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Community structure and species composition of a periodically flooded Restinga forest in Caraguatatuba, São Paulo, Brazil

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Abstract: The aim of this study was to characterize the structure and composition of the tree and shrub community in a 77-ha fragment of Restinga forest in Caraguatatuba, São Paulo, Brazil. In this fragment, forty 20 × 20-m plots (1.6 ha) were systematically allocated and all trees with a stem diameter at breast height (DBH) ≥4.8 cm were sampled. Sixteen plots were randomly chosen to also sample individuals with a DBH of between 1 and 4.8 cm. All individuals were tagged, identified to species level, and their diameters and heights were measured. A total of 2587 individuals (1616 ind./ha) from 119 species and 42 families were found with a DBH >4.8 cm, and 2659 individuals (4154 ind./ha) from 125 species and 38 families were found with a DBH >1 cm. The richest families were Myrtaceae, Lauraceae, and Fabaceae, and the most abundant species were *Diospyros brasiliensis* (Ebenaceae), *Anaxagorea dolichocarpa* (Annonaceae), and *Euterpe edulis* (Arecaceae). The structure of the studied site was similar to that of other Restinga forest sites, but the forest composition was quite distinct. Implications for the conservation and restoration of Restinga forests in this region are discussed in light of the results obtained.
Keywords: *white sandy soil, coastal sandy forest, waterlogging, coastal plain vegetation, Atlantic Forest.*

Estrutura e composição de espécies de uma floresta de Restinga periodicamente alagada em Caraguatatuba, São Paulo, Brasil

Resumo: O objetivo deste estudo foi caracterizar a estrutura e composição da comunidade arbórea e arbustiva em um fragmento de 77 ha de floresta de Restinga em Caraguatatuba, São Paulo. Neste fragmento, 40 parcelas de 20 × 20 m (1,6 ha) foram distribuídas sistematicamente e todas as árvores com diâmetro do tronco na altura do peito (DAP) ≥4,8 cm foram amostradas. Além disso, 16 parcelas foram escolhidas aleatoriamente para amostrar também todos os indivíduos com DAP entre 1 e 4.8 cm de DAP. Todos os indivíduos foram marcados, identificados ao nível de espécie e tiveram seu diâmetro e altura medidos. Para indivíduos acima de 4,8 cm de DAP, foi amostrado um total de 2587 indivíduos (1616 ind./ha) em 119 espécies e 42 famílias. Para indivíduos acima de 1 cm de DAP, foi amostrado um total de 2659 indivíduos (4154 ind./ha) em 125 espécies e 38 famílias. As famílias mais ricas foram Myrtaceae, Lauraceae e Fabaceae. As espécies mais abundantes foram *Diospyros brasiliensis*, *Anaxagorea dolichocarpa* e *Euterpe edulis*. Quando comparado com outros locais de florestas de Restinga, a estrutura florestal do fragmento estudado é semelhante a outras florestas de Restinga. No entanto, a composição da floresta é bastante distinta, evidenciando a heterogeneidade das florestas de Restinga ao longo da costa do Brasil. Implicações para a conservação e restauração das florestas de Restinga são destacadas.
Palavras-chave: *solo arenoso, floresta sobre areia, alagamento, vegetação da planície costeira, Mata Atlântica.*

Introduction

The Atlantic Forest domain harbors a great diversity of forest types, whose characteristics are defined primarily by climatic and topographic factors. However, soils are also an important factor for determining some forest types, such as Restinga forests (also called coastal sandy forests), which are established on Quaternary marine sand deposits. In such edaphic communities, variations in soil properties (e.g., soil texture, nutrient levels, and aluminum content) and groundwater dynamics largely determine variations in forest structure and composition (Scarano 2002, Magnago et al. 2012, Oliveira et al. 2014). As the water table is usually shallow in Restinga forests, tree roots are often subjected to some level of waterlogging (Maun 1994, Scarano 1998). Restinga forests subjected to long-lasting or permanent flooding tend to have low species richness and can show patterns of high species dominance (Galvão et al. 2002, Kurtz et al. 2013), while forests with intermittent flooding regimes tend to harbor more species (Guedes et al. 2006, Marques et al. 2009, Magnago et al. 2012). Although these diversity patterns are well known, there are uncertainties regarding some aspects of Restinga forest structure, such as stem density (Guedes et al. 2006, Marques et al. 2009, Magnago et al. 2012, Oliveira et al. 2014), patterns of species abundance, and the distribution and identity of the most abundant species (Galvão et al. 2002, Martins et al. 2008, Menezes et al. 2010, Assis et al. 2011, Oliveira et al. 2014). Therefore, new inventories are required to improve our understanding of Restinga forest structural and compositional variation.

In the state of São Paulo, Brazil, more surveys have been conducted on rainforests on clayey soils than on Restinga forests (Lima et al. 2015), so information gaps of the Restinga forest still remain along the 400-km coastline (Marques et al. 2011, Lima et al. 2015 and references therein). The south coast of São Paulo has been the most studied (Carvalhaes 1997, Sugiyama 1998, Sztutman & Rodrigues 2002, Carrasco 2003, Lima et al. 2011, Oliveira et al. 2014), while studies in central and northern regions have concentrated on the municipalities of Bertioga (Guedes et al. 2006, Lopes 2007, Martins et al. 2008) and Ubatuba (Cesar & Monteiro 1995, Assis 1999, Assis et al. 2011). Although Caraguatatuba is the largest coastal plain in the northern region, only one study has been conducted in this municipality (Mantovani 1992).

Since the 1970s, the Caraguatatuba region and surroundings municipalities have been converted into urban areas, livestock farms, and more recently, industrial areas. Currently, 63% of the Caraguatatuba coastal plain has been deforested, and most of the forest remnants are small and scattered across the landscape (Souza 2006, Souza & Luna 2008). Knowledge of the different types of vegetation in this region is fundamental to future conservation and restoration strategies. In this study, the structure and composition of a forest fragment in this poorly studied region of the coastal plain were investigated, and the importance of the area for regional conservation strategies was highlighted.

Material and Methods

1. *Study site*

The study was conducted in a ~77-ha Restinga forest fragment on the sandy coastal plain of Caraguatatuba on the north coast of São Paulo state, Brazil (23°38′22″S, 45°26′59″W (WGS-84); Figure 1). The study siteIt is located on property owned by a local resident, and is surrounded by a heterogeneous matrix of urban occupation eastward, pastures on its southern and western limits, and low-altitude rainforests on the northern boundary. The terrain is almost flat, and the elevation varies between 6 and 8 m above sea level. Due to variations in microtopography, the lowest areas are more susceptible to flooding, and are flooded for between a few days to over a month during rainy periods, particularly the summer. Even in the driest period of the year, the water table is shallow (~30–50 cm), so the area floods after occasional heavy rain. Only a small proportion of our study site is established on sand ridges with well-drained soils. Evidence of palm-heart harvesters, hunting, and domestic animals were found in our study site. Although no evidence of selective wood extraction was found during the fieldwork, it is possible that *Tabebuia cassinoides* was extracted in the past for its traditional use in handicrafts and oar-making (Borges & Peixoto 2009). However, our study site seems to be relatively well-conserved, because there were no signs that any major disturbances had occurred there, as observed in aerial photographs taken from 1967 to 2016, except for a small-scale deforestation event that occurred in a 100-m strip in 1990. Information regarding the secondary vegetation in this strip is provided as Supplementary Material.

The dominant soils in the region are Quartzarenic Neosols and Spodosols, according to Oliveira et al. (1999). These soils are sandy to sandy-clayey, very acidic, infertile, and have a high aluminum content (Table 1). The climate is tropical rainforest (*Af*, following the Köppen classification), with hot, wet summers and cool, dry winters. The average annual temperature is 24.9 °C, and the average temperatures of the hottest and coldest months are 26.5 °C and 20 °C, respectively. The average annual precipitation is 1758 mm. The dry season runs from April to September, and the driest month is July (average of 62.5 mm of precipitation). The wet season runs from October to March and the wettest month is January, with an average of 251.6 mm of precipitation (CEPAGRI 2016).

2. *Data collection and analysis*

Forty 20×20-m plots (total of 1.6 ha) were sampled from January 2013 to July 2014. The plots were 80 m apart, systematically distributed in the area (Figure 1), and at least 30 m from the edge of the fragment. Only trees with a stem diameter at breast height (DBH) ≥4.8 cm were included in all 40 plots. Individuals with a DBH of between 1 and 4.8 cm, which included shrub species, were additionally sampled in 16 randomly taken plots (Figure 1). All trees and shrubs were tagged and had their diameters measured and their heights estimated. For multi-stemmed individuals, all stems were measured if at least one of them reached the DBH cutoff. After collection, plant specimens were identified by referring to the literature, checking herbarium specimens, and/or consulting experts. Easily identified species, such as *Calophyllum brasiliense*, *Euterpe edulis*, and other palms, were identified in the field. Vouchers of the species identified by experts and/or after herbarium checks were deposited in the herbarium of the Universidade de São Paulo, Campus Piracicaba (ESA) under the collection numbers of M.P. Pansonato. Some unicates that were not deposited in the ESA are available at the Laboratório de Ecologia de Florestas Tropicais of the Universidade de São Paulo. The nomenclature followed that of the Angiosperm Phylogeny Group IV (APG IV 2016).

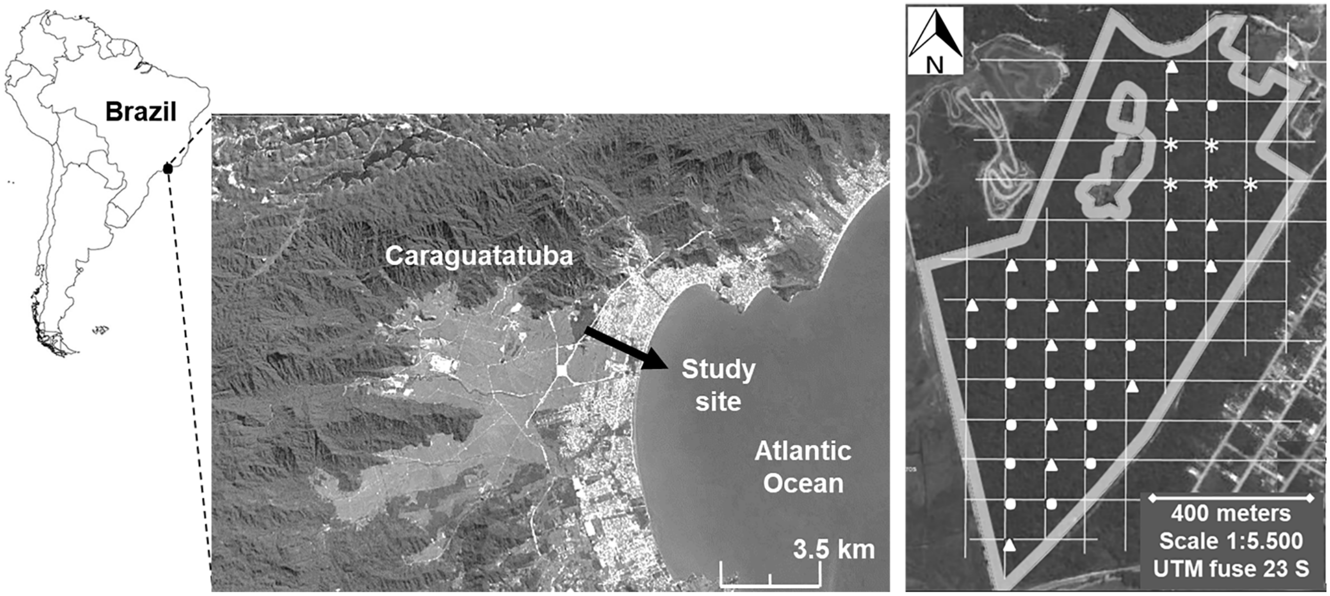

Figure 1. Location of the study site on the coastal plain of Caraguatatuba, SP, Brazil. In the central image, note the continuous forest cover (dark grey) surrounding the study site. In the right image, plots distributed systematically along the Restinga forest fragment are shown. Dots are plots sampled for DBH ≥ 4.8 cm; Triangles are plots sampled for DBH ≥ 1 cm; Asterisks represents the five plots located on degraded strip (see supplementary material).

Table 1. Mean and amplitude (within parentheses) of topsoil (0 - 5 cm) chemical properties in the study site. Samples were collected in the center of each sampled plot.

pH	P	K	Ca	Mg	H+Al	CEC[1]	V[2]
(CaCl2)	(mg/dm^3)			-----------------------(mmolc/dm^3)--------------------		-	(%)
3.1	23.4	1.8	12.1	7.3	357.6	378.7	7.1
(2.7 - 4.4)	(6 - 38)	(0.6 - 3.2)	(3 - 31)	(1 - 14)	(22 - 726)	(27.9 - 755)	(2 - 38)

[1] cation exchange capacity; [2] base saturation.

In order to compare our results with those in the literature, the forest structure and composition data are shown separately for three groups with distinct inclusion criteria: i) DBH ≥1 cm from 16 plots; ii) DBH ≥4.8 cm from 40 plots; iii) DBH ≥10 cm from 40 plots. For each inclusion criteria, the number of individuals per hectare, relative density, basal area, relative dominance, the percentages of multi-stemmed individuals and singletons (species with one individual in the total sample), and the Shannon diversity index (H'; Magurran 1988) were calculated using FITOPAC 2.0 (Shepherd 2009). In order to obtain a better comparison of the values among the three DBH inclusion criteria, the number of species in the DBH ≥4.8 cm and DBH ≥10 cm inclusion criteria were rarefied by sample (20×20-m plots), and the mean species richness values for 0.64 ha and 1 ha, and their respective confidence intervals, were calculated. Sample-based rarefaction curves were calculated using the *vegan* package (Oksanen et al. 2016) in R 3.4.4 (R Foundation for Statistical Computing, Vienna, Austria).

Results

A total of 4222 individuals from 44 families and 141 species were sampled (Table 2). The results varied with the DBH inclusion criteria under consideration (Tables 3 and 4; see also Supplementary Material tables S1 and S2). The smaller the DBH, the greater the tree density, species richness, and Shannon diversity index. The estimated species richness varied between 93 and 114 species per hectare for DBH ≥4.8 cm, and between 73 and 89 species per hectare for DBH ≥10 cm (Supplementary Material Figure S1). Sampling smaller individuals (between 1 and 4.8 cm DBH) had only a minor effect (~3% increase) on the estimated basal area. The proportions of multi-stemmed individuals were similar among the three DBH inclusion criteria (Table 3), and 76 out of 141 species (53.9%) had at least one multi-stemmed individual. Canopy height varied between 14 and 20 m, with emergent trees reaching up to 25 m.

The richest family in all of the DBH inclusion criteria was Myrtaceae, which had nearly twice the number of species than the second-richest (Lauraceae) (Supplementary Material Table S2). The peak in Myrtaceae, Rubiaceae, and Melastomataceae richness was found in the DBH ≥1 cm group, as some species in these families do not have large diameters. The most abundant family in all of the DBH inclusion criteria was Ebenaceae, which was represented by only one species (*Diospyros brasiliensis*), and Myrtaceae was the second-most abundant family for all DBH inclusion criteria because of the abundance of many species (Supplementary Material Table S2). Annonaceae, Arecaceae, and Lauraceae were the most abundant families in the two lowest DBH inclusion criteria, being replaced by Euphorbiaceae and Bignoniaceae, in addition to Lauraceae, when DBH ≥10 cm.

Table 2. Species list and voucher numbers in the herbarium of the Universidade de São Paulo - Campus Piracicaba (ESA) of a Restinga forest in Caraguatatuba - SP, Brazil.

Family/Species	Voucher
Anacardiaceae	
Tapirira guianensis Aubl.	ESA134411
Annonaceae	
Anaxagorea dolichocarpa Sprague & Sandwith	ESA134412
Guatteria australis A.St.-Hil.	ESA134413
Xylopia langsdorfiana A.St.-Hil. & Tul.	ESA134414
Aquifoliaceae	
Ilex dumosa Reissek	ESA134415
Ilex pseudobuxus Reissek	ESA134416
Ilex theezans Mart. ex Reissek	ESA134417
Araliaceae	
Dendropanax monogynus (Vell.) Seem.	ESA134418
Oreopanax capitatus (Jacq.) Decne. & Planch.	
Schefflera angustissima (Marchal) Frodin	ESA134419
Arecaceae	
Astrocaryum aculeatissimum (Schott) Burret	
Attalea dubia (Mart.) Burret	
Bactris setosa Mart.	
Euterpe edulis Mart.	
Geonoma schottiana Mart.	
Bignoniaceae	
Handroanthus albus (Cham.) Mattos	ESA134420
Handroanthus umbellatus (Sond.) Mattos	ESA134421
Jacaranda puberula Cham.	ESA134422
Tabebuia cassinoides (Lam.) DC.	ESA134423
Tabebuia sp. Gomes ex DC.	
Boraginaceae	
Cordia sellowiana Cham.	
Calophyllaceae	
Calophyllum brasiliense Cambess.	ESA134424
Celastraceae	
Maytenus gonoclada Mart.	ESA134425
Clethraceae	
Clethra scabra Pers.	ESA134426
Clusiaceae	
Garcinia gardneriana (Planch. & Triana) Zappi	ESA134427
Cyatheaceae	
Cyathea atrovirens (Langsd. & Fisch.) Domin	
Ebenaceae	
Diospyros brasiliensis Mart. ex Miq.	ESA134428
Elaeocarpaceae	
Sloanea guianensis (Aubl.) Benth.	ESA134429
Euphorbiaceae	
Alchornea triplinervia (Spreng.) Müll. Arg.	ESA134430
Aparisthmium cordatum (A.Juss.) Baill.	ESA134431
Mabea piriri Aubl.	
Maprounea guianensis Aubl.	ESA134433
Fabaceae	
Albizia pedicellaris (DC.) L.Rico	
Andira fraxinifolia Benth.	ESA134434
Hymenolobium janeirense Kuhlm.	
Inga edulis Mart.	
Inga sessilis (Vell.) Mart.	ESA134435
Inga striata Benth.	ESA134436
Machaerium nyctitans (Vell.) Benth.	
Ormosia arborea (Vell.) Harms	ESA134437
Pterocarpus rohrii Vahl	ESA134438
Lacistemataceae	
Lacistema lucidum Schnizl.	
Lamiaceae	
Aegiphila integrifolia (Jacq.) Moldenke	
Vitex polygama Cham.	
Lauraceae	
Aiouea saligna Meisn.	ESA134439
Aniba viridis Mez	ESA134440
Cryptocarya mandioccana Meisn.	
Endlicheria paniculata (Spreng.) J.F.Macbr.	ESA134441
Nectandra grandiflora Nees	
Nectandra oppositifolia Nees	ESA134442
Ocotea aciphylla (Nees & Mart.) Mez	ESA134443
Ocotea brachybotrya (Meisn.) Mez	
Ocotea lanata (Nees & Mart.) Mez	ESA134444
Ocotea mosenii Mez	ESA134445
Ocotea pulchella (Nees & Mart.) Mez	ESA134446
Ocotea venulosa (Nees) Baitello	ESA134447
Persea willdenovii Kosterm.	
Malvaceae	
Eriotheca pentaphylla (Vell. & K.Schum.) A.Robyns	ESA134448
Melastomataceae	
Clidemia cf. *urceolata* DC.	
Huberia ovalifolia DC.	ESA134449
Miconia cinnamomifolia (DC.) Naudin	
Miconia dodecandra Cogn.	ESA134450
Miconia prasina (Sw.) DC.	ESA134451
Miconia pusilliflora (DC.) Naudin	ESA134452
Ossaea sp. DC.	
Tibouchina pulchra Cogn.	ESA134454
Tibouchina stenocarpa (Schrank & Mart. ex DC.) Cogn.	ESA134453
Meliaceae	
Cabralea canjerana (Vell.) Mart.	
Guarea macrophylla Vahl	ESA134455
Trichilia pallens C.DC.	
Monimiaceae	
Mollinedia cf. *ovata* Ruiz & Pav.	

Continuation Table 2.

Family/Species	Voucher
Mollinedia schottiana (Spreng.) Perkins	ESA134456
Moraceae	
Ficus enormis Mart. ex Miq.	
Ficus gomelleira Kunth	ESA134458
Ficus insipida Willd.	
Ficus pulchella Schott	ESA134457
Sorocea jureiana Romaniuc	ESA134459
Myrtaceae	
Blepharocalyx salicifolius (Kunth) O.Berg	ESA134460
Calyptranthes concinna DC.	
Calyptranthes lucida Mart. ex DC.	ESA134461
Eugenia astringens Cambess.	ESA134462
Eugenia brasiliensis Lam.	ESA134463
Eugenia cerasiflora Miq.	ESA134464
Eugenia cereja D.Legrand	
Eugenia melanogyna (D.Legrand) Sobral	
Eugenia monosperma Vell.	ESA134465
Eugenia neoglomerata Sobral	ESA134466
Eugenia oblongata O.Berg	ESA134467
Eugenia stigmatosa DC.	ESA134468
Eugenia sulcata Spring ex Mart.	ESA134469
Marlierea clausseniana (O.Berg) Kiaersk.	ESA134470
Marlierea racemosa (Vell.) Kiaersk.	ESA134471
Marlierea tomentosa Cambess.	ESA134472
Myrcia brasiliensis Kiaersk.	ESA134473
Myrcia glabra (O.Berg) D.Legrand	ESA134474
Myrcia hexasticha Kiaersk.	ESA134475
Myrcia multiflora (Lam.) DC.	ESA134476
Myrcia pubipetala Miq.	ESA134477
Myrcia racemosa (O.Berg) Kiaersk.	ESA134478
Myrcia spectabilis DC.	ESA134479
Myrcia splendens (Sw.) DC.	ESA134480
Psidium cattleianum Sabine	ESA134481
Syzygium jambos (L.) Alston *	ESA134482
Nyctaginaceae	
Guapira hirsuta (Choisy) Lundell	ESA134483
Guapira opposita (Vell.) Reitz	ESA134484
Pisonia sp. L.	ESA134485
Ochnaceae	
Ouratea multiflora (Pohl) Engl.	ESA134486
Ouratea parviflora (A.DC.) Baill.	ESA134487
Olacaceae	
Heisteria silvianii Schwacke	ESA134488
Peraceae	
Pera glabrata (Schott) Poepp. ex Baill.	
Phyllanthaceae	
Hyeronima alchorneoides Allemão	ESA134432

Continuation Table 2.

Family/Species	Voucher
Piperaceae	
Piper gaudichaudianum Kunth	ESA134489
Podocarpaceae	
Podocarpus sellowii Klotzsch ex Endl.	ESA134490
Primulaceae	
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	ESA134491
Myrsine guianensis (Aubl.) Kuntze	
Myrsine venosa A.DC.	ESA134492
Stylogyne lhotzkyana (A.DC.) Mez	ESA134493
Rosaceae	
Prunus myrtifolia (L.) Urb.	ESA134494
Rubiaceae	
Amaioua intermedia Mart. ex Schult. & Schult.f.	ESA134495
Cordiera cf. *myrciifolia* (K.Schum.) C.H.Perss. & Delprete	ESA134496
Ladenbergia hexandra (Pohl) Klotzsch	
Posoqueria latifolia (Rudge) Schult.	ESA134497
Psychotria hastisepala M. Arg.	
Psychotria hoffmannseggiana (Willd. ex Schult.) M. Arg.	ESA134498
Psychotria mapourioides DC.	
Rudgea coriacea (Spreng.) K.Schum.	ESA134499
Rutaceae	
Zanthoxylum rhoifolium Lam.	
Sapindaceae	
Matayba intermedia Radlk.	ESA134500
Sapotaceae	
Ecclinusa ramiflora Mart.	ESA134501
Manilkara subsericea (Mart.) Dubard	ESA134502
Pouteria beaurepairei (Glaz. & Raunk.) Baehni	ESA134503
Pouteria psammophila (Mart.) Radlk.	ESA134504
Siparunaceae	
Siparuna brasiliensis (Spreng.) A.DC.	ESA134505
Styracaceae	
Styrax glabratus Schott	ESA134506
Symplocaceae	
Symplocos estrellensis Casar.	
Theaceae	
Laplacea fructicosa (Schrad.) Kobuski	
Thymelaeaceae	
Daphnopsis racemosa Griseb.	ESA134507
Daphnopsis schwackeana Taub.	
Urticaceae	
Cecropia glaziovii Snethl.	ESA134508
Cecropia pachystachya Trécul	
Coussapoa microcarpa (Schott) Rizzini	ESA134509

* Exotic species.

Table 3. Community-level attributes for three diameter at breast height (DBH) inclusion criteria of a Restinga forest fragment located on coastal plain of Caraguatatuba, Brazil.

Atribute	DBH inclusion criteria		
	≥ 1 (0.64 ha)	≥ 4.8 (1.6 ha)	≥ 10 (1.6 ha)
Total of individuals	2659	2587	1268
Individuals/ha#	4154 ± 1127	1616 ± 393	792 ± 263
Basal area (m^2/ha)#	31.76 ± 13.3	30.9 ± 10.9	27.08 ± 11.1
Multi-stemmed (%)	14.7	15.7	13.4
Total of species	125	119	95
Species/ha*	--	104 (93-114)	81 (73-89)
Species/0.64ha*	125	90 (77-103)	69 (59-79)
Shannon	3.64	3.61	3.41
Singletons (%)	24.8	24.4	26.3
Families	38	42	37

These values represent the mean ± standard deviation. * These values were estimated by sample-based rarefaction methods. See Supplementary Material for complete rarefaction curves.

Table 4. Relative densities (%) and ranking order (within parentheses) of 15 most abundant species for DBH ≥ 1 cm and their values for larger diameter at breast height (DBH) inclusion criteria sampled in a Restinga forest fragment located on coastal plain of Caraguatatuba, Brazil.

Species	DBH inclusion criteria		
	DBH ≥ 1 (0.64 ha)	DBH ≥ 4.8 (1.6 ha)	DBH ≥ 10 (1.6 ha)
Diospyros brasiliensis	13.8 (1)	19.1 (1)	23.8 (1)
Anaxagorea dolichocarpa	11.5 (2)	6.3 (2)	2.4 (12)
Euterpe edulis	5.7 (3)	6.3 (3)	0.2 (50)
Tabebuia cassinoides	5.1 (4)	3.5 (7)	4.5 (5)
Guarea macrophylla	4.2 (5)	2.6 (10)	0.6 (32)
Nectandra oppositifolia	3.8 (6)	3.1 (8)	4.5 (4)
Eugenia monosperma	3.3 (7)	5.1(4)	3.5 (8)
Sloanea guianensis	3.3 (8)	4.2 (5)	4.7 (3)
Aniba viridis	2.8 (9)	0.9 (28)	0.2 (57)
Bactris setosa	2.7 (10)	0.4 (43)	-
Guapira opposita	2.4 (11)	1.4 (17)	1.5 (15)
Schefflera angustissima	2.4 (12)	2.8 (9)	3.4 (9)
Alchornea triplinervia	2.3 (13)	3.5 (6)	5.7 (2)
Stylogyne lhotzkyana	2.3 (14)	0.6 (36)	0.2 (58)
Myrcia racemosa	1.9 (15)	1.4 (19)	0.5 (36)

A strong dominance by one species, in terms of the number of individuals, was observed in all of the DBH inclusion criteria considered. *Diospyros brasiliensis* had the highest abundance, basal area, and frequency values in all of the DBH inclusion criteria (Table 4 and Supplementary Material Table S1). *Anaxagorea dolichocarpa*, *Euterpe edulis*, and *Alchornea triplinervia* were the second-most abundant species in DBH ≥1 cm, DBH ≥4.8 cm, and DBH ≥10 cm, respectively (Table 4 and Supplementary Material Table S1). For DBH ≥1 cm, the threatened species *E. edulis* and *Tabebuia cassinoides* were also well represented as regenerating individuals (Table 4). Only one exotic species (*Syzygium jambos*) was sampled, with three individuals. *Nectandra oppositifolia* had relatively high basal area values because it can grow to a great size (DBH ≥60 cm). *Tapirira guianensis*, *Calophyllum brasiliense*, and *Manilkara subsericea* had the highest DBH and height values. Only around 10 species were present in more than a half of the plots, and almost a quarter of the species were only found in one plot, irrespective of DBH.

Discussion

Tree density in the study area (1616 ind./ha for DBH ≥4.8 cm) was lower than the average density estimated from 14 Restinga forests in São Paulo state (1442–2756 ind./ha, average 1907 ind./ha; see Lima et al. 2015 and references therein). In addition, the tree density for DBH ≥1 cm (4154 ind./ha) had similar values to the only study of our knowledge that has used this inclusion criteria (3533–4256 ind./ha, average 3895 ind./ha in Oliveira et al. 2014). Differences in tree density could be caused by abiotic factors such as flooding period (Menezes et al. 2010, Marques et al. 2015). Restinga forests that are susceptible to flooding seem to have a greater stem density than those that are not (Guedes et al. 2006, Magnago et al. 2012). However, some studies have found the opposite pattern (e.g., Marques et al. 2009) or no significant differences in stem density between flooded and unflooded Restinga forests (Oliveira et al. 2014). This suggests that other ecological factors could also be relevant, such as successional stage (Chazdon 2003).

In general, forests in early successional stages tend to have greater stem density and lower biomass than old-growth forests (Chazdon et al. 2009). Thus, the low density found in our study site when compared with other Restinga forests could be indicative of the relatively well-conserved status of this site, besides the five recognized secondary plots (see Supplementary Material Table S3). However, the lower density observed could also have been a consequence of harvesting *Euterpe edulis* (101 ind./ha), which probably had long-lasting effects that continue today. In addition, the selective extraction of *Tabebuia cassinoides* individuals (56 ind./ha), which is not currently evident but probably occurred in the past, could also have contributed to the low stem density values obtained. Despite their high relative abundances in this study, these species are usually found at much higher densities in Restinga forests that are susceptible to flooding (for example, 639 ind./ha of *E. edulis* in Rotta et al. 1997, 365 ind./ha in Vanini 1999, and 293.8 ind./ha in Oliveira et al. 2014). However, the *E. edulis* density found for DBH ≥1 cm (237 ind./ha) may indicate that its population is increasing, and could achieve similar values of density as those reported in the above-mentioned studies. Of course, this will only occur if selective extraction ceases or is drastically reduced.

Basal area values (30.9 m^2/ha for individuals with DBH ≥4.8 cm) were slightly above the average of other Restinga forests in Brazil (27.3 ± 11.1 m^2/ha; Lima et al. 2015 and references therein). The relationship between flooding and basal area that we observed is not supported by the literature, as flooded and periodically flooded sites usually have forests with lower basal areas than unflooded sites (Sztutman & Rodrigues 2002, Guedes et al. 2006, but see Marques et al. 2009). Restinga soils subjected to flooding usually have higher nutrient availability than dry, well-drained sandy soils (Magnago et al. 2012). In a study that compared flooded and unflooded Restinga forests, the relative growth rate was higher on poorly drained soils than on well-drained soils (Marques et al. 2009). It is possible that species that are able to deal with flooding benefit from the higher levels of nutrients available in these sites and accumulate biomass, so have larger basal areas. Large basal areas may also be related to a relatively advanced successional stage (Chazdon 2003), which is the case in our study site (but see Supplementary Material Table S3).

Although multi-stemmed individuals are considered a common feature of Restinga forests (Silva 1990), the average proportion of multi-stemmed individuals in this study was only 14.6%, which is similar to that found by Lima et al. (2011) in a Restinga forest with a mixture of periodically flooded and unflooded plots in Ilha do Cardoso State Park. The proportion of species with multi-stemmed individuals (53.9%) was within the range of other Atlantic Forest types (44–68%; Lima et al. 2011), and lower than the proportion (74%) observed by Lima et al. (2011) in a Restinga forest in southern São Paulo state. The development of multi-stemmed trees has been related to increased light interception, and resprouting and survival after physical damage (Martini et al. 2008). In our study site, the growth of multi-stemmed trees could be related to both of the above-mentioned factors, as well as the open canopies of Restinga forests (Araújo & Lacerda 1987, Sugiyama 1998) and soil instability, which is a common feature of flooded sites and can make species more susceptible to uprooting during storm events (Fraser 1962, Kurtz et al. 2013). The consistency in the proportion of multi-stemmed individuals among the three DBH inclusion criteria sampled in our study site indicates that this feature generally appears in trees at early life stages.

The overall species richness (119 species) was relatively high in comparison with the results obtained by previous studies on other Restinga forests with similar sampling efforts. Only two Restinga forest sites in Brazil have had higher richness values reported for trees with a DBH ≥4.8 cm (Espírito Santo, 159 species and 2 ha sampled, Leite 2010; and Santa Catarina, 128 species and 1 ha sampled, Negrelle 1995). Local environmental heterogeneity may contribute to the establishment of a large number of species (Lundholm 2009). In our study site, variations in environmental features could be mainly related to different levels of waterlogging (Pansonato M.P., pers. obs.) and soil properties. When richness values were rarefied to a common sampling effort (0.64 ha), a richness increase was observed when small individuals were included, probably because of the inclusion of shrub and treelet species in the Myrtaceae, Rubiaceae, and Melastomataceae families.

The Shannon diversity index value was relatively high (H' = 3.61) in comparison to other flooded and unflooded Restinga forests (Menezes et al. 2010 and references therein; Assis et al. 2011 and references therein), particularly considering the high relative abundance of *Diospyros brasiliensis* (ca. 20%), which tends to reduce Shannon values due to reduced equability. Restinga forests with lower species richness than our study site have higher values of diversity (e.g., 71 species and 0.5 ha sampled, H' = 3.703, Fabris & Cesar 1996; 84 species and 0.4 ha sampled, H' = 3.897, Urbanetz et al. 2010; 94 species and H' = 3.637 per hectare, Lima et al. 2011), probably because of higher equability among species. The proximity of our study site to continuous areas of rainforest on clayey soils may have facilitated constant colonization by propagules that originated in the continuous forest and this would tend to increase species richness. Furthermore, if local factors in our study site favored the establishment of certain species, they would also have had their density greatly increased by having a source of propagules in nearby rainforests.

As expected, Myrtaceae was the richest family in our study area. This is a major floristic pattern in the Atlantic Forest (Mori et al. 1983, Scudeller et al. 2001). Lauraceae, Fabaceae, Rubiaceae, and Melastomataceae were also very rich families, as previously found in other studies on Restinga forests (Guedes et al. 2006, Lopes 2007, Martins et al. 2008, Assis et al. 2011, Magnano et al. 2012). Our study site was dominated by *Diospyros brasiliensis* (Ebenaceae), which was the most representative species in terms of density, frequency, and basal area. This species occurs in the coastal plain forests of Rio de Janeiro, São Paulo, and Paraná (Ivanauskas 1997, Santos & Sano 2007, Martins et al. 2008), as well as in the lowlands and riverine forests. It has also been recorded in semi-deciduous forests in São Paulo and Pernambuco states (Soares et al. 2005, Holanda et al. 2010), although this should be viewed with caution, as the misidentification of this species is common (Santos & Sano 2007). Despite species identification, the highest density recorded for this species until now was 59 ind./ha in a seasonal semi-deciduous forest in Pernambuco state (Holanda et al. 2010).

Additionally, this species was found to be dominant in the subcanopy layer of a Restinga forest in a floristic inventory conducted in the nearby municipality of Bertioga, although species abundances were not quantified in this study (Martins et al. 2008). The high abundance of *Diospyros brasiliensis* in our study site (309 ind./ha or 19.1% of all individuals for DBH ≥4.8 cm) is, therefore, very peculiar. The high abundance of *Anaxagorea dolichocarpa* (Annonaceae) (102 ind./ha or 6.3% of all individuals for DBH ≥4.8 cm) is also unusual in Restinga forests.

Sandy coastal plains are geologically recent, and are considered as a subset of species that were originally present in the surrounding Atlantic Forest (Rizzini 1979, Araújo 2000). However, when the densities of some species are compared between coastal plains and adjacent slope forests, they usually differ widely (Scarano 2002, Assis et al. 2011). Some indicator species in coastal plain forests, such as *Ilex theezans* (Marques et al. 2011), confirm this hypothesis. *Calophyllum brasiliense*, *Andira fraxinifolia*, *Myrcia multiflora*, and *Ocotea pulchella* are more abundant in Restinga forests than in slope forests along the Brazilian coast (Lima et al. 2015 and references therein). Low floristic similarities between Restinga forests and nearby rainforests on clayey soils may be caused by soil characteristics (Araújo 2000, Assis et al. 2011). However, the unusual abundance of *Diospyros brasiliensis* and *Anaxagorea dolichocarpa* in our study site should not be solely attributed to general soil characteristics, but colonization processes such as founder effects (Grime 1998) and mass effects (Shmida & Ellner 1984) should also be considered. Further studies on species similarity that take into account species abundance are needed, as they would improve our understanding of differences in species distributions between rainforests on clayey soils and Restinga forests, as well among Restinga forests.

Our study site is located in a region under strong anthropogenic pressure with only a few forest fragments remaining. The recent construction of a road across the Caraguatatuba coastal plain has altered the drainage pattern in a small proportion of the southern part of our study site (Pansonato M.P., pers. obs.). This has also occurred in several areas along the BR-101 highway, and has reduced vegetation cover on the coastal plain (Souza 2006). Therefore, the long-term monitoring of the structure and composition of our study site would improve our understanding of the effects of road construction on coastal plain forests in São Paulo. Furthermore, recent ongoing projects related to transport and seaport infrastructure are generating a high demand for compensatory forest restoration on the northern coast of São Paulo. Knowledge of the local vegetation may provide guidelines for the restoration initiatives, and providing information on local species composition could encourage the use of native local species in restoration initiatives. Forest structure data could help to establish restoration strategies that accelerate the recovery of the main attributes of vegetation.

Our study site is important for both biodiversity conservation and ecosystem services. Its location is strategic in connecting slope forests and the coastal plain, and it probably acts as a stepping stone that facilitates the movement of animals (e.g., seed dispersers) across the landscape. In addition, as our study site is one of the largest Restinga forest remnants in the region, it may function as a source of propagules to recolonize nearby smaller fragments, and areas under secondary succession. Because of the high frequency of heavy rain, many areas on the Caraguatatuba coastal plain are frequently flooded (Boulomytis et al. 2015), so the conservation of this Restinga forest remnant is important because it could act as a water sink that mitigates overflow events (Neary et al. 2009). As overflow events are capable of transporting sediments, Restinga forest remnants probably contribute to sediment retention by preventing sediments being deposited in watercourses or urban areas (Carter 1988). Finally, the Restinga forest studied is only partly protected by ecological-economic zoning, which recommends a soil occupation rate of 20% (Estado de São Paulo, 2017). Given the importance of our study site to the landscape and its proximity to urban areas, we recommend the creation of a Private Reserve of Natural Heritage for its long-term conservation.

Supplementary material

The following online material is available for this article:

Figure S1 - Rarefaction sample-based curves and their respective confidence intervals. A) DBH ≥4.8 cm. B) DBH ≥10 cm.

Table S1 - Parameters of the species sampled for three diameter inclusion criteria of a Restinga forest fragment located on coastal plain of Caraguatatuba, Brazil. N: Number of individuals, Ind./ha: Individuals per hectare, RD: Relative density, BA: Basal area and RDo: Relative dominance. Data ordered by their N for DBH ≥4.8 cm.

Table S2 - Parameters of the families sampled for three diameter inclusion criteria of a Restinga forest fragment located on coastal plain of Caraguatatuba, Brazil. N: Number of individuals, Ind./ha: Individuals per hectare, RD: Relative density, BA: Basal area, RDo: Relative dominance and Nsp: Number of species. Data ordered by their N for DBH ≥4.8 cm.

Table S3 - Parameters of the 72 species sampled in five secondary plots of a Restinga forest fragment located on coastal plain of Caraguatatuba, Brazil. N: Number of individuals, RD: Relative density and Ind./ha: Individuals per hectare. Data ordered by their N for DBH ≥4.8 cm.

Author Contributions

Marcelo Petratti Pansonato: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Renato Augusto Ferreira de Lima: Contribution to data analysis and interpretation; Contribution to critical revision, adding intelectual content.

Alexandre Adalardo de Oliveira: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to critical revision, adding intelectual content.

Ricardo Bertoncello: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to critical revision, adding intelectual content.

Adriana Maria Zanforlin Martini: Substantial contribution in the concept and design of the study; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intelectual content.

Conflicts of interest

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

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