

Structure, diversity, and spatial patterns in a permanent plot of a high *Restinga* forest in Southeastern Brazil

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RESUMO

(Estrutura, diversidade e padrões espaciais em uma parcela permanente de floresta alta de *Restinga* no Sudeste do Brasil) Nós investigamos a estrutura, diversidade e distribuição de espécies arbóreas em uma parcela de 10,24 ha de uma floresta alta de *Restinga* (FAR) no Sudeste do Brasil. Nós amostramos 15.040 indivíduos pertencentes a 45 famílias, 87 gêneros e 116 espécies (densidade= 1.468 árvores ha⁻¹, e área basal= 28,0 m² ha⁻¹). A riqueza média foi menor que outros tipos de florestas tropicais e outras FAR amostradas em menor intensidade, provavelmente pela juventude e hidromorfia dos solos na área de estudo. A densidade, área basal, composição e diversidade arbórea variaram consideravelmente de acordo com a classe de tamanho considerada. A parcela estudada teve uma densidade similar a outras florestas tropicais, mas com menor área basal (menos indivíduos > 60 cm de diâmetro) e maior densidade de árvores pequenas. Fustes múltiplos não foram frequentes (11% dos indivíduos), mas foram comuns entre as espécies (74% das espécies). A distribuição espacial foi predominantemente agregada, um padrão comum a outros tipos de florestas tropicais. Além do substrato arenoso, a parcela estudada e outras florestas de areia branca do mundo tiveram padrões muito similares de estrutura, riqueza e diversidade. Assim, consideramos a FAR como um subtipo evidente de floresta de areia branca.

Palavras-chave: classes de tamanho de árvores; Floresta Atlântica, fustes múltiplos; riqueza de espécies

ABSTRACT

(Structure, composition, and diversity of a high *Restinga* forest in the Southern Atlantic Forest) We assessed the structure, diversity and distribution of tree species in a 10.24-ha permanent plot of high *Restinga* forest (HRF) in southeastern Brazil. We sampled 15,040 individuals belonging to 45 families, 87 genera and 116 species (density= 1,468 trees ha⁻¹, and basal area= 28.0 m² ha⁻¹). Mean richness was lower than other types of tropical forests and other HRFs that have been less intensively sampled, which is probably due to the younger age and hydromorphy of the soils in the study site. Tree density, basal area, species composition, and diversity all varied considerably depending on the size class considered. The studied plot had a density similar to other tropical forests but with a smaller basal area (fewer individuals > 60 cm in diameter), and higher density of smaller trees. Multi-stemmed individuals were not frequent (11% of the trees), though they were widespread among species (74% of the species). Spatial distribution was predominantly clumped, a pattern common to other types of tropical forests. Besides growing over white-sand soils, the PEIC plot and other white-sand forests of the world also had very similar patterns of community structure, richness and diversity. Therefore, we consider the HRF as a recognizable subtype of white-sand forest.

Key words: Atlantic Forest; multi-stemmed trees; species richness; tree size classes

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Introduction

One useful way to study tropical forests is via large permanent inventory plots (Condit 1998), specially designed for the study large-sized, long-lived organisms such as trees. Recently, numerous plots have been established in a variety of types of forests around the world (Losos *et al.* 2004). However, these permanent plots are restricted to particular types of soils, primarily oxisols and ultisols (Ashton 2004). Still, surprisingly diverse forests grow on a larger number of soil types, including relatively nutrient-poor, white-sand soils (Newbery 1991; Phillips *et al.* 1994). In Brazil, besides the widespread Amazon *campinaranas* (Anderson 1981), some coastal forests also grow on sandy soils (mainly spodosols), the *Restinga* forests. These forests are known to be lower and less species rich than surrounding rain forests, although species rich *Restinga* forests may also be found (César & Monteiro 1995; Guedes *et al.* 2006; Negrelle 2006).

But what is the typical structure and composition of *Restinga* forests? How is it different from forests that grow on non-sandy soils? How clumped are trees of different species on such nutrient poor-soils? Is there any evidence of species being more associated to habitat characteristics than in forests on richer soils? The answer to these and many other questions are still unavailable because detailed accounts of *Restinga* forests are largely missing. Plots over 1-ha are rare (Assis *et al.* 2004; Negrelle 2006), and therefore there is not enough data to properly assess general community-level patterns, *Restinga* population distributions, habitat associations or other features related to the ecology of these forests. For instance, the occurrence of multi-stemmed trees, cited as being typical of *Restinga* species (Sugiyama 1998; Guedes *et al.* 2006), has never been properly assessed. In addition, this lack of knowledge also prevents a proper comparison of *Restinga* forests with other forest types.

Restinga forests are part of the *Restinga* vegetation complex (or simply *Restinga*), a typical feature of Brazilian coastal plains. By definition, it is the vegetation that grows over tertiary or quaternary marine sand deposits. So, although the *Restinga* forest may be seen as a climax formation in the *Restinga* complex, it is a very young type of forest, geologically speaking. Besides its young age, the limiting soil conditions makes it a very promising setting in which the mechanisms that control the floristic composition and structure of tropical forests can be better understood (Scarano 2009). For instance, a low degree of endemism is expected because soils are much younger than other forests on soils developed *in situ* (Anderson 1981). In this scenario, one may ask if the *Restinga* composition is the result of simple historical events or if there is local and specific ecological processes (*e.g.* competition, facilitation or herbivore pressure – Scarano 2002; Fine *et al.* 2009) that control species establishment and growth. Therefore, the study of tropical forests under such extreme conditions can give us a broader perspective on their structure, composition, and diversity.

In addition, *Restingas* are very important systems for physical and biological conservation of Atlantic Forest areas. Besides the more obvious important linked to the prevention of sea erosion, *Restingas* can shelter considerable populations of species that are rare in other Atlantic forest types (Scarano 2009). This type of vegetation is restricted to narrow spaces along the Atlantic Ocean coastline, places where human settlements are major and constant threats to biodiversity (Rocha *et al.* 2007). More specifically, high *Restinga* forests (HRF) represent one of the most rare and threatened vegetation types of the already deforested Brazilian Atlantic Forest (Ribeiro *et al.* 2009).

Aiming to describe and understand more precisely the composition, structure, diversity, and spatial patterning of *Restinga* forests at different scales, we present a study of a 10.24-ha plot established in the high *Restinga* forest of the Parque Estadual da Ilha do Cardoso (PEIC), at 25° S latitude. The main goal of this study was to detect general community-level patterns of the plot tree community. We evaluated several different characteristics of the community such as tree density, basal area, and species richness and how these characteristics vary among different tree size classes. We also assess the frequency and specificity of multi-stemmed individuals in the community. Spatial analyses were carried out for the most abundant species, aiming to describe general patterns of species aggregation.

Methods

Study area

This study was conducted in the Parque Estadual da Ilha do Cardoso (PEIC), a 13,500-ha continental island located in Cananéia County, in the extreme southern tip of São Paulo State, southeastern Brazil (Fig. 1). Although at 25° S latitude, the climate is tropical and wet with no dry season (mean annual water surplus = 1,330 mm – *Af sensu* Köppen (1948) climate classification). Mean annual temperature is 22.4 °C (average daily maximum and minimum are 26.1 and 18.0 °C), mean minimum temperature of the coldest month is 12.6 °C, and average annual precipitation is 2,261 mm. Only one month (August) has an average precipitation below 100 mm and the average rainfall for the three driest months is 314 mm (DAEE/SP, 2010). Data collection was carried out in a 10.24-ha (320×320 m) permanent plot established in 2002 (25°04'41"S and 47°55'53"W), subdivided into 256 subplots of 20×20 m (400 m²). The terrain is flat (altitude between 3 and 8 m above sea level) and developed over the sedimentary rocks of the Cananéia Formation (Upper Pleistocene). The soils are young (around 5,000 years), sandy (90–100%, mainly fine-grained sand), strongly acidic (pH in water between 3.9–5.0), hydromorphic, and with variable content of organic matter (Gomes *et al.* 2007). The *plot soil* survey classified them as *aquodic quartzipsamments* (lower parts, periodic flooded), wet spodosols (arenic/oxyaquic

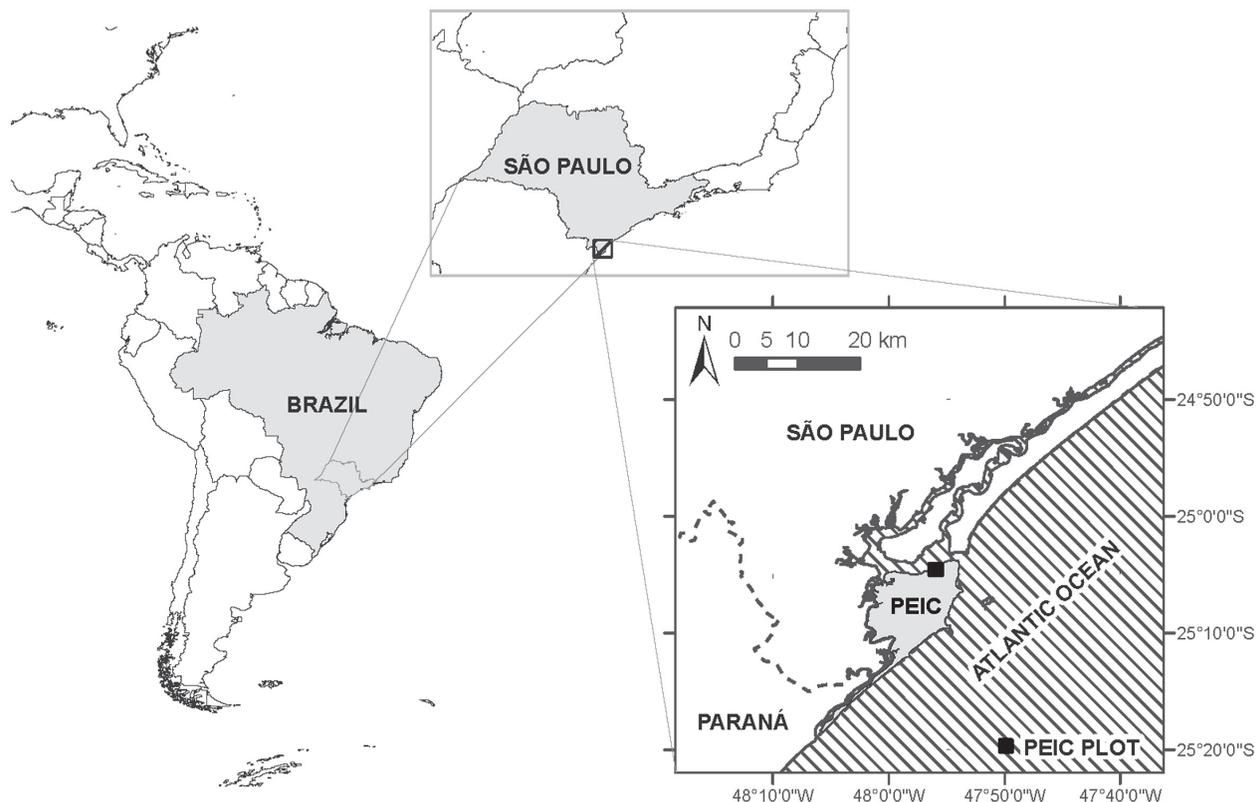


Figure 1. Location of the Parque Estadual da Ilha do Cardoso (PEIC) and the PEIC 10.24-ha forest plot.

alorthod and histic alaquod) and thionic histosols (terric sulfisaprists – soil maps, profiles and details on physical and chemical properties can be found in Gomes *et al.* 2007). The plot vegetation represents one type of the Atlantic Forest, the high *Restinga* forest (HRF), a type of forest which grows over marine sand deposits and is equivalent to Lowland tropical rain forest (Holdridge *et al.* 1971). Vegetation over marine sand deposits covers approximately 18% of the island. The PEIC has no main geographical barriers except rivers separating it from the continent, which is one of the largest and better conserved landscapes of the Atlantic Forest (Ribeiro *et al.* 2009). Therefore, there is no evidence of dispersal limitation from the continent and other forest types of the island. In addition, there is no evidence of any recent human disturbance inside the PEIC plot, although it is possible that low intensity selective timber extraction occurred before the establishment of the park in 1962.

Tree census

Tree census followed the Center for Tropical Forest Science protocol (Condit 1998) except that it only included individuals with stem girth at breast height ≥ 15 cm, equivalent to diameter at breast height (dbh) ≥ 4.8 cm. All individuals were tagged, mapped and identified to the species level. The diameter of each stem of each individual was measured to the nearest 1 mm and the number of stems of multi-stemmed individuals (*i.e.* with ramifications of the trunk

below 1.3 m) was counted. Tree height was measured to the nearest 0.5 m for most individuals and was used to estimate mean and maximum canopy heights. Species identifications were based on several reference collections and the relevant literature. Vouchers were deposited in the Universidade de São Paulo (Campus Piracicaba) herbarium (ESA) under the collection numbers of D. Sampaio. We followed the APG II (2003) system. The plot was first censused in 2002 and then again in 2004/2005; because of improved species-level identifications in the second census, data presented here refer to the individuals found alive during the second census.

Forest structure and diversity

In addition to the total plot density and basal area, the relative values of density and basal area were calculated for each species following Mueller-Dombois & Ellenberg (1974). Stems were assumed to have a cylindrical shape to calculate tree basal area. In order to assess forest stratification we divided the sample according to different diameter size classes: ≥ 4.8 cm; ≥ 10 cm; ≥ 20 cm; and ≥ 30 cm dbh. For multi-stemmed individuals, the diameter of the largest stem was used to determine the size class. We estimated the maximum richness using different non-parametric estimators (e.g. Michaelis-Menten, first and second order Jackknife), performed using 5,000 randomizations by the EstimateS software (Colwell 2006). The choice of using the first order Jackknife to discuss the results was made empiri-

cally, based on the number of samples required to estimate the total plot richness and on the tendency of stabilization of the curve, following Colwell and Coddington's (1994) recommendations. Average values of density, basal area, richness, singletons, and Fisher's alpha and Berger-parker index (Magurran 2004) per hectare were estimated from all possible 1-ha square plots that could be fit in the 10.24-ha plot ($n = 144$ plots). The number of singletons per hectare is used here as a practical definition of rare species and the Berger-parker index refers to the relative abundance of the most common species. All the analyses were completed for the four size classes in order to assess possible differences in the vertical structure of the forest.

Multi-stemmed individuals

The numbers of stems per individual were evaluated for each species, to detect if the distribution of the number of individuals in different stem categories (1 to 10 stems per individual) was significantly different than the distribution observed for the community as a whole. The distribution observed for each focal species was compared to 1000 random distributions, obtained by randomly selecting from the community a number of individuals equal to the abundance of the focal species in the plot. For each category of number of stem per individual, we observed the proportion of random distributions (simulations) smaller than the number observed for the species in the category. When this proportion was equal to or greater than 95%, the observed number was considered to be different than the expected by chance for the whole community (randomization test *sensu* Manly 2006). To test if the species with the highest proportions of multi-stemmed individuals were also the most abundant species in the plot, we compared the density of each species that had more multi-stemmed individuals than expected by chance with the density of all other species in the plot. Simulation procedures were also used to run this test. In both analyses, we excluded some palms (*Euterpe edulis*, *Geonoma schottiana* and *Syagrus romanzoffiana*) that have strictly monopodial growth habits and one gymnosperm species (*Podocarpus sellowii*).

Spatial distribution

To describe the spatial patterns of species, the Morisita Index of Dispersion (ID, Krebs 1999) was calculated based on the 20×20 m subplots for each species with more than 70 individuals ($n = 40$ species). The observed value of the index for each focal species was compared with a null model that assumed complete spatial randomness of the individuals (Poisson distribution). This model was generated from 1000 simulations for the same number of individuals of the focal species. For each simulation, the null ID value was calculated and the distribution of values obtained was used to calculate the probability of the type I error on the statistical inference (Manly 2006). This approach was only used in the ≥ 4.8 and ≥ 10 cm dbh size classes because of

the small number of individuals per species in the bigger size classes. The routines used to generate the null models of multi-stemmed individuals (described above) and of complete spatial randomness were developed in R (R Development Core Team 2008) and are available upon request from the authors.

To explore spatial patterns at scales larger than 20 m, we carried out spatial autocorrelation analyses. For the same 40 species with $n > 70$, the Moran's index (I) was calculated for different distance classes up to 200 m (correlograms, Legendre & Legendre 1998) based on the distance between the 20×20 m subplots. The global significance of the correlogram was tested using the Bonferroni method (Legendre & Fortin 1989) and in cases of significant correlograms, the values of the coefficients were tested for each scale individually. This test was performed using a Monte Carlo permutation routine that assigned randomly the observed densities for each subplot 1000 times to construct the confidence envelopes around the null model at each given scale. Positive and significant values indicate positive autocorrelation at a given distance class, whereas negative and significant values indicate the opposite. The absence of significant values indicates a random or regular distribution at the given distance class. Finally, to illustrate the existing types of spatial distribution, species were separated into general patterns of spatial distribution (see results for patterns description). The assignment of species to each pattern was based on the visual inspection of the correlogram and of the distribution map of the species in the plot. The definition of patterns was subjective but we do believe that they are representative examples and that they may be useful to assess what mechanisms are influencing species distributions.

Results

Forest diversity and composition

We sampled 15,040 individuals that represented a total basal area of 290 m² (Tab. 1). These individuals belonged to 45 families, 87 genera and 116 species. Based on this sample, a total of 126 ± 3.1 (Jackknife 1) tree species was estimated for the HRF of the PEIC. Fisher's alpha was 17.1 ± 0.6 (Shannon = 3.58) for the entire plot, but the value was slightly greater when calculated for samples of 1-ha (17.9). In the 1-ha subsamples, the number of singletons (13.7 singletons ha⁻¹) was greater than that obtained for the 10.24-ha plot (9 singletons). In contrast, the Berger-Parker index of dominance was more or less the same independent of the sample size. The rarefaction curve indicated 5.5 ha as the area at which 95% of the total richness was found. In addition, the number of singletons leveled-off around nine after about 6.5 ha.

Areaceae was the most abundant family, followed by Myrtaceae, Lauraceae, Annonaceae and Rubiaceae. Together they accounted for 58.8% of the sampled individuals. The

Table 1. Total and per hectare values of the main structure and diversity parameters in different size classes in a 10.24-ha plot of high *restinga* forest. *n* = total number of individuals; BA = Basal area; Singletons = species with only one individual in the sample. Brackets refer to the 2.5 and 97.5 percentiles of the distribution obtained from 144 one-hectare plots inside the 10.24-ha plot.

Parameter	Size class (cm)			
	≥ 4.8	≥ 10	≥ 20	≥ 30
<i>n</i>	15,040	6,229	2,199	807
<i>n</i> ha ⁻¹	1,467.6 [1292–1681]	642.2 [527–725]	224.8 [185–273]	82.3 [60–108]
BA (m ²)	289.9	251.4	183.0	115.9
BA ha ⁻¹	27.99 [25.2–33.2]	24.61 [21.3–29.8]	17.88 [13.9–23.4]	11.30 [7.7–16.7]
Species	116	103	76	52
Species ha ⁻¹	79.1 [65–89]	62.3 [50–70]	38.7 [29–47]	17.1 [9–26]
Singletons	9	11	12	19
Singletons ha ⁻¹	13.7 [8–19]	13.7 [9–20]	12.9 [8–19]	8.8 [2–17]
Fisher's alpha	17.11 ± 0.59	17.53 ± 0.71	15.47 ± 0.81	12.72 ± 0.92
Fisher's alpha ha ⁻¹	17.93 [14.2–21.1]	17.14 [12.3–20.1]	13.64 [8.4–14.5]	6.76 [2.8–12.4]
Berger-Parker	0.20	0.08	0.18	0.29
Berger-Parker ha ⁻¹	0.20 [0.12–0.28]	0.11 [0.07–0.18]	0.21 [0.12–0.35]	0.31 [0.19–0.48]

most abundant species in the plot was *Euterpe edulis* with 293.8 ± 154.9 trees ha⁻¹, and a frequency of 99.6%. The 40 most abundant species in the plot are listed in Tab. 2. *Calophyllum brasiliense*, *Ocotea pulchella*, *Albizia pedicellaris*, *Tapirira guianensis*, *Euterpe edulis* and *Manilkara subsericea* were the species with the largest contribution to basal area (50.2%). Myrtaceae was the richest family (21% of species), followed by Lauraceae (10%), and Fabaceae (5%). Twenty five families had just one species in the plot. The full list of species names and abundances from the 2004/2005 census can be found at http://ecologia.ib.usp.br/labtrop/doku.php?id=labtrop:01_projetos:02_pp:pp_peic:pp_peic#lista_de_especies.

Forest structure

The increase in tree diameter from 4.8 to 10 cm resulted in the exclusion of 8,811 individuals, that is, almost three fifths of all individuals in the sample (58.6%). In turn, the total number of singletons increased with the size class considered. There was a tendency for higher diversity and smaller dominance in the ≥ 10 cm size class (Tab. 1). With respect to dominance, there was a shift in the dominant (*i.e.* more-abundant species) species among the size classes. *Euterpe edulis* was dominant in the size class ≥ 4.8 cm, *Ocotea pulchella* was dominant in the mid-size classes (≥ 10 and ≥ 20 cm) and *Calophyllum brasiliense* was dominant above 30 cm dbh. The six species with the greatest contribution to basal area (cited above) were also the most common species in the plot canopy (78.3% of trees ≥ 30 cm dbh). *Albizia pedicellaris* attained the greater average and overall dbh in the plot (34.4 and 85.4 cm, respectively), followed

by *Calophyllum brasiliense* (mean dbh = 33.1 cm). Together, these two species accounted for 82% of trees ≥ 50 cm dbh in the plot. Besides these two species, only five others exceeded 50 cm dbh (*i.e.* *Eugenia sulcata*, *Myrcia glabra*, *Manilkara subsericea*, *Ocotea pulchella*, and *Tapirira guianensis*). All species with individuals present in the plot canopy (dbh ≥ 30 cm) had individuals < 10 cm dbh. In contrast, 26 species did not exceed 15 cm dbh. There was considerable variance in abundance and, consequently, in species rank order among the different size classes (Tab. 2). Many species' (45%) abundances gradually declined with increasing size class (*e.g.* *Euterpe edulis*, *Xylopia langsdorffiana*, *Amaioua intermedia*, *Andira anthelmia* and *Schefflera angustissima*). Small-sized species, as expected, declined drastically with an increase in size class (25% of species), with no or extremely low contributions to the > 20 cm dbh size class (*e.g.* *Miconia cubatanensis*, *Marlierea racemosa*, *Guatteria australis*, *Garcinia gardneriana*, *Alibertia myrciifolia*, and *Ilex amara*). Other species, however, presented a smoother decline in abundance with size classes, reflecting peaks of abundance at larger size classes (17.5% of species) or abundance values more similar among classes (12.5%). *Ocotea pulchella*, for instance, had more individuals > 40 cm than < 10 cm dbh, showing a peak of abundance between 20 and 25 cm dbh. Examples of these general patterns of species diameter distribution are illustrated in Fig. 2.

Multi-stemmed individuals

We found 84 species (72%) and 1,623 individuals (10.8%) with two or more stems (mean ± sd: 1.17 ± 0.60 stems individual⁻¹). Only 233 trees (1.5%) of 36 species (31%) had more

Table 2. The 40 most abundant species found in a 10.24-ha plot of high *restinga* forest and their correspondent abundance, aggregation (Morisita's index of dispersion) and distribution pattern (DP). In parentheses, the species rank order in the size classes considered (species with the same abundance received the same rank to avoid overestimation of the real number of ranks per size class). See text for more detail on the distribution patterns of species. Legend to distribution patterns: A – no spatial autocorrelation; B – small isolated patches; C – more than one clump forming large stripes or larger patches more or less isolated; D – big patches covering large areas of the plot; E – no evident pattern.

Species and author	Abundance (species rank)								Morisita's index		DP
	≥ 4.8 cm	≥ 10 cm	≥ 20 cm	≥ 30 cm	≥ 4.8 cm	≥ 10 cm					
<i>Euterpe edulis</i> Mart.	3008 (1)	109 (19)	8 (30)	2 (28)	1.192***	1.696**			D		
<i>Xylopia langsdorffiana</i> A. St.-Hil. & Tul.	946 (2)	136 (15)	10 (32)	3 (26)	1.281***	1.813***			D		
<i>Amaioua intermedia</i> Mart.	837 (3)	400 (2)	32 (17)	1 (34)	1.410***	1.431***			B		
<i>Schefflera angustissima</i> (Marchal) Frodin	574 (4)	287 (7)	86 (7)	23 (6)	1.219***	1.285***			A		
<i>Andira anthelmia</i> (Vell.) J.F.Macbr.	548 (5)	278 (8)	34 (15)	4 (18)	1.120**	1.223**			D		
<i>Ocotea pulchella</i> (Nees) Mez	537 (6)	518 (1)	400 (1)	171 (2)	1.839***	1.876***			D		
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	526 (7)	309 (6)	50 (11)	5 (15)	1.400***	1.065 ^{ns}			D		
<i>Ternstroemia brasiliensis</i> Cambess.	526 (7)	384 (3)	45 (13)	7 (11)	3.167***	2.977***			C		
<i>Tapirira guianensis</i> Aubl.	505 (9)	357 (5)	186 (3)	93 (3)	1.375***	1.295***			B		
<i>Myrcia racemosa</i> (O. Berg) Kiaersk.	444 (10)	72 (24)	3 (50)	1 (34)	1.479***	2.504***			C		
<i>Calophyllum brasiliense</i> Cambess.	410 (11)	365 (4)	294 (2)	230 (1)	1.237***	1.279***			E		
<i>Calyptanthes concinna</i> DC.	323 (12)	187 (11)	73 (8)	12 (7)	1.979***	2.502***			B		
<i>Miconia cubatanensis</i> Hoehne	267 (13)	26 (44)	-	-	2.732***	-			D		
<i>Ocotea aciphylla</i> (Nees) Mez	261 (14)	140 (14)	67 (9)	10 (10)	1.871***	1.868***			D		
<i>Pouteria beaurepairei</i> (Glaz. & Raunk.) Baehni	251 (15)	189 (10)	59 (10)	6 (13)	1.160*	1.282*			D		
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	250 (16)	44 (31)	4 (46)	1 (34)	2.114***	-			C		
<i>Psidium cattleianum</i> Afzel. ex. Sabine	238 (17)	200 (9)	38 (14)	2 (28)	1.325**	1.376***			E		
<i>Manilkara subsericea</i> (Mart.) Dubard	226 (18)	170 (12)	106 (5)	44 (5)	1.863***	2.139***			D		
<i>Byrsonima ligustrifolia</i> A. Juss.	214 (19)	124 (17)	24 (21)	- (54)	2.876***	2.216***			E		
<i>Marlierea racemosa</i> (Vell.) Kiaersk.	190 (20)	16 (56)	3 (50)	1 (34)	4.021***	-			C		
<i>Eugenia sulcata</i> Spring ex Mart.	183 (21)	99 (20)	27 (20)	5 (15)	1.414**	1.319 ^{ns}			E		
<i>Ilex theezans</i> Mart. ex Reissek	180 (22)	154 (13)	92 (6)	11 (8)	5.784***	5.020***			B		
<i>Aparisthium cordatum</i> Baill.	179 (23)	21 (50)	-	-	3.150***	-			B		
<i>Balizia pedicellaris</i> (DC.) Barneby & J.W. Grimes	163 (24)	134 (16)	107 (4)	92 (4)	1.125 ^{ns}	1.178 ^{ns}			A		
<i>Maytenus robusta</i> Reissek	154 (25)	30 (39)	3 (49)	-	2.488***	-			D		
<i>Myrcia</i> sp.	144 (26)	43 (32)	-	-	1.716***	-			A		
<i>Myrcia ilheosensis</i> Kiaersk.	134 (27)	118 (18)	48 (12)	1 (34)	5.229***	4.932***			B		
<i>Myrcia brasiliensis</i> Kiaersk.	119 (28)	78 (21)	31 (18)	7 (11)	1.349 ^{ns}	1.193 ^{ns}			A		
<i>Heisteria silvianii</i> Schwacke	115 (29)	59 (26)	12 (30)	1 (34)	3.085***	-			C		
<i>Myrcia multiflora</i> (Lam.) DC.	111 (30)	78 (21)	20 (24)	-	4.491***	5.479***			B		
<i>Guatteria australis</i> A. St.-Hil.	104 (31)	5 (72)	2 (56)	1 (34)	1.721**	-			E		
<i>Clusia criuva</i> subsp. <i>parviflora</i> Vesque	101 (32)	74 (23)	23 (22)	1 (34)	3.092***	2.843***			C		
<i>Ormosia arborea</i> (Vell.) Harms	95 (33)	64 (25)	23 (22)	4 (18)	1.204 ^{ns}	-			A		
<i>Myrcia bicarinata</i> (O. Berg) D. Legrand	94 (34)	57 (28)	7 (38)	2 (28)	10.015***	-			B		
<i>Matayba intermedia</i> Radlk.	93 (35)	58 (27)	34 (15)	11 (8)	1.676**	-			C		
<i>Alibertia myrciifolia</i> K. Schum.	92 (36)	4 (73)	-	-	1.835**	-			E		
<i>Myrcia glabra</i> (O. Berg) D. Legrand	80 (37)	56 (29)	31 (18)	6 (13)	2.216***	-			C		
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	79 (38)	14 (59)	-	-	3.656***	-			C		
<i>Ilex amara</i> (Vell.) Loes	74 (39)	22 (49)	-	-	1.990**	-			A		
<i>Posoqueria latifolia</i> (Rudge) Schult.	74 (39)	35 (34)	4 (46)	1 (34)	1.706*	-			E		

* $p < 0.05$; ** $p < 0.01$; *** $p = 0.001$; ns = not significant.

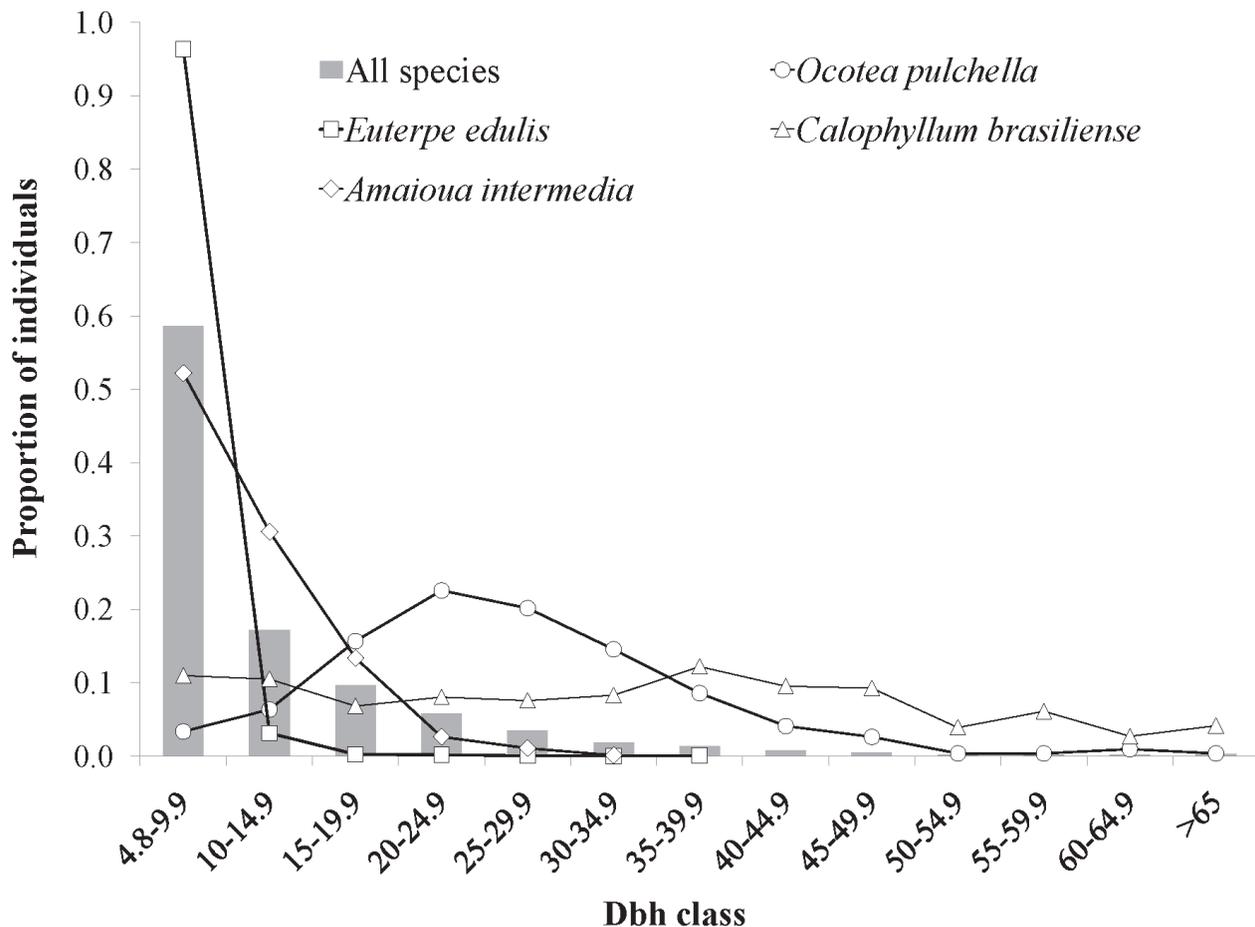


Figure 2. Overall size distribution and examples of species with different patterns of distribution in the PEIC plot. Dbh classes divided in 5 cm intervals.

than three stems. Eighteen species had significantly more stem ramifications than expected for the community as a whole, whereas another 26 species had fewer multi-stemmed individuals than expected. *Marlierea racemosa* had the highest number of stems (10) and also the highest proportion of multi-stemmed individuals (50.5%). The mean abundance of species with significantly more stems per individual (185.1 ± 256.7 trees) was marginally greater ($p = 0.041$) than the abundance of the other species in the plot (95.8 ± 154.3 trees). Among the species with significantly fewer multi-stemmed individuals, only *Blepharocalyx salicifolius* did not have any multi-stemmed individuals in the plot. Some of the significantly less-ramified species had high densities in the plot ($n < 500$), such as *Amaioua intermedia*, *Schefflera angustissima*, *Andira anthelmia*, *Ocotea pulchella*, and *Tapirira guianensis* (Tab. 3), besides the monopodial palm *Euterpe edulis*.

Spatial distribution

Among the 40 most abundant species, dispersion patterns of three (*Albizia pedicellaris*, *Myrcia brasiliensis* and *Ormosia arborea*, pattern A in Tab. 2) were not significantly different from random at the 20 m scale. At larger scales, three other species (*Schefflera angustissima*, *Myrcia* sp. and *Ilex amara*) were also not clumped. All other species had clumped pat-

terns at one or more distance classes, with *Myrcia bicarinata*, *Myrcia ilheosensis*, *Myrcia multiflora*, *Marlierea racemosa* and *Ilex theezans* having the highest aggregation indexes. In the size class ≥ 10 cm dbh, the random distribution was maintained for *Albizia pedicellaris* and *Myrcia brasiliensis*. The species *Pera glabrata*, clumped in the ≥ 4.8 cm size class, was not different from random in the ≥ 10 cm class. Other species were still clumped but had considerable increases (e.g. *Myrcia racemosa* and *Myrcia multiflora*) or decreases (e.g. *Byrsonima ligustrifolia* and *Ilex theezans*) in the Morisita index of dispersion in the size class ≥ 10 cm dbh. Visual inspection of the auto-correlograms and the distribution maps of the most abundant species in the plot ($n > 70$ individuals) suggested the existence of five general distribution patterns (Fig. 3 and Tab. 2). For certain species the individuals were clumped in small patches (e.g. *Ilex theezans*, pattern B), whereas others were concentrated in larger and specific areas of the plot (e.g. *Ocotea aciphylla* and *Ternstroemia brasiliensis*, patterns C and D). Besides a significant auto-correlation at some distances, eight species did not display an evident pattern of distribution (e.g. *Calophyllum brasiliense*, pattern E). It is noteworthy that several Myrtaceae species (e.g. *Myrcia ilheosensis*, *Myrcia multiflora* and *Myrcia bicarinata*) were the most strongly clumped species on the plot.

Table 3. Number of individuals per category of number of stems for species with more or less multi-stemmed individuals than expected by chance.

Species	Number of stems				
	1	2	3	4	>5
More multi-stemmed individuals than expected					
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	58	13	8		
<i>Ecclinusa ramiflora</i> Mart.			1		
<i>Gordonia fruticosa</i> (Schrader) H. Keng	14				1
<i>Guarea macrophylla</i> Vahl	13	5			
<i>Guatteria australis</i> A. St.-Hil.	78	18	5	2	1
<i>Hirtella hebeclada</i> Moric. ex A.P. DC.	12	7	1	2	
<i>Marlierea racemosa</i> (Vell.) Kiaersk.	94	37	31	16	12
<i>Maytenus robusta</i> Reissek	106	28	15	5	1
<i>Mollinedia schottiana</i> (Spreng.) Perkins	12	4	2	1	2
<i>Myrceugenia myrcioides</i> (Cambess.) O. Berg	2			1	
<i>Myrcia insularis</i> Kiaersk.	2				1
<i>Myrcia racemosa</i> (O. Berg) Kiaersk.	294	87	46	13	4
<i>Myrcia</i> sp.	94	30	11	6	3
<i>Ocotea aciphylla</i> (Nees) Mez	204	29	11	8	9
<i>Ocotea pulchra</i> (Nees) Mez	43	8			
<i>Ocotea venulosa</i> (Nees) Mez	37	5	1	1	
<i>Ternstroemia brasiliensis</i> Cambess.	448	65	8	5	
<i>Xylopia langsdorffiana</i> A. St.-Hil. & Tul.	478	241	133	55	38
Less multi-stemmed individuals than expected					
<i>Aiouea saligna</i> Meisn.	41	1			
<i>Amaioua intermedia</i> Mart.	769	53	12	3	
<i>Andira anthelmia</i> (Vell.) J.F. Macbr.	499	32	11	4	2
<i>Aparisthium cordatum</i> Baill.	163	11	3	2	
<i>Balizia pedicellaris</i> (DC.) Barneby & J. W. Grimes	161		2		
<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg	53				
<i>Calophyllum brasiliense</i> Cambess.	403	6	1		
<i>Calyptanthes concinna</i> DC.	306	16	1		
<i>Eugenia umbelliflora</i> O. Berg	63	3			
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	246	4			
<i>Heisteria silvianii</i> Schwacke	112	3			
<i>Ilex theezans</i> Mart. ex Reissek	166	13	1		
<i>Jacaranda puberula</i> Cham.	55	2	1		
<i>Manilkara subsericea</i> (Mart.) Dubard	211	14		1	
<i>Myrcia brasiliensis</i> Kiaersk.	116	2		1	
<i>Myrcia glabra</i> (O. Berg) D. Legrand	76	1	1		
<i>Myrcia ilheosensis</i> Kiaersk.	127	6	1		
<i>Myrcia multiflora</i> (Lam.) DC.	111		1		1
<i>Ocotea pulchella</i> (Nees) Mez	504	26	3	3	
<i>Ormosia arborea</i> (Vell.) Harms	92	2	1		
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	510	12	3		1
<i>Posoqueria latifolia</i> (Rudge) Schult.	70	3	1		
<i>Pouteria beaurepairei</i> (Glaz. & Raunk.) Baehni	230	16	3		1
<i>Rapanea venosa</i> (A. DC.) Mez	43	1			
<i>Schefflera angustissima</i> (Marchal) Frodin	569	5			
<i>Tapirira guianensis</i> Aubl.	481	19	5	2	

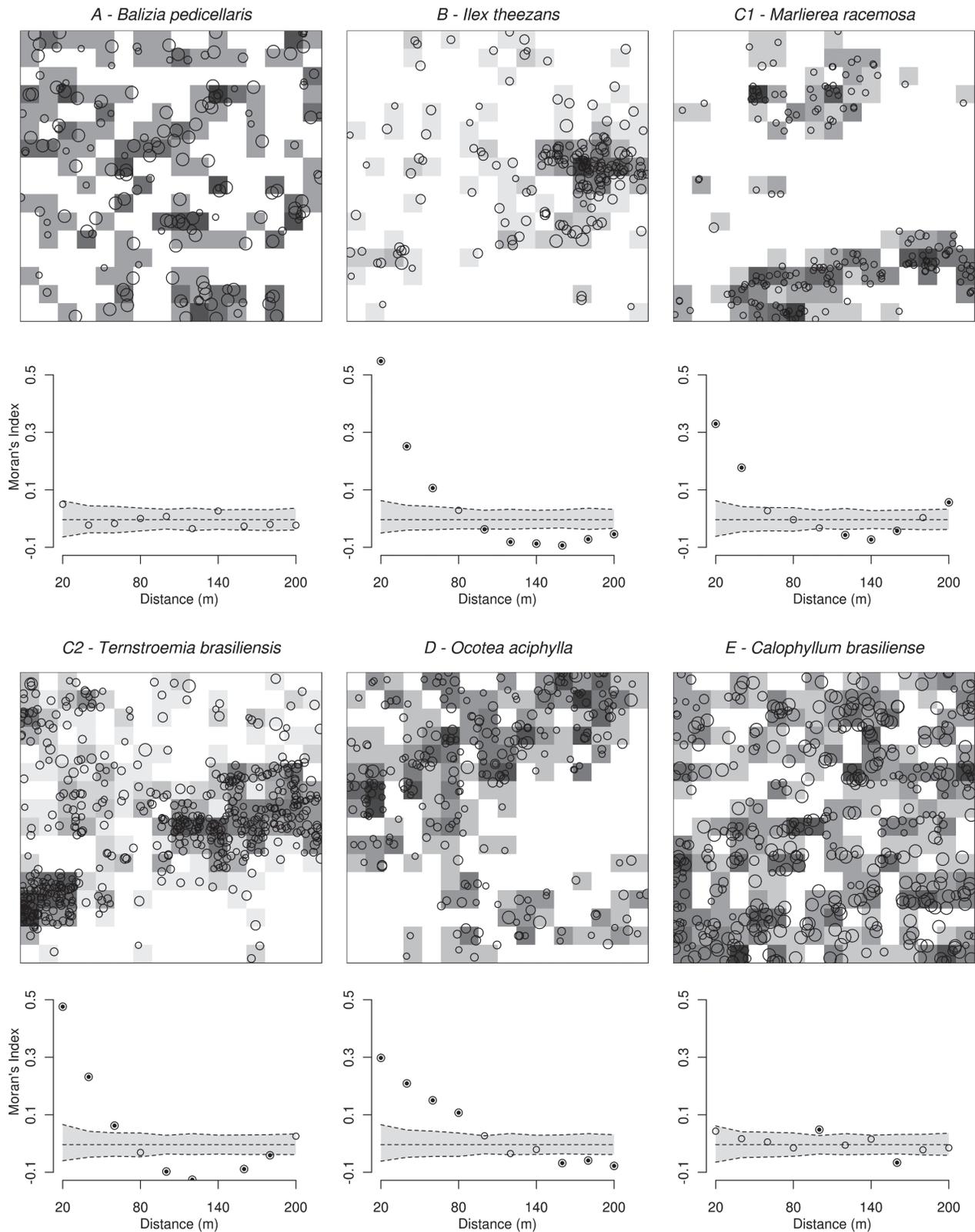


Figure 3. Illustrative maps of the general distribution patterns suggested for the most abundant tree species in the 256 subplots (20×20 m) surveyed. Circles vary in size according to tree size. More dark colors indicate subplots with higher values of abundance, while the white color indicate subplots with zero individuals of a given tree species. Legend to patterns: A – no spatial autocorrelation (A); B – small isolated patches (B); C – more than one clump forming large stripes (C1) or larger patches more or less isolated (C2); D – big patches covering large areas of the plot (D); E – and no evident pattern (E).

Discussion

Forest diversity and composition

The mean richness obtained (79 species ha⁻¹) was lower than other Brazilian sites of HRF (92 and 128 species ha⁻¹ – Assis *et al.* 2004 and Negrelle 2006, respectively; note that both studies used non-contiguous plots). Even the studies with much smaller sampling efforts attained similar or higher species richness (César & Monteiro 1995; Guedes *et al.* 2006). One possible explanation for this result may lie in the particularities of the PEIC plot substratum, which is young (< 5000 years), very acid, hydromorphic and periodically flooded (Gomes *et al.* 2007). Besides the little time that species had for colonization, such features impose important constraints on the establishment of some species (Dumont *et al.* 1990; Marques *et al.* 2009). Lower richness was also found when comparing trees \geq 10 cm dbh of two nearby non-HRF sites (109 – Melo 2000; and ca. 108 species ha⁻¹ – R.A.F. Lima, unpublished data).

The number of rare species (*i.e.* singletons) per hectare represented 17% of the plot richness, a value quite similar to other HRFs (14 to 17%, Assis *et al.* 2004; Negrelle 2006) and lower than that observed values for forests on non-sandy soils (> 23% - Melo 2000, Melo *et al.* 2000; Guilherme *et al.* 2004; Losos 2004). In addition, Fisher's alpha were much smaller than in 10 other tropical forest plots (values from 23 to 181) evaluated by Condit *et al.* (2004), except by the Mudumalai dry deciduous forest plot (5.9). Therefore, lower richness, rarity and diversity may be characteristic to HRFs relative to forests on richer soils. However, studies with standardized sampling methods and in HRF on soils with different features (age, acidity and/or flooding regime) are still needed to test this suggestion.

Arecaceae was the most abundant family, a common finding in many other Atlantic Forests. Exceptions are found where there is illegal palm-heart harvesting (César & Monteiro 1995; Guilherme *et al.* 2004; Guedes *et al.* 2006), an activity not seen inside the plot. Myrtaceae also deserves special mention because it harbored twice as many species as the second richest family of the plot. This pattern was not observed in other CTFS plots (Ashton *et al.* 2004), or inventories of forests on white-sand soils in South America (Phillips & Miller 2002) and Asia (Proctor *et al.* 1983; Newbery 1991; Davies & Becker 1996), where Myrtaceae does not exceed 7% of the total tree richness. However, nearby Atlantic Forest types have similar richness per family, with similar or higher Myrtaceae richness (Melo *et al.* 2000; Guilherme *et al.* 2004), suggesting an important effect of the geographic region on the general pattern of HRF floristic composition.

To the best of our knowledge, this is the largest survey ever carried out in a high *restinga* forest or in any other forest on white-sand soils. Magurran (2004) has suggested that sample sufficiency is attained when the species ac-

cumulation curve crosses the Michaelis-Menten model curve, which was observed around 4.4 ha. This also can be interpreted as the sampling area needed to confidently estimate the richness observed in the plot. According to the first and second order Jackknife estimators, these areas would be 3.4 and 2 ha, respectively. The suggestion of Colwell & Coddington (1994) that sample sufficiency is attained when all species have at least two individuals proved to be impracticable because the number of singletons virtually leveled-off after about 6.5 ha. This indicates that the presence of naturally rare species (\leq 1 trees ha⁻¹) in the PEIC plot is not merely a sampling artifact. Therefore, the 10.24-ha plot was appropriate to describe the composition of the studied HRF, but it was insufficient to characterize the population structure of rare species. Anyhow, these results indicate the use of contiguous plots of at least 6 ha to properly assess species richness and composition of HRF on similar soils.

Forest structure - The PEIC plot had a density similar to other non-HRF Atlantic Forest sites (Melo 2000, R.A.F. Lima, unpublished data) but with less basal area. In addition, among the other 42 sites consulted (*e.g.* Phillips *et al.* 1994; Losos *et al.* 2004), only four had basal areas smaller than the one found here, three of them also being found on white-sand soils. This result corroborates the connection between forest structure and soil properties suggested by Phillips *et al.* (1994) and Uhl & Murphy (1981). The pattern found here was also found by other authors when comparing white-sand forests to other types of tropical forests (Proctor *et al.* 1983; Davies & Becker 1996; Nebel *et al.* 2001; Miyamoto *et al.* 2003) and it is primarily due to the higher proportion of trees < 10 cm dbh and to the smaller proportion of large trees. In the PEIC plot the mean number of trees \geq 60 cm dbh per hectare was six, whereas in other forest types it varied between eight and 33 trees (mean \pm sd: 19 ± 7 , Losos *et al.* 2004). Three factors are probably impeding species to attain large sizes: low soil fertility, higher light availability at ground level, which may induce individuals to cease vertical growth earlier, and lower potential size of *Restinga* species (Luizão *et al.* 2007; Scarano 2009). Future studies monitoring *Restinga* species growth controlling these three factors would be particularly useful to better understand the mechanisms giving rise to structure in such forests.

The considerable change in species rank order among size classes, including changes in the most abundant species in the sample, confirms that the contribution of a given species also depends on the tree-diameter cutoff (Valencia *et al.* 2004; Kenfack *et al.* 2007). And these changes are not related exclusively to the presence of small-sized species in the understory. Different from expected, almost one third of the species did not have a constant decrease in the number of individuals with an increase in diameter. This result may be a remnant of recent successional changes in the community. For instance, species that had peaks of density in larger size classes (*e.g.* *Ternstroemia brasiliensis*, *Ocotea pulchella*, *Myrcia ilheosensis*, *Ilex theezans*) are also abun-

dant in forest borders or in younger successional stages of *Restinga* vegetation of PEIC (Sugiyama 1998). On the other hand, species that had densities more constant among size classes were often emergent tree species (e.g. *Calophyllum brasiliense*, *Albizia pedicellaris*, *Manilkara subsericea*), which may have regeneration strategies different from other species, including different mortality and growth rates and/or seed production strategies (Clark & Clark 1987; Swaine & Hall 1988). So, the successional stage of the community (i.e. age of the substratum) and the regeneration strategies of its species are perhaps the two main determinants of the vertical composition and structure of HRFs.

Multi-stemmed individuals

The occurrence of multi-stemmed individuals has been noted by different authors as a common feature of *Restinga* species (Sugiyama 1998; Guedes *et al.* 2006) and as an important regeneration mechanism in *Restinga* forests (Assumpção & Nascimento 2000). Indeed, 74% of the species showed at least one multi-stemmed individual in the PEIC plot, a proportion that was higher than the one found for three other types of tropical forests of southeastern Brazil (ca. 44 – 68% – Lima *et al.*, unpublished data). Nevertheless, the total number of multi-stemmed individuals was quite close to the numbers obtained for these forests, showing no evidence that this phenomenon is more common in the HRF tree individuals. Why there would be more species with multi-stemmed individuals in the HRF than in other comparable types of forest remains unclear.

There was evidence that the average abundance of species with more multi-stemmed individuals was larger than other species, suggesting that this trait may influence species survival. For instance, a larger number of stems per individual may be beneficial in terms of light interception efficiency and survival after physical damage, an advantage which is well documented for species able to survive and resprout after being damaged (Paciorek *et al.* 2000; Martini *et al.* 2008). However, among the ten most abundant species in the plot ($n > 400$) only three had a greater number of stems than expected. Hence, the ability to produce multi-stemmed trees is not mandatory for successful establishment, at least in terms of density. In addition, resprouting after damage is not the only reason why individuals have more than one stem. Multi-stemmed individuals, for instance, may be linked to a higher availability of light that would stimulate a premature ramification. In any case, our prediction is that species with a high proportion of multi-stemmed individuals would show a smaller number of stems per individual in shaded environments. And if the species also have a lower density of individuals, then we could start to infer about the competitive benefits of multi-stemmed individuals.

Spatial distribution

Although some studies indicate that species' dispersion patterns are predominantly aggregated (e.g. Armesto *et al.* 1986), there is little information on multi-species patterns

of dispersion at different scales. Li *et al.* (2009) found that 92% of species were aggregated at scales < 50 m, and Condit *et al.* (2000) found similar results for scales < 30 m. These scales correspond to our patterns B and C, but in the PEIC plot 25% of the most abundant species were aggregated at scales > 70 m. Clumped distributions are generally the result of association to discrete habitats, patterns of seed dispersal, interspecific interactions (e.g. competition, facilitation), and/or expanding or contracting distributions (Hutchings 1997; Valencia *et al.* 2004; Law *et al.* 2009; Li *et al.* 2009), whereas large clumps can be related to environmental heterogeneity. In the PEIC plot, species distributed over large patches (patterns C and D) suggested species associated with habitat, probably soil. Species with distributions practically opposite in respect to particular places were relatively common and intriguing (e.g. *Ocotea pulchella* and *Ternstroemia brasiliensis*). Such places may indicate (un)favorable abiotic conditions where more stress-tolerants do well, or where more competitive species (e.g. ground bromeliads) may exclude others. Or it may indicate an association with resource availability (nutrients or light). It is noteworthy that similar distribution patterns can be generated from different mechanisms (Harms *et al.* 2001).

In forests with restrictive soil conditions, such as the HRF, patterns of aggregation are particularly interesting. Higher aggregation in the larger size classes, for instance, would indicate a greater degree of habitat association (Condit *et al.* 2000). Examples of this result in the PEIC plot are *Myrcia racemosa* and *Myrcia multiflora*. The opposite could indicate dispersal-limited species, such as *Byrsonima ligustrifolia* and *Ilex theezans*. Although the number of individuals in the larger size classes was limited to properly assess such processes, this approach should be extended to a larger number of species, perhaps including individuals < 4.8 cm dbh. Condit *et al.* (2000) suggested that changes in the patterns of aggregation among size classes are small (although the proportion of species with significant values of aggregation presented by these authors was considerably lower for $\text{dbh} \geq 10$ cm). Examples from other types of forests also suggest that the abiotic conditions are not able to explain the distribution of the majority of forest species (Harms *et al.* 2001; Valencia *et al.* 2004). Nevertheless, in the PEIC plot we believe that there is a higher degree of habitat association, particularly regarding the type of soil, flooding regime, and canopy gap distribution that combined generate very distinct habitats for tree establishment.

Concluding remarks

The structural features observed in the Atlantic HRF were very close to those found for other white-sand forests around the world. Common in South America and Asia, and known by several local names (e.g. *heath forests*, *campinaranas*, *kerangas*, *varillal alto* – Anderson 1981), white-sand forests develop on acid, sandy soils with low availability of nutrients (Proctor *et al.* 1983; Ashton 2004; Luizão *et al.* 2007). These features act simultaneously to

generate forests whose characteristics are shorter stature, lower species diversity, and roots more concentrated in the superficial soil horizons (Davies & Becker 1996; Miyamoto *et al.* 2003; 2007). For these reasons, we recognize the Atlantic HRF as a type of white-sand forest. Although forest structure and probably functioning are similar among white-sand forests, species composition seems to be linked to local biogeographical issues. This is in accordance with the Walter's biome classification (Walter 1986), in which the HRF should be classified as a Psammobiome I, *i.e.* a pedobiome within the Tropical Rain Forest Zonobiome, which is functionally and structurally determined by the sandy soil condition. Finally, we do believe that this similarity may be extended to other Neotropical forests over white-sand soils, such as the Brazilian *muçunungas* (Simonelli *et al.* 2008) or the 'river' HRF of Peru (Nebel *et al.* 2001).

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