries expanded the deforestation (Sales et al., 2018). Other factors such as agricultural expansion, cutting down trees for charcoal production, the installation of urban centers, the construction of road networks, the coastal occupation and the introduction of alien species all contributed to this degradation and suppression process, reducing the Atlantic Forest of Rio de Janeiro to an estimated area of only 917,196 ha (SOS MATA ATLÂNTICA 2019). The studies carried out in coastal forests of the central and eastern portions of Rio de Janeiro (e.g. Sá 1992, 2002, 2006; Conde et al., 2005; Araujo et al., 2009; Barros 2008; Patzlaff 2016; Machado 2018; Barros et al., 2020) show that the forests were affected in different ways by these activities.

The multiple land uses to which coastal forests have been subjected represent a major factor in shaping tree species composition, increasing the occurrence of some species in some places and reducing to rare occurrences or eliminating species in others, while the generalist species and those which are more adapted to disturbances have been able to expand their distribution (e.g. *Anadenanthera colubrina* (Vell.) Brenan, *Piptadenia gonoacantha* (Mart.) J.F.Macbr., *Piptadenia paniculata* Benth., *Pseudopiptadenia contorta* (DC.) G.P.Lewis & M.P.Lima and *Pterogyne nitens* Tul.). The parameters from the phytosociological analyzes carried out in these areas (e.g. Sá 2006; Barros 2008; Patzlaff 2016; Machado 2018) show the contribution of these species to the structure of the sampled forests. In the municipalities of Maricá and Niterói, this was enhanced mainly by the intentional production of charcoal, an activity that was very important for the development of large urban centers, such as Rio de Janeiro and Niterói. What is behind these species and parameters is the current expression of the forests devastated by these human activities (Barros 2008; Patzlaff 2016). Thus, the results indicate that this Leguminosae distribution in Seasonal and Ombrophilous Forests can be influenced by not only geographic and climatic factors, but also by human interventions. As pointed out by Carvalho et al. (2006), these aspects have been little discussed in comparative analyses, but they could lead to new avenues of research in floristic composition and beta-diversity. Regarding the Leguminosae, Ribeiro & Lima (2009) argue that, in addition to its diversification into seasonal environments, the association of the family with nitrogen-fixing bacteria has been identified as an efficient strategy for occupancy in nutrient and regeneration-poor environments, which are common in the Atlantic Forest.

Costa et al. (2009) argue that more than 70% of the original area covered by Semi-Deciduous Forests in Rio de Janeiro state have already been lost and has currently a low coverage of remnants in Conservation Units (CU), especially in the Integral Protection category. This situation harsh is not restricted to the state of Rio de Janeiro, it can be observed throughout the dry forest extension area. Durigan et al. (2000) consider the Semi-Deciduous Forest to be the most rapidly and extensively devastated vegetation throughout its natural occurrence area. This is a critical situation intensified by the high beta-diversity among the remaining Neotropical Seasonal Forest fragments, since 23 to 73% of the species found in each of the areas are exclusive, indicating high levels of endemism (DRYFLOR 2016). Therefore, the most effective strategy to reduce the extinction of these species would be to consider these remnants individually and to adopt less orthodox conservation measures, which include protecting a group of separate areas. This strategy is also supported by the high degree of phylogenetic geographic structure of the SDTF, mainly due to its limited dispersion (Pennington et al., 2009), which further reinforces the urgent conservation priority.

Conservation Units of different categories have already been created in coastal forest stretches located in the central and eastern portion of the state of Rio de Janeiro (Table 5), but the protection of these areas is hardly effective, as most have not been properly implemented and its enforcement is still very precarious. These municipalities cover 6,845 km^2 (Araruama, Armação de Búzios, Arraial do Cabo, Cabo Frio, Campos dos Goytacazes, Mangaratiba, Maricá, Niterói, São Pedro da Aldeia and Saquarema). However, when the extension of these ten municipalities is contrasted with the extension of protected areas, the CUs only cover 312 km^2, i.e., a small extension of areas is really protected. These forests are basically protected by nine CUs, five of which belong to the Integral Protection group, and the other four are in the Sustainable Use category. However, the Environmental Protection Area category stands out in the municipalities of Campos dos Goytacazes and Mangaratiba, while different categories occur in Niterói, Maricá and in the Região dos Lagos, which overlap in certain locations. It can also be observed that only part of the Ilha de Marambaia extension is included in Mangaratiba's Environmental Protection Area, which refers to the island portion.

These ten municipalities are amongst those with the greatest concentration of Rio de Janeiro endemic flora (Table 5). Four Leguminosae tree species are endemic and threatened with extinction (Table 4), being categorized as Vulnerable (*Machaerium firmum* (Vell.) Benth., *M. obovatum* Kuhlm. & Hoehne, *Swartzia glazioviana* (Taub.) Glaz.) or Endangered (*Bauhinia albicans* Vogel). Other Leguminosae species also stand out in the coastal stretch such as *Apuleia leiocarpa* (Vogel) J.F.Macbr. (Vulnerable) and *P. echinata* (Lam.) Gagnon, H.C.Lima & G.P.Lewis (Endangered) (Lima et al., 2013; Lima et al., 2018). Thus, this study used data present in NeoTropTree, but it additionally covered several coastal areas, thereby improving local floristic knowledge by conducting new collections. The study also worked with the collections of Herbaria in the state of Rio de Janeiro, identifying and reviewing collections to expand our dataset.

Table 5. Conservation Units implemented in a coastal forests stretch inserted in the central and eastern portion of the state of Rio de Janeiro. E.S. = Endemic Species and E.S.T.E. = Endemic species threatened with extinction (Rosa et al., 2018). Municipalities area (IBGE, 2020).

Municipality	Area	E.E.	E.E.A.E.	Conservation Unit	Group	Area (ha)	Source
Araruama	638.150	5	2				
Armação de Búzios	70.978	26	24				
Arraial do Cabo	152.105	29	27	Costa do Sol State Park	Integral Protection	9,841	INEA 2020
Cabo Frio	413.575	37	33				
Saquarema	352.130	33	30				
São Pedro da Aldeia	332.922	19	18				
Campos dos Goytacazes	4031.989	27	15	Serra do Itaoca EnvironmentalProtection Area	Sustainable Use	600	Farias et al. 2014
				Taquaruçu State Park	Integral Protection	65	Abreu Filho & Kristosch 2008
Mangaratiba	358.563	27	23	Mangaratiba EnvironmentalProtection Area	Sustainable Use	2,125.43*	INEA 2015
Maricá	361.572	35	32	Serras de Maricá Municipal Wildlife Refuge	Integral Protection	8,938.27	Maricá 2011
Niterói	133.757	51	45	Morro do Morcego, da Fortaleza de Santa Cruz e os Fortes do Pico e do Rio Branco Environmental Protection Area	Sustainable Use	141	Niterói 2018
				Lagunas e Florestas de Niterói Environmental Protection Area	Sustainable Use	5,139**	Niterói 2018
				Serra da Tiririca State Park	Integral Protection	3,493	Niterói 2018
				Nature Municipal Park	Integral Protection	918	Niterói 2018
Total (sq. km2)	6,845.741					312,607	
Total (ha)	684,574.1					31,260.7	

*** The Mangaratiba Environmental Protection Area does not cover the entire length of Marambaia, only the island (hillside forest).**

**** The Environmental Protection Area of the Niterói Lagoons and Forests overlaps with the Serra da Tiririca State Park (PESET).** Thus, the value shown in the table is given by the total area minus the PESET area, so that a value larger than the real one would not be presented.

The results of our analyses reinforce the need to preserve the remaining vegetation of these coastal forests included in the central and eastern portion of Rio de Janeiro state. The floristic differentiation supported by an exclusive group of Leguminosae species shows that the extent of dry forests may be greater than currently acknowledged. The patterns of diversity, endemism and phylogenetic niche conservatism indicate SDTF as a stable biome and limited by dispersion. Such uniqueness justifies conservation action given especially the speed at which these forests have been modified by human activities.

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Author Contributions

Davi Nepomuceno da Silva Machado: Plant collection in forested areas, data analysis, interpretation and manuscript preparation.

Marcelo Trindade Nascimento: Dry Forest floristic data contribution from Southeastern Brazil, data interpretation and critical revision of the manuscript.

Ana Angélica Monteiro de Barros: Contribution to the floristic data, collection of plants from forests of the Niterói and Maricá stretches and critical revision of the manuscript.

Richieri Antônio Sartori: Contributed to data processing in statistical packages and interpretation; critical review of the manuscript.

Cláudio Belmonte de Athayde Bohrer: Contributed to data processing in statistical packages and interpretation; critical review of the manuscript.

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Haroldo Cavalcante de Lima: Contributed to the study concept and design; collected plants in forest areas; data analysis and interpretation, and preparation of the manuscript.

Conflicts of interest

The authors declare they have no conflicts of interest related to the publication of this manuscript.

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