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Habitat specialization and phylogenetic structure of tree species in a coastal Brazilian white-sand forest

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Abstract

Aims

The coastal Brazilian rainforest on white-sand (restinga) ranks among the most fragmented forest types in the tropics, owing to both the patchy distribution of sandy soils and widespread coastal development activities. Here we study the environmental and evolutionary determinants of a forest tree assemblage at a single restinga forest in Southeastern Brazil. We also explore the ability of competing hypotheses to explain the maintenance of species diversity in this forest type, which includes contrasting extremes of edaphic conditions associated with flooding stress.

Methods

The study was conducted in a white-sand forest permanent plot of 10.24 ha on the coastal plain of Southeastern Brazil. This plot was divided into 256 quadrats of 20 × 20 m, which were classified into two main edaphic habitats (flooded and drained). Trees with a diameter ≥1 cm at breast height were identified. We assembled DNA sequence data for each of the 116 morphospecies recognized using two chloroplast markers (*rbcL* and *matK*). A phylogenetic tree was obtained using the maximum likelihood method, and a phylogenetic distance matrix was produced from an ultrametric tree. We analyzed similarity in floristic composition and structure between habitats and related them to cross-plot distances using permutation procedures. Null model torus shift simulations were performed to obtain a statistical significance level for habitat association for each species. The phylogenetic structure for the two habitats and for each 20 × 20 m quadrat was calculated using the mean phylogenetic distance weighted by species abundance and checked for significance using the standardized effect size generated by 5000 randomizations of phylogenetic tip labels.

Important Findings

Our results indicate that partitioning among edaphic habitats is important for explaining species distributions and coexistence in restinga forests. Species distributions within the plot were found to be non-random: there was greater floristic similarity within than between habitats, and >40% of the more abundant species were positively or negatively associated with at least one habitat. Patterns of habitat association were not independent of phylogenetic relatedness: the community was overdispersed with respect to space and habitat type. Closely related species tended to occur in different habitats, while neighboring trees tended to belong to more distantly related species. We conclude that habitat specialization is important for the coexistence of species in restinga forests and that habitat heterogeneity is therefore an essential factor in explaining the maintenance of diversity of this unique but fragile and threatened type of forest.

Keywords: habitat association, torus-translation test, phylogenetic community structure, niche partitioning, edaphic condition

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INTRODUCTION

Tropical forests harbor a large number of tree species. Understanding the underlying processes driving the origin and maintenance of this extraordinary diversity remain a central goal in tropical biology (Brokaw and Busing 2000; Chave *et al.* 2004; Denslow 1987; Dobzhansky 1950; Grubb 1977). Ecologists need to understand how nearly 300 tree species that require the same set of resources in similar ways can coexist within a hectare (Oliveira and Mori 1999; Valencia *et al.* 1994).

Habitat specialization to environmental conditions is one of the earliest-described and best-documented hypotheses proposed to explain the diversity of tree species in tropical forests (Ashton 1969; Brown *et al.* 2013; Condit *et al.* 2002, 2013; Humboldt and Bonpland 1815; Richards 1952). Tree species show spatial associations with soil and topographic conditions, sometimes at scales of only several meters (Clark *et al.* 1999; Davies *et al.* 1998; Harms *et al.* 2001; Valencia *et al.* 2004), and soil resource availability may also determine the distribution of tree species according to their functional traits (Katabuchi *et al.* 2012). Such patterns of habitat association have been traditionally linked to niche differentiation (Ashton 1969; Pacala and Tilman 1994; Silvertown 2004). However, two different niche-based processes may result in habitat association: habitat filtering and limiting ecological similarity. Habitat filtering is the process by which species occurrences are determined by their ability to establish, grow and reproduce in particular abiotic conditions (Keddy 1992). In contrast, similar species can strongly compete for resources in such a way that ecological similarity could be limited and lead to a shift in ecological strategies, such as differences in habitat preferences (MacArthur and Levins 1967; Pacala and Tilman 1994). Different patterns of species coexistence in a community are expected depending on the relative importance of these processes. We expect the coexistence of ecologically similar species if habitat filtering is stronger or the coexistence of ecologically different species if competition is more important. However, associations of species occurrence with habitat can be interpreted as the result of either one of these processes when the ecology of the species is poorly known (Brown *et al.* 2013; Condit *et al.* 2013; Jabot *et al.* 2008; Kraft *et al.* 2008; Tuomisto *et al.* 2003). Assessing phylogenetic relationships among species in a community may help us to distinguish between these processes (Kraft *et al.* 2007; Webb *et al.* 2002).

Phylogenies provide information about the degree of relatedness of species in a community; they permit the assessment of patterns of trait evolution and hence, of the importance of niche-based processes in determining community structure. The phylogenetic structure of a community may be clustered or overdispersed, reflecting that species that co-occur are respectively more closely or more distantly related than expected with respect to the phylogeny of the regional species pool. Absence of phylogenetic structure suggests that phylogenetic distances among species in the community are not different from those of assemblages randomly drawn from the species pool (Mouquet *et al.* 2012; Webb *et al.* 2002). Assuming conservatism of ecological traits (i.e. closely related species tend to have similar niches), phylogenetic clustering is often interpreted as evidence of habitat filtering, a process by which species with similar niches are clustered in the environmental conditions to which they are adapted. The opposite pattern, i.e. phylogenetic overdispersion, can be interpreted as a consequence of biological interactions (e.g. competition) that limit the similarities between species and favor the coexistence of species with different ecological strategies (Webb *et al.* 2002). Although a lack of conservatism or lability in functional traits in the regional species pool may change the interpretation of the processes behind the phylogenetic community structure (Losos 2008; Mouquet *et al.* 2012), the premise of niche conservatism has gained support from phylogenetic studies of both animals and plants (see Webb *et al.* 2002) and a recent study using 17 functional traits for 4672 individuals from 668 tropical tree species (Baraloto *et al.* 2012). In this study a molecular phylogenetic tree based on DNA sequence of two plastid loci (*rbcL* and *matK*) suggested that phylogenetic distances provide information on niche overlap in tropical tree communities.

The use of phylogenetic information has brought new interest to community forest assembly studies in the tropics. Some studies have found that habitats may have different phylogenetic structures, with different niche processes acting more strongly in each of them (Ding *et al.* 2012; Kembel and Hubbell 2006; Kraft and Ackerly 2010; Kress *et al.* 2009; Pei *et al.* 2011). Successional forests in Costa Rica, e.g. show variation in the phylogenetic overdispersion intensity at multiple scales (Letcher 2010), supporting a forest succession model. This model predicts a prevalence of stochastic (i.e. dispersion) and habitat filtering processes at early successional stages and shifting to a prevalence of biotic interactions at later stages (Chazdon 2008). In contrast, a study of a gradient of precipitation and soil in French Guiana found an aggregated phylogenetic community pattern, suggesting that habitat filtering is a major process of community assembly in this tropical forest (Baraloto *et al.* 2012). Similarly, the phylogenetic structure of tree communities in the Northwest of South America is related to the degree of seasonal flooding and precipitation, with the more stressful environments showing stronger phylogenetic clustering (González-Caro *et al.* 2014).

Areas of sandy soils associated with Quaternary marine regressions along seashores in Southeastern Brazil create strong gradients associated with edaphic conditions (Gomes *et al.* 2007; Scheel-Ybert 2000) and are subject to recent plant colonization and primary succession. These sandy coastal plains are covered with a mosaic of vegetation types varying from sparse herbaceous communities to scrublands and tall forests (Lacerda *et al.* 1993). The forests associated with this system grow in poor edaphic conditions (i.e. low nutrients, flooding or poor water retention) and are considered marginal

to Atlantic rain forests that occur on more clay- and nutrient-rich soils. Despite the different edaphic conditions, the restinga forest shares most of its species with other Atlantic forest formations (Bergamin *et al.* 2012; Scarano 2002) but is less diverse (Marques *et al.* 2010) and contains more locally dominant species (Bergamin *et al.* 2012). Previous studies have shown that restinga forests contain a large proportion of tree species with spatially aggregated populations (Lima *et al.* 2011), with edaphic associations (Magnago *et al.* 2012) and differential plant establishment related to flooding gradients (Scarano 2006; Scarano *et al.* 1997).

Here we investigate the spatial patterns of tree populations in a 10.24-ha restinga forest plot with respect to edaphic habitat specialization and phylogenetic structure. First, we analyze the importance of edaphic conditions for species distributions. Then, we assess the relationship of the patterns of species associated with edaphic habitats to the phylogenetic structure of this forest community. Habitat differences are based on the degree of exposure to flooding, which imposes root anoxia, a strong constraint on tree species establishment and growth (Scarano 2006). We hypothesize that (i) species distribution and community composition are related to edaphic conditions; (ii) habitat filtering is more important than limiting similarity in these limiting soil conditions; and (iii) the more heavily flooded habitat acts as a stronger ecological filter to species composition.

MATERIALS AND METHODS

Study site and plot tree census

This study was conducted in a 10.24-ha (320 × 320 m) permanent plot (25°04′41″S and 47°55′53″W) at the Parque Estadual da Ilha do Cardoso, a 13 500-ha continental island located near the southern tip of São Paulo State, Brazil. The Island is separated from the mainland by a small channel of <100 m at the closest point. The climate is tropical with a mean annual temperature of 22.4°C, mean minimum temperature of the coldest month of 12.6°C and average annual precipitation of 2261 mm with only 1 month (August) with average monthly precipitation falling <100 mm. The permanent plot was established between 2002–04 in flat terrain (3–8 m above sea level, a.s.l.) on a young marine sandy geological deposit of approximately 3000–5000 years (Gomes *et al.* 2007). The vegetation in the plot is tall restinga forest, which was described in detail by Lima *et al.* (2011). In this study, we used data from the 2009 census, which follows the Center for Tropical Forest Science protocols (Condit 1998), including all individual trees and shrubs with stem diameter at breast height ≥1 cm.

Characterization of edaphic habitats

In general, the soils in the plot have a high content of fine sand and are unconsolidated. The higher elevation areas (5–7 m a.s.l.) within the plot are well drained but may occasionally be flooded for short periods during heavy rains. These areas are associated with a thicker and darker podsol layer and are the older and more weathered marine deposits in the region (ca. 5000 years before present, y.b.p.). They are here referred to as the 'Drained habitat' (DH). The 'Flooded habitat' (FH) dominates the northern part of the plot and is characterized by the lowest elevations (ca. 3 m a.s.l.), youngest soils (ca. 1600 y.b.p.), and the lack of a podsol layer. In the more convex topography, such as in the southern portion of the plot, the soils have a thicker organic surface layer and are referred to as the 'Humic habitat' (HH). The Humic and FH are strongly associated with poorly drained areas that experience the highest intensity of waterlogging. The plot area was divided into 256 quadrats of 20 × 20 m and all quadrats were assigned into one of the three edaphic habitats (Fig. 1). Quadrats with <70% of the area classified as a single habitat were considered transition zones and were not considered in the habitat association analyses. Because the HH contributes only 7% of the plot area (Table 1) we focused on the two main habitat types, i.e. the extremes of the edaphic gradient in the plot. Both edaphic habitat types are strongly correlated with elevation, seeing that pedogenesis in restingas is tightly associated with the shallow water table and flood regime (Gomes *et al.* 2007).

Phylogeny

We collected fragments of tissue (ca. 10 cm^2) and herbarium samples (vouchers can be found at the ESA herbarium), one to three individuals per morphospecies, from trees sampled at random in the plot. We assembled DNA sequence data for each of the 116 species of vascular plants previously found in the plot (Lima *et al.* 2011) using two chloroplast markers: *rbcL* (5-end fragment of the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit gene) and *matK* (maturase K-like gene). Most of the sequences were produced using Sanger sequencing (ABI3730, Applied Biosystems, Foster City, CA, USA) from DNA extracted from trees tagged in the plot (Table S1, see online supplementary material), but for some species we complemented these by accessions from other sources (Table S2, see online supplementary material). For primers and sequencing details, see Gonzalez *et al.* (2009) and Dunning and Savolainen (2010). A multiple alignment was generated using MAFFT (http:align.bmr.kyushu-u.ac.jp/mafft). The aligned matrix consisted of 1346 bp, 690 for the *matK* and the rest for the *rbcL* region. Because both markers are from the chloroplast genome, they were treated as a single partition. The GTR+I+G model of evolution was selected for this dataset using jModelTest (Posada 2008), and a phylogenetic analysis was performed by Maximum Likelihood using the PhyML software (Guindon *et al.* 2010). We used *Selaginella uncinata* as an outgroup for rooting the tree because the plot includes one gymnosperm (*Podocarpus selowii*) and one tree-fern (*Cyathea microdontha*). To obtain an ultrametric tree we produced a chronogram using Penalized Likelihood implemented by the function *chronoPl* of package ape in R (Paradis *et al.* 2004) with the parameter lambda set to 0.

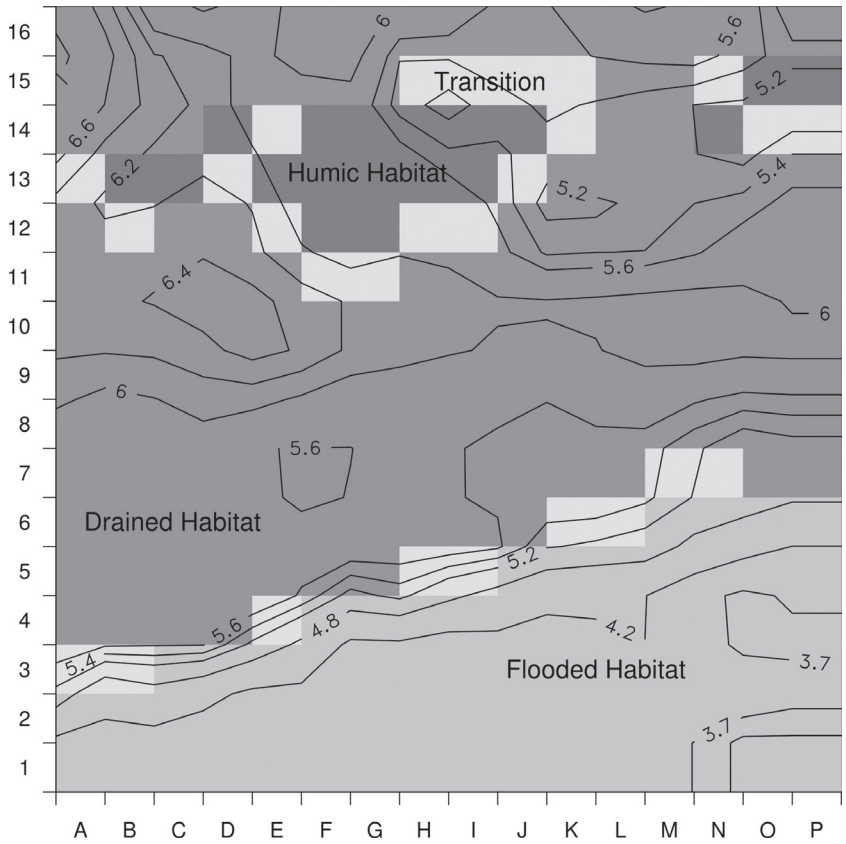

Figure 1: habitat classification based on edaphic conditions in the Parque Estadual da Ilha do Cardoso Plot. Transition type was defined as a quadrat characterized by <70% of a single edaphic type. Lines represent topographic levels.

Table 1: description of edaphic habitats

	Drained	Flooded	Humic	Transition	All habitats
Number of quadrats	143	68	18	27	256
Area (ha)	5.72	2.72	0.72	1.08	10.24
Number of trees	23236	9219	3254	4379	40088
Density (ha^{-1})	3669–4418	3120–3629	4159–4793	3690–4390	3533–4256
Richness (# sp/ha)	98–110	99–109	95–103	96–103	101–112

Tree density and species richness per hectare were calculated from the simulation of 25 random sample quadrats with replacement. Values represent the 95% confidence interval limits from 5000 simulations.

Statistical analyses

Species assemblage. We analyzed similarity of floristic composition and structure of habitats and related them to the cross-plot distance using the procedure described in Valencia *et al.* (2004). First we calculated the Sorensen quantitative similarity index, which incorporates abundance data (Magurran 2004) for each of the 32640 pairs of the 256 20 × 20 m quadrats in the plot and the distance between them. To compare habitats we calculated the mean similarity within and between habitats in the range of 60–200 m distance where the impact of distance on similarity was slight. We used a jackknife re-sampling approach to generate confidence intervals for these mean similarities, taking a random sample of 128 from the 256 quadrats without replacement, and repeated the procedure 1000 times.

Habitat community similarity. Habitat association was investigated using a null simulation that explicitly incorporates spatial autocorrelation, eliminating the need to assume independence among stems and keeping intact critical properties of the spatial structure of both the habitats and plant populations (Harms *et al.* 2001). The randomization

algorithm comprises the following steps: (i) the habitat map was shifted by 20 m along both the x and y coordinates and the species map remained fixed; (ii) strips of quadrats moved beyond a border of the plot were placed inside the opposite border; (iii) for each shift, the relative density of the species in each habitat was re-calculated; (iv) steps one to three were repeated until the habitat map returned to the original position; and (v) the observed species density in each habitat was then compared with the distribution of densities generated by the shifted maps. To increase the number of simulations, we used three other base habitat maps following Harms *et al.* (2001): (i) mirror, (ii) rotated and (iii) mirror and rotated. This approach increased our number of simulations to 1024 without changing the spatial structure of the habitats. We considered positive associations significant when 95% of the simulated values were smaller than those observed and negative habitat associations significant when 95% were larger than the observed values.

Phylogenetic structure. We first produced a phylogenetic distance matrix from the ultrametric tree generated using the *cophenetic* function from the ape package (Paradis *et al.* 2004). This procedure computes patristic distances (the sum of the lengths of the branches separating two tips) between all pairs of tips in the phylogenetic tree. We then analyzed the phylogenetic structure for the two main habitats (DH and FH) and for each 20×20 m quadrat by calculating the mean observed phylogenetic distance (MPD) weighted by abundance. We checked for significance using the standardized effect size (SES), i.e. the difference between the observed MPD and mean MPD generated by 5000 randomizations of taxa labels in the phylogenetic distance matrix in a scale of standard deviation of the pseudovalues of the MPD. This test determines whether and which quadrats are phylogenetically clustered, overdispersed or not structured (Webb 2000). We used the same procedure to test for phylogenetic structure within the main habitats using the whole list of species and abundances in each main habitat (DH and FH) as a community entry to calculate the MPD. Because the net relatedness index, a common metric used in community phylogenetic studies, is equal to −1*SES (Kembel *et al.* 2010), we report only the SES. Analyses were performed using the picante package (Kembel *et al.* 2010) in R.

RESULTS

Phylogenetic tree

The phylogenetic tree reconstruction based on the plastid gene regions *rbcL* and *matK* yielded a phylogenetic hypothesis that is consistent with the known relationships for the angiosperms (Fig. 2) with two exceptions: (i) the Chloranthaceae was placed as a sister clade to the monocots instead of within the magnoliids, but this lacks support and (ii) the dicots in the old sense appeared as monophyletic with high support despite having a very short branch (see phylogram in Fig. S1, see online supplementary material). The phylogenetic community structure is sensitive to the more recent relationships, i.e. those placed towards the tips of the tree, and these incongruences with the current angiosperm consensus phylogeny (Soltis *et al.* 2011) are for very deep nodes and have little impact on changing the relative phylogenetic distances among species.

Habitat community similarity

The two main habitat types, Flooded (FH) and Drained (DH), correspond to 82.4% of the entire plot area. Only a small portion of total plot area was classified as an HH (7.0%), and the remaining quadrats (10.5%) were transitional forest (Fig. 1 and Table 1). The species density between habitats did not differ significantly but FH tended to support fewer trees (Fig. 3).

Quadrats that are closely located (up to 40 m) were more similar in floristic composition and structure (Fig. 4), and as expected, the mean Sorensen similarity index showed more within- than between-habitat similarity at all scales inside the plot. The within-habitat mean similarity between 60 and 200 m for DH (0.484±0.018) did not differ from the mean similarity inside the FH (0.480±0.013), but both were larger than the mean similarity between habitats (0.423±0.019).

Habitat associations

Of the 116 morphospecies identified in the plot, 99 had at least 20 individuals and these were included in a more detailed analysis of habitat association. We found that 52 of these 99 species (52.5%) displayed significant habitat associations, with 19 (19.2%) species positively associated and 14 (14.1%) species negatively associated with the FH. In contrast, 10 (10.1%) showed positive and 20 (20.2%) showed negative associations with the well-drained habitat. Several species had opposite associations between DH and FH: of 23 species, 16 were positively associated with DH and negatively associated with FH, and 7 species showed the opposite pattern (Table 2). All species positively associated with DH have densities at least 2.4 times greater in DH than in FH, and for two of these species the difference was 5-fold greater in DH: *Blepharocalyx salicifolius* (9.1×) and *Miconia cubatanensis* (5.9×). In contrast, 12 species had a 3-fold greater tree density in FH than in DH, and nine of these had a 5-fold greater density in FH: *Mollinedia schottiana* (15.0×), *Tibouchina trichopoda* (12.9×), *Tabebuia cassinoides* (12.1×), *Marlierea racemosa* (10.1×), *Eugenia neoglomerata* (6.1×) *Hedyosmum brasiliense* (6.0×) *Astrocaryum aculeatissimum* (5.5×), *Guarea macrophylla* (5.3×) and *Miconia chartacea* (5.0×).

Habitat phylogenetic structure

When the whole habitat community was considered, the MPDs for both habitat classes were very similar and were both significantly larger than expected (MPD_{DH} = 1.321, SES_{DH} = 2.137, P_{DH} = 0.022; MPD_{FH} = 1.318, SES_{FH} = 2.064, P_{FH} = 0.024). The average MPD (± standard deviation) for the 256 quadrats was 1.286±0.035; only one quadrat had a

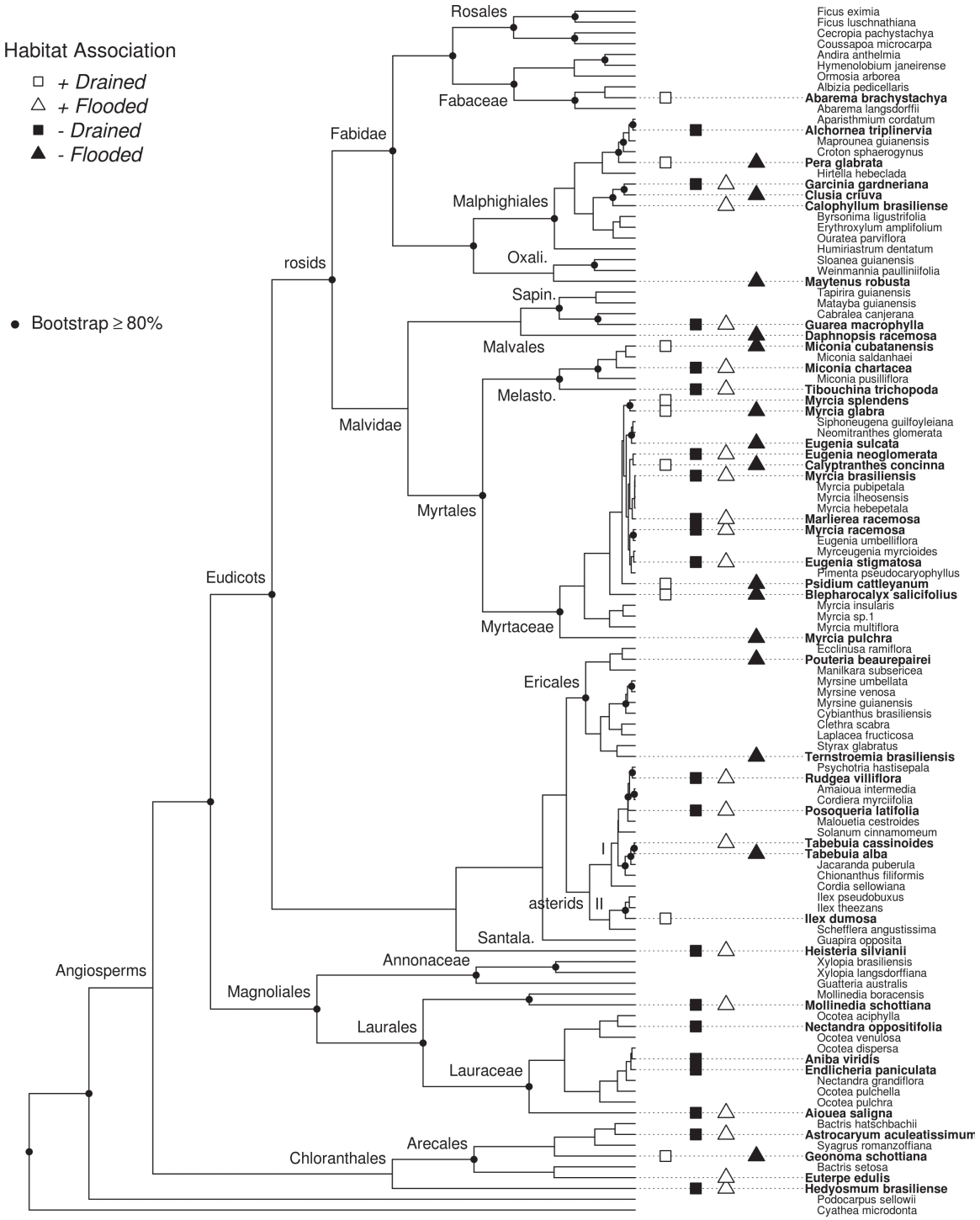

Figure 2: phylogenetic tree based on two chloroplast markers (*rbcL* and *matK*) and species habitat associations (bold tips).

smaller MPD than the average MPD simulated by the null model, and the difference was not significant. The mean MPD for the DH and FH quadrats were almost identical to the overall mean, 1.286 for the FH and 1.285 for the DH quadrats. The observed MPD was significantly greater than the mean distance produced by the null model for 24.6% of the 65 FH quadrats and for 24.0% of the 146 DH quadrats. All other quadrats, 75.4% in FH and 76.0% in DH, could not be distinguished from phylogenetically random communities generated by the null model (Fig. 3). Nevertheless, the bootstrap confidence interval (99%) of the mean SES per quadrat in FH (1.46–1.68) and in DH (1.43–1.63) did not reach zero. These

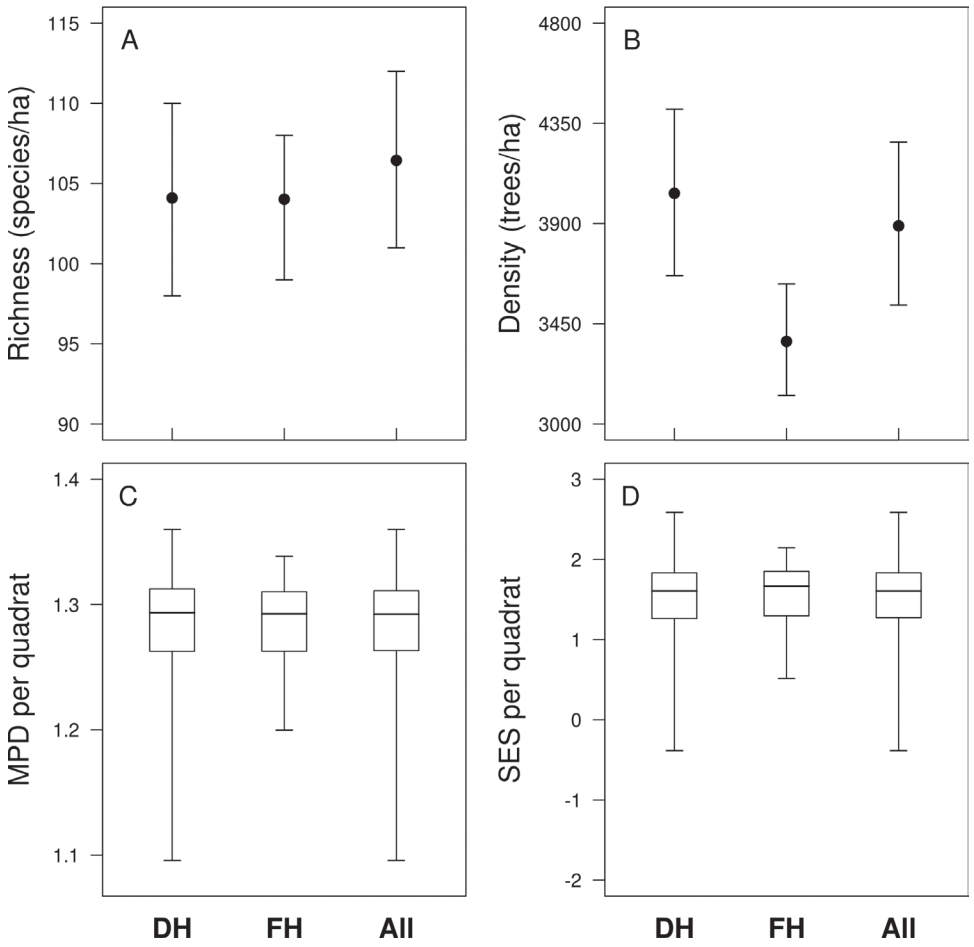

Figure 3: richness and phylogenetic structure of the sampled restinga tree community. Means and 95% confidence intervals of number species (**A**) and of tree density (**B**). Quadrats (20 × 20 m) quantile distribution for MPD (**C**) and for MPD SES (**D**). Means and confidence intervals in (A) and (B) were built using a bootstrap approach re-sampling 25 quadrats 5000 times. FH: flooded habitat; DH: drained habitat; All: both habitats.

results show that phylogenetic overdispersion was detected at both scales in the plot: (i) at the entire habitat scale and (ii) within quadrats of each habitat. This highlights that co-occurring species are phylogenetically more distantly related than expected. At the same time, species that occur in the same habitat, but not necessarily near each other, are also more distantly related than expected.

DISCUSSION

Our results indicate that habitat specialization related to edaphic habitats is important for explaining species coexistence in restinga forests. First, we found that species distributions within the plot are not random. There was greater floristic similarity within than among habitats, and half of the more abundant species were positively or negatively associated with one of the two main habitat types. Second, the patterns of habitat associations were not independent of phylogenetic relatedness; the community is overdispersed with respect to space and habitat type, i.e. closely related species tend to occur in different habitats and trees in close proximity belong to more distantly related species. These results indicate that habitat specialization is important for species coexistence in restinga forests and that edaphic habitat heterogeneity promotes diversity in such forests.

Contrary to expectation, we found no or only weak indication that the more stressful habitat (FH) is a stronger ecological filter than the less stressful one. Species diversity and within-habitat floristic variation did not differ between habitats, although there was a slight tendency for greater species composition heterogeneity in the less stressful habitat as the scale increases. At the scale analyzed in this study, the pattern of greater similarity at small scales could have been generated by dispersal limitation processes. From another standpoint, flood tolerance, both to waterlogging and submergence, requires adaptations (e.g. carbohydrate reserves) to cope with conditions that may result in death for the majority of plant species, e.g. through the reduced energy production caused by anoxia in plant tissues (see Parolin and Wittmann 2010). In Amazonian flooded forests, species substitution along flooding gradients has been viewed as the result of a process of continuous adaptations along the gradient from the more

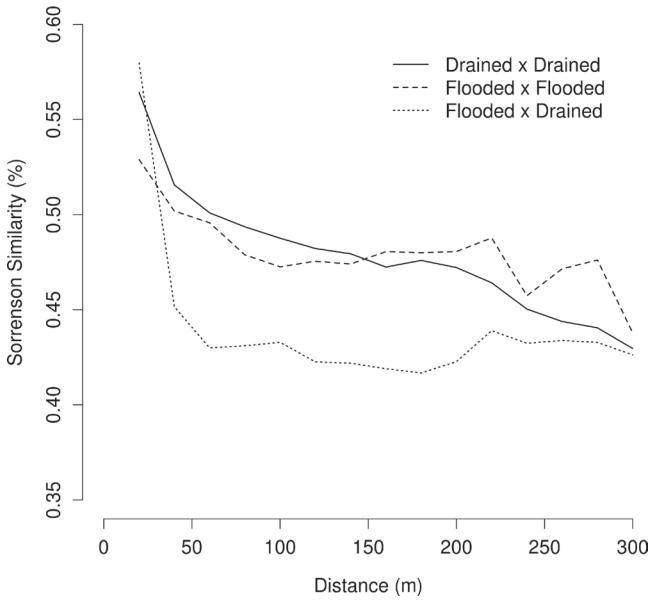

Figure 4: main within- and between-habitat floristic similarity based on the quantitative Sorensen index. The index includes all trees and shrubs of >1 cm diameter at breast height in quadrats of 20 × 20 m at the Ilha do Cardoso Permanent Plot.

suitable and diverse habitat (*terra firme*) to the more stressful and less diverse habitat (*low igapó*) (Kubitzki 1989; Wittmann *et al.* 2011). We found no difference in species diversity and habitat variation between the two main habitats, despite the difference in flooding conditions. This may be related to other soil properties not measured in this study, such as fertility, which may counterbalance the negative effects of flooding, as reported for a white-sand forest in the Amazon region (Damasco *et al.* 2013). In addition, the soil in the whole plot is extremely nutrient-poor (oligotrophic) white-sand; therefore, the difference in flooding may not lead to great differences in stress for plant growth and establishment.

Nonetheless, the two main habitats have different species assemblages, and at least half of the more abundant species prefer one or the other habitat class. These findings are concordant with similar analyses conducted in other tropical forest plots with substantial local habitat heterogeneity (Comita *et al.* 2007; Gunatilleke *et al.* 2006; Itoh *et al.* 2010; Valencia *et al.* 2004) and confirm the importance of edaphic variation in explaining the spatial occurrence of many tree species. Differing species compositions in different edaphic conditions indicate that habitat variation is important in promoting diversity (Tuomisto *et al.* 2003, 1995), as beta diversity increases with increasing edaphic heterogeneity.

Our phylogenetic results indicate that closely related species prefer different habitats, suggesting that habitat specialization is an important process in structuring restinga forests. The species in the plot are an assemblage of many lineages of angiosperms, and sister-species pairs with opposite habitat preferences are scattered through the plot phylogeny. There is great diversity in the evolutionary responses to waterlogging and/or submergence in plant lineages (Parolin and Wittmann 2010), and thus adaptive transitions may occur from different genetic backgrounds. However, the phylogeny is incomplete

Table 2: tree density (ha^{-1}) for the whole plot and for each edaphic habitats

	Habitat types		
	Drained	Flooded	Whole plot
Abarema brachystachya	7.0^{+}	2.6	5.0
Aiouea saligna	6.5^{-}	10.3^{+}	8.7
Alchornea triplinervia	5.9^{-}	8.5	7.5
Aniba viridis	22.2^{-}	35.3	31.10
Astrocaryum aculeatissimum	3.8^{-}	21.0^{+}	8.2
Blepharocalyx salicifolius	16.8^{+}	1.8^{-}	11.4
Calophyllum brasiliense	42.5	47.1^{+}	43.7
Calyptranthes concinna	84.4^{+}	29.0^{-}	66.9
Clusia criuva	14.7	3.7^{-}	11.1
Daphnopsis racemosa	9.6	2.6^{-}	8.3
Endlicheria paniculata	38.6^{-}	52.9	48.0
Eugenia neoglomerata	1.7^{-}	10.7^{+}	5.0
Eugenia stigmatosa	25.9^{-}	56.2^{+}	37.5
Eugenia sulcata	44.2	20.2^{-}	36.9
Euterpe edulis	385.1	505.1^{+}	408.6
Garcinia gardneriana	48.3^{-}	145.2^{+}	94.1
Geonoma schottiana	304.9^{+}	112.9^{-}	233.1
Guarea macrophylla	12.6^{-}	67.3^{+}	35.5
Hedyosmum brasiliense	1^{-}	6.2^{+}	3.7
Heisteria silvianii	20.1^{-}	34.9^{+}	25.7
Ilex dumosa	36.7^{+}	14.3	27.5
Marlierea racemosa	13.1^{-}	133.1^{+}	62.0
Maytenus robusta	72.6	21.7^{-}	60.70
Miconia chartacea	4.4^{-}	22.1^{+}	9.80
Miconia cubatanensis	86.4^{+}	14.7^{-}	61.20
Mollinedia schottiana	2.6^{-}	39.3^{+}	17.40
Myrcia brasiliensis	16.4^{-}	29.4^{+}	22.30
Myrcia glabra	11.9^{+}	4.4^{-}	9.20
Myrcia pulchra	20.3	6.2^{-}	16.00
Myrcia racemosa	74.1^{-}	103.7^{+}	85.10
Myrcia splendens	25.3^{+}	7	18.20
Nectandra oppositifolia	1.4^{-}	5.1	3.90
Pera glabrata	272.7^{+}	111^{-}	215.10
Posoqueria latifolia	14.7^{-}	27.6^{+}	20.90
Pouteria beaurepairei	38.3	16.9^{-}	32.70
Psidium cattleyanum	28^{+}	10.7^{-}	23.20
Rudgea villiflora	18.2^{-}	44.1^{+}	25.20
Tabebuia alba	9.8	2.6^{-}	8.20
Tabebuia cassinoides	0.7	8.5^{+}	2.60
Ternstroemia brasiliensis	67.5	12.5^{-}	51.00
Tibouchina trichopoda	1.2^{-}	15.8^{+}	5.10

(+) and (−) signs indicate positive and negative associations based on torus-translation simulation with alpha = 0.05.

in that it does not include all the living close relatives of the plot species. It thus remains unclear whether the ancestors of the species pairs in the plot were white-sand specialists, whether the species with opposite habitat preferences in the plot are indeed sister species, or alternatively, whether they are more closely related to non-white-sand species. The strong pattern of the habitat divergence among close relatives seen in the plot may, therefore, be the result of competition related to the local ecological divergence of species that share a recent ancestor, or reflect ecological divergences under different evolutionary/ecological contexts.

While phylogenetic overdispersion was found in ~25% of the quadrats in our plot, in the remaining 75% of the quadrats the phylogenetic pattern could not be differentiated from a random pattern. A random pattern is expected when neutral processes are stronger than deterministic ones, or when different deterministic processes obscure patterns. However, not a single quadrat was phylogenetically clustered. One plausible hypothesis is that deterministic processes that could generate phylogenetic clustering are not important to the community assembly. This suggests that the assembly of restinga forests has some component of neutrality at the quadrat scale.

The restinga forest grows on a relatively recent substrate and very few plant species seem to be endemic to this vegetation type (Scarano 2002). Moreover, the characteristic tree species of restinga forests are locally abundant but also occur in other adjacent formations (Bergamin *et al.* 2012). These restinga forest indicator species have a broad geographic distribution (Bergamin *et al.* 2012) that is generally associated with broad ecological niches (Morin and Chuine 2006). In this sense, the assembly of the restinga tree community may be best seen as the result of immigration events from adjacent formations filtered by harsh environmental conditions (i.e. white-sand nutrient-poor soils). Our results suggest that both interactions and neutral processes may be important once this harsh ecological filter is passed. We observed greater similarity in species composition among quadrats at small scales (up to 50 m, essentially means adjacent quadrats), and this pattern may be produced by dispersal limitation, because the same species are found in neighboring quadrats. Our phylogenetic results indicate overdispersion at very small scales (within a quadrat), which could be produced by competition. In this way it is noteworthy that neutral (dispersal limitation) and deterministic (competition) processes could be acting simultaneously at the fine scale of this study.

Based on our results and evidence from other studies described above we propose a conceptual model for restinga forests in which the hierarchical importance of assembly processes change with the spatial scale: ecological filters are more important at the regional scale, mostly related to the harsh oligotrophic edaphic conditions in white-sand soils, whereas species interactions and neutral processes are more important at finer scales. A recent meta-analysis of plant community studies emphasizes the general importance of scale for assembly rules and supports the theoretical consideration that processes leading to assembly rules act at different scales for trees (Götzenberger *et al.* 2012). In our view, restinga is a promising system to reveal that theoretical consideration and to test the changes in assembly processes at different scales.

Stress gradient theory predicts that the balance between positive and negative interactions will change along an environmental gradient, with competition being more important at the more suitable extreme of the gradient (Bertness and Callaway 1994). Although white-sand soil and flooded forests are stressful habitats compared to other tropical forests, the restinga forest occurs in a somewhat more favorable part of the coastal plain gradient at the local scale (i.e. no salt spray, no extreme soil temperatures, no extremely young soils), and our findings do not counter this theory. In fact, Castanho *et al.* (2012) found facilitation between adult tree and seedling species in a more open physiognomy vegetation on the same island, suggesting a feedback process of facilitation between tree species along successional stages towards the development of the forest structure. Like competition, positive interspecific interactions may also favor phylogenetic overdispersion because plant–plant facilitation tends to occur between phylogenetically distant species (Valiente-Banuet and Verdú 2007; Verdú *et al.* 2009). A study of coastal dune plant communities across the globe found that phylogenetic clustering decreases along successional gradients from open to scrub-like vegetation structures (Brunbjerg *et al.* 2014). Future studies should examine the positive and negative associations between plants along a broader restinga gradient to assess how the balance of these interactions (i.e. net interactions) affects phylogenetic community structure. This will provide a better understanding of how these communities are assembled along broader environmental gradients and of the underlying evolutionary forces. That information shall also provide insights into the long-term successional dynamics of these forests, which may base management policies for this unique, fragile and threatened type of forest.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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