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Title: An endangered tree fern increases beta-diversity at a fine scale in the Atlantic Forest Ecosystem

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Highlights

- We demonstrate that a “heterogeneity enhancer” increase diversity in the Restinga, a stressful tropical ecosystem.
- Our results highlight the importance of evaluate the role played by individual species at different diversity scales.
- Plant-plant interactions may increase diversity.
- Conservation effort towards both the area and nurse species are crucial to maintaining plant diversity in Restinga forest.

Abstract

Some species make substantial contribution to habitat heterogeneity, supporting species coexistence. *Dicksonia sellowiana* Hook., an endangered tree fern, is a known phorophyte for epiphytes, has the potential to be such a taxon. We tested the hypothesis that *D. sellowiana* increases plant diversity in Brazilian Restinga forest, a biodiversity hotspot, by augmenting the habitat heterogeneity at a fine scale. To do this we quantified α-diversity and β-diversity in three habitat types: on the tree fern trunks, immediately beneath the trunks and away from the trunks. In total, 40 ferns were sampled. Overall we recorded 2602 individuals belonging to 61 phanerophyte species in 30 families. The number of individuals sampled varied among habitats but rarefaction showed that richness did not differ. In contrast, species composition varied markedly amongst habitats. Both statistical approaches detected high levels of β-diversity, particularly between the species found in the vicinity of the fern, and those in the samples away from the trunks. Indicator species analysis was used to identify the species characteristic of the different habitats. About 30% of the species were exclusively found in "away plots", 17% were exclusively "below plots" and 15% were found only on the trunks, 13% were found on the trunks and below them, 12% on "bellow" and "away plots", 10% of species occurred in all areas and 3% were found on trunks and "away plots". Our results lead us to conclude that the endangered fern *D. sellowiana* plays an important role in promoting habitat heterogeneity within the Restinga forest. As this iconic species is threatened, its overexploitation may lead to impoverishment of plant communities. Conservation effort towards both the area and this species are crucial to maintaining Restinga plant diversity.

Keywords: *Dicksonia sellowiana;* conservation; spatial heterogeneity; species coexistence; Restinga

1. Introduction

Structural elements of the landscape contribute to maintain biodiversity by promoting environmental heterogeneity and species coexistence (Fischer et al., 2006). This "keystone structure" varies at different scales between ecosystems: for instance, a river and a tree hollow both promote diversity by providing aquatic habitat (Gibbons and Lindenmayer, 2000; Tews et al., 2004; Fischer et al., 2006). All other things being equal, the expectation is that gamma diversity will be higher in more heterogeneous habitats (Mouquet et al., 2002). In this case, heterogeneity depends on the identities of the species present as well as on the physical environment. Some species are likely to make substantial contributions to habitat heterogeneity and as such should be conservation priorities (Mills et al., 1993; Fischer et al., 2006) – an especially urgent challenge when these taxa are themselves endangered. These species should be a priority focus for conservation strategies.

The Atlantic Forest is one of the 34 global "hotspots" of biodiversity because of its high degree of endemism, diversity and threats (Mittermeier et al., 2004). Its high biodiversity is partly related to the high environmental diversity (Silva and Casteleti, 2005), which in turn contribute to a wide variation in species composition, resulting in different vegetation types (Lautert et al., 2015). One of these vegetation types is the Restinga, which consists of pioneer and heterogeneous sandy coastal plain vegetation under marine influence (Scarano, 2002). This formation varies from shrub vegetation to closed forests, and is distributed over soil mosaics extending inland from the coastal zone (Lacerda et al., 1982). The Restinga vegetation is considered more stressful for its inhabitant plant species than the Atlantic Forest core, due to nutrient and water shortage (Scarano, 2009).

Under the limiting conditions of the Restinga forest, the tree fern *Dicksonia sellowiana* Hook. (Dicksoniaceae) is the most important phorophyte for several epiphytes and also support many other plant species growing on its trunk or settling successfully due to the availability of nutrients such as potassium (Fraga et al., 2008; Mielke, 2002; Martinelli and Moraes, 2013). For this reason, *D. sellowiana* has been historically exploited for landscaping and as a natural substrate for other plants (Cortez, 2001; Faria et al., 2001; Mielke, 2002). As a slow growing species, it takes around 50 years for an individual to reach the adult stage (Fernandes, 2000), making its cultivation an economically non-viable alternative according to harvesters (Martinelli and Moraes, 2013). Consequently, the continued indiscriminate exploitation means that this species is both nationally (MMA, 2014) and regionally (São Paulo, 2004) endangered. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) lists American populations of *Dicksonia* in Appendix II. Despite the illegality of exploitation and commerce, continuing indiscriminate exploitation and deforestation may cause its extinction in a near future (Martinelli and Moraes, 2013).

It is known that *D. sellowiana*, as other tree ferns (Medeiros et al., 1993; Gaxiola et al., 2008) and also some tree species (Dias and Scarano, 2007), acts as substrate for developing seedlings. However, whether this feature affects diversity patterns within the regenerating layer remains unknown. Thus, in this paper we test the hypothesis that *D. sellowiana* promotes habitat heterogeneity at a fine scale. We argue that this species has the potential to increase niche complementarity and support plant species coexistence by promoting environmental heterogeneity, thereby elevating local β-diversity. To test our hypothesis, we selected 3 habitat zones– 1) on the tree fern trunk itself, 2) below the tree fern trunks and 3) at a distance away from the trunks to provide a measure of species composition in the absence of possible influence of the existent tree ferns. We compared α-diversity (species richness) and β-diversity (species similarity) across these zones and ask if: (i) the flora found on the tree ferns trunks is different from the flora found on the ground below and away from the trunks; (ii) some plant species occur exclusively on the tree ferns; (iii) the presence of *D. sellowiana* increases β-diversity.

2. **Methods**

2.1. Study area

The study was carried out at Ilha do Cardoso State Park (ICSP), a legally protected area that is 13,500 ha, located on the southern coast of São Paulo state (25°03'-25°18'S, 47°53'-48°05'W), Brazil. The regional climate is Cfa - with hot summer - according to the new Köppen's climate classification for Brazil (Alvares et al., 2013). It has an annual rainfall between 1,800-2,000 mm, while temperatures range from 19-27 °C (Melo and Mantovani, 1994). The soils have been described as podzol hydromorphic (Pfeifer et al., 1989). The vegetation is classified within the Atlantic Rain Forest domain (Melo & Mantovani 1994). However, a remarkable feature of ICSP is the diversity of physiognomies, ranging from coastal vegetation to montane forest formation, presenting ecotone zones between physiognomies (Bernardi, 2001). Specifically, the sampling area represents an ecotone between the coastal shrubs and lowland forest.

2.2. Species description

Dicksonia sellowiana Hook. (Dicksoniaceae) is a tree fern occurring from southeast Mexico to Uruguay. It is restricted to the Atlantic rain forest of South America, i.e. within Brazil to the south and southeast of the country (Fraga et al., 2008, Noben et al., in press). It reaches up to 10 m height and its fronds can extend to 5 m (Tryon and Tryon, 1982). It is estimated that in the last ten years 75% of *D. sellowiana* populations have decreased in Brazil (Martinelli and Moraes, 2013). For this reason, this species is assessed as endangered (EN), according to criterion A2abcd (IUCN 2014) related to population decline (Martinelli and Moraes, 2013).

2.3. Data collection

Based on our previous knowledge about the study site, we chose an area within the Restinga forest with high density of individuals of *D. sellowiana*. Thus, we selected the 40 tallest individuals of *D. sellowiana* - at least 3 m apart from each other in a1.5 hectares area. Species richness was assessed in three different habitats: (1) count of the phanerophyte species (Angiosperm) growing on each *D. sellowiana* individual, randomly selected (not sequentially; "on trunk" plots); (2) count of the Angiosperm species growing in 1 m^2 at random plots on the forest floor under the canopy of each fern ("below" plots) and (3) count of the Angiosperm species in forty 1 m^2 random plots located on the forest floor, but at least two meters apart from the canopy of each fern ("away" plots). Because of the harvest of *D. sellowiana* trunks in the area, the tallest individuals within the sampled population of *D. sellowiana* had 1.0-1.5 m in height. As the canopy of *D. sellowiana* extends at most 1 m from its trunk we assumed that plots located further than 2 m were not currently under the influence of *D. sellowiana*. All plants found in each of these habitats were identified to species or genus level. Species name follows the "List of Species of the Brazilian Flora" (BFG, 2015).

2.4. Statistical analysis

To estimate the species richness (α-diversity) of the three habitats we used the extrapolated rarefaction method using the EstimateS software (Colwell et al., 2012; Colwell, 2013). This method estimates species richness based on the number of individuals found in the largest sample, which was 2075 in this study. This method also allows the comparisons of α-diversity between samples with different sizes, in our case, the area of tree ferns and plots. A Kruskal-Wallis test (using the software Past v. 2.17) was conducted to evaluate differences in the numerical abundance (number of individuals) in the plots among habitats.

β-diversity provides the link between local (α-diversity) and regional diversity (γ-diversity; Whittaker, 1960). Estimates of β-diversity can be influenced by both local and regional diversity (α and γ diversity). The Raup-Crick test (β_{RC}; Chase et al., 2011), however, provides a means of determining whether the composition of habitats is more different than expected on the basis of null models constructed using known γ diversity (the species list across all sites). β_{RC} ranges from -1 to 1: values approaching 1 represent communities more different than expected by chance; 0 represents no difference between communities and -1 represents communities more similar than expected by chance. The Raup-Crick analysis was conducted using the vegan package in R (Oksanen et al., 2013; R Core Team, 2014), with the code provided by Chase et al. (2011).

In addition, we calculated the multivariate dispersion of the three habitats – an approach regarded as an informative method of estimating β-diversity (see Anderson et al., 2011). This method begins by calculating Bray-Curtis pairwise distances between the 120 samples. The “betadisper” function in vegan (Oksanen et al., 2013) was then used to compute multivariate dispersion of the samples, relative to the habitats (groups) they belong to. Finally, in order to determine which species are significant indicators of three habitat types (on, below and away from the fern trunk) we used the indicator value function (IndVal) in the R package indicspecies (Dufrêne and Legendre, 1997; Cáceres and Legendre, 2009). Indval analysis determines groups of indicator species for each habitat by measuring the species association to each habitat (or combination of habitats). Indicator species can be – but are not restricted to - the most abundant species within a habitat.

3. **Results**

We sampled 2,602 plant individuals belonging to 61 species and 30 families; 40% of the species are endemic to Brazil (BFG, 2015). The number of individuals sampled was significantly different among habitats (Kruskal-Wallis $H = 82.99$ $p < 0.0001$, Fig. 1). The highest number of individuals was found in the plots away the tree fern trunks (Table 1).

Rarefaction analysis showed that α-diversity (measured as species richness) did not differ between habitats (Fig. 2). Our analysis, however, uncovered high levels of β-diversity. The Raup-Crick analysis showed that the highest difference in species composition ($\beta_{RC} = 1$, in other words the maximum possible β-diversity) was between the assemblages found on the trunk of *D. sellowiana* and found on the plots away from trunks. In addition, the composition of species growing immediately below and away from trunks was also significantly different from that expected by chance (β_{RC} =0.97). The composition of species was similar on the trunks and in the plots below trunks (β_{RC} =0.13, Table 4).

The analysis of dispersion, an approach regarded as an informative method of estimating β-diversity (see Anderson et al., 2011), also revealed highly significant differences between habitats in β-diversity (ANOVA $F_{2,115}$=5.94, p=0.003). The Tukey's test showed significant differences in pairwise comparisons between trunks and plots away (p= 0.03) and between plots below and plots away (p= 0.004); no significant differences were found between trunks and plots below (p= 0.74; Fig. 2), which is consistent with the Raup-Crick analysis.

The indicator analysis identified species representative of each habitat type (see Table 5). Interestingly, for the "away" habitat, the indicator species with the highest significance values (*Myrcia splendens*, *Coccosypselum lanceolatum* and *Calyptranthes concinna*), were also the most abundant ones. Similarly, the most abundant species from the "below" trunk habitat (*Anthurium* sp.) was also an indicator of this group, while *Ilex dumosa* and *Calophyllum brasiliensis* were indicator species for the "below-away" habitats. The three most abundant species found "on the trunk" habitat were indicators of this unit combined with the trunk-away habitats (*Clusia criuva*, *Ocotea pulchella* and *Ternstroemia brasiliensis*; Tables 3 and 5).

4. Discussion

Our results confirm that *D. sellowiana* promotes habitat heterogeneity and enables species coexistence. Although α-diversity (number of species) was similar across the habitats we found differences in species composition (β-diversity) in the three habitats associated with this tree fern. The fact that the tree fern is a threatened species underlines the risk that species extinctions pose for the maintenance of biodiversity worldwide.

Dicksonia sellowiana may facilitate species coexistence both by inhibiting the dominance of some woody species and by providing habitat for the establishment of epiphytes and hemi-epiphytes. Research carried out in New Zealand (Gaxiola et al., 2008) and North America (Cretaz and Kelty, 2002) revealed that tree ferns can affect the secondary succession in their neighborhood by inhibiting the growth of understory species through the release of allelochemicals. This process is likely to limit the extent to which potential competitors could become dominant. On the other hand, tree ferns can be suitable sites for the establishment of plants (Newton and Healey, 1989; Coomes et al., 2005; Derroire et al., 2007; Gaxiola et al., 2008). *Dicksonia sellowiana* acts as a litter trap and has physicochemical properties that make it an excellent natural substratum, explaining its historical use in gardening. It can also offer an opportunity for seedlings to reach better light conditions and provides protection against herbivory, trampling or water saturation. In addition, plants growing on tree fern trunks can escape infertile soil (Assis et al., 2011) and seasonal flooding (Pedroni, 2001; Oliveira and Joly, 2010; Assis et al., 2011), conditions that can occur in stressful habitats as those found in the Restinga (Scarano, 2009).

In stressful tropical ecosystems, such as the Restinga forest, some species may play a key role in promoting diversity. The structure and functioning of this ecosystem seems to be dependent on certain species that act as 'nurse' species tolerant to stress that ameliorate the local habitat and enable the establishment of less tolerant species (Scarano, 2009). One example is the hemi-epiphytic genus *Clusia* (Franco and Nobel, 1989; Young et al., 1995; Zaluar and Scarano, 2000; Scarano, 2002; Dias and Scarano, 2007). Because *D. sellowiana* acts as a substratum for the establishment of *Clusia*, its contribution is even more important in maintaining the diversity of the Restinga forests. In this case, while many species depend on the genus *Clusia* for their establishment, our results demonstrate that seedlings of *Clusia* are more abundant on tree fern trunks than on ground. Our results also reveal *Clusia criuva* as an indicator species for the "on-away" group, two markedly different habitats in terms of species composition. This result indicates that tree fern trunks may provide a source of nutrients for *Clusia* development because the growth during the epiphytic phase is dependent on the accumulated nutrient-rich humus in the crown of the host species (Putz and Holbrook, 1989).

Our study highlighted the role of spatial heterogeneity linked to the presence of a single species, in increasing β-diversity at the small local scale - an area less than 2 m^2, on the forest floor. Other systems may exhibit different relationships between diversity and scale. For example, in a meta-analysis Tamme et al. (2010) found a direct relationship between diversity and environmental heterogeneity at a broad spatial scale (more than 10 m), while relationships were found to be neutral or negative on fine spatial scales (<1.0 m^2). *D. sellowiana* may also contribute to the vertical heterogeneity in tropical forest as its trunk can reach up to 10 m of height, capturing different amounts and quality of light compared to the light reaching on the forest floor. This vertical heterogeneity may help explain the contribution of *D. sellowiana* to increase diversity at this fine local scale.

Besides the illegal harvest, forest fragmentation and climate change are also important threats to the Atlantic forest and several of its species. Currently, this biome is reduced to small forest patches (Ribeiro et al., 2009), which has led to range reductions for numerous plant species (Scarano and Ceotto, 2015). Moreover, climate change can may trigger increases in sea-level, putting coastal zones at risk (IPCC, 2014), with the possible extinction of species with narrow geographical distribution (Leão et al., 2014). Considering that species composition varies widely because of environmental diversity, Lautert et al. (2015) suggests that biodiversity conservation should take into account the various Atlantic Forest vegetation types rather than dealing with this domain as a homogeneous unit. Therefore, we can conclude that *D. sellowiana* promotes spatial turnover within specific habitats at a fine scale and thus should be a focus of conservation action plans. Despite the legal protection, several species have still been illegally harvested within protected areas in the Atlantic forest, including this tree fern species. The design of protected areas should be based on a management plan that considers the area of occupancy of threatened species and its specific habitats, to guarantee the regulation and actions to prevent illegal uses.

5. Conclusion

We demonstrated that a single and endangered species contributes to the spatial variation in diversity found in the Atlantic Forest hotspot, mainly for epiphytes and hemi-epiphytes. The three habitats examined in this research support similar levels of species richness, once differences in numerical abundance are accounted for. Species composition, in contrast, differs substantially across habitats. This confirms our hypothesis that *D. sellowiana* promotes biological diversity by increasing environmental heterogeneity and spatial turnover. However, as this tree fern is an endangered species, its continuous illegal overexploitation may lead to an impoverishment of the Restinga forest. Our results emphasize that conservation efforts should consider not only the extinction risk of this species, but also their ecological functions - crucially to support epiphytes and hemi-epiphytes. This is even more important in restricted and threatened ecosystems where diversity could be positively related to the presence of few species.

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Legend of figures

Figure 1- Rank abundance plots (log abundance v. species rank) for the different habitat zones: left to right, on trunk, below trunk and away from trunk.

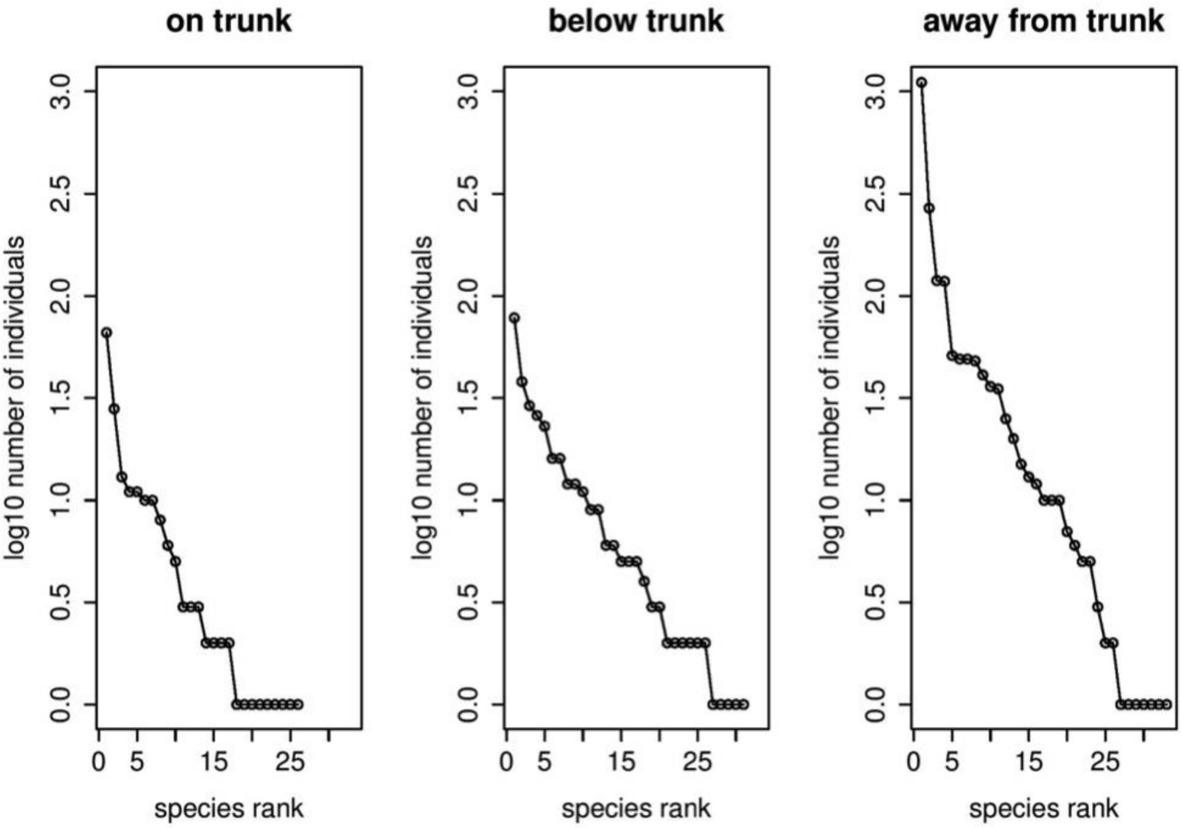
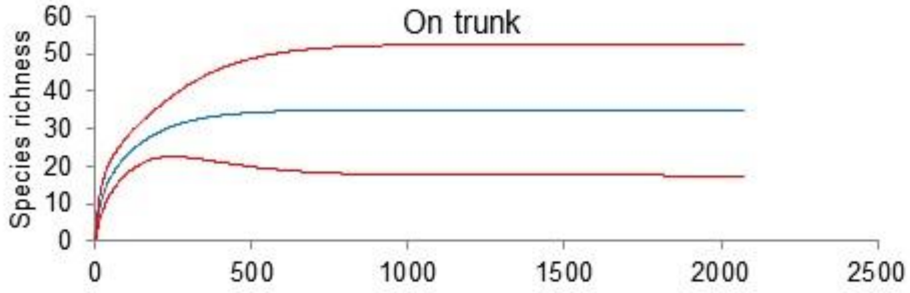
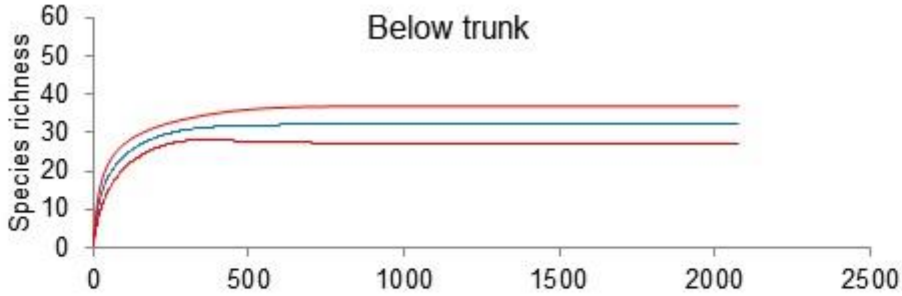


Figure 2. Estimated richness from the three habitat zones calculated with EstimateS software (Colwell et al., 2012; Colwell, 2013). In each case extrapolated rarefaction was based on 2075 individuals (the maximum in any one habitat). Blue lines represent the mean estimated richness and the red lines the 95% confidence interval.


On trunk
Species richness
60
50
40
30
20
10
0
0
500
1000
1500
2000
2500


Below trunk
Species richness
60
50
40
30
20
10
0
0
500
1000
1500
2000
2500

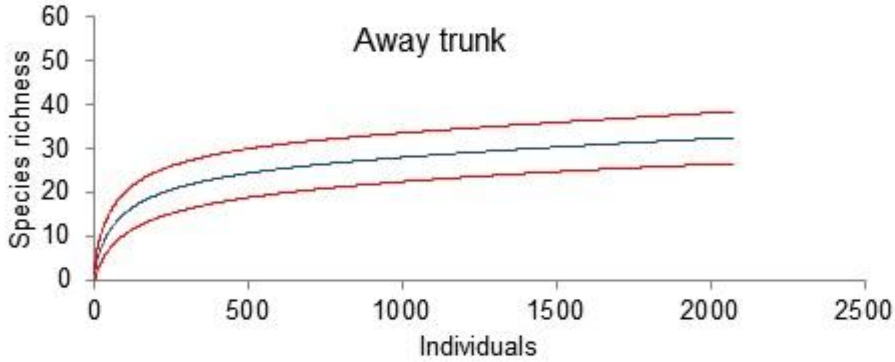

Away trunk
Species richness
60
50
40
30
20
10
0
0
500
1000
1500
2000
2500
Individuals

Table 1. Number of families, species and individuals of plants within the Restinga forest at Ilha do Cardoso State Park, Brazil.

Plots	Families	Species	n# of individuals
trunk	19	25	194
below	20	30	333
away	15	33	2,075

Table 2. Most abundant plant families in the different habitat zones (on trunk, below trunk and away from the trunk) within Restinga forest at Ilha do Cardoso State Park, Brazil. In parenthesis, the percentage of each family in relation to the total sampled individuals.

Plots	1º	2º	3º
Trunk	Myrtaceae (14%)	Bromeliaceae (12%)	Aquifoliaceae and Orchidaceae (8%)
Below	Myrtaceae (16%)	Bromeliaceae (10%)	Aquifoliaceae, Arecaceae, Cyperaceae, Melastomataceae and Primulaceae (6%)
Away	Myrtaceae (47%)	Rubiaceae (23%)	Aquifoliaceae (17%)

Table 3. Most abundant plant species in the different habitat zones (trunk, below trunk and away from the trunk) within Restinga forest at Ilha do Cardoso State Park, Brazil. In parenthesis, are the percentage of each species in relation to the total sampled individuals within each habitat.

Plots	1º	2º	3º
Trunk	*Clusia criuva* 66/194 (34%)	*Ternstroemia brasiliensis* 28/194 (14%)	*Ocotea pulchella* 13/194 (7%)
Below	*Anthurium* sp 78/333 (23%)	*Ilex dumosa* 38/333 (11%)	*Calophyllum brasiliensis* 29/333 (9%)
Away	*Myrcia splendens* 1108/2075 (53%)	*Coccosypselum lanceolatum* 269/2075 (13%)	*Calyptranthes concinna* 119/2075 (6%)

Table 4. Raup-Crick result showing the dissimilarities between the zones. 0 indicates no difference between zones; 1 communities maximum dissimilarity relative to that expected by random chance and -1 maximum similarity relative to that expected by random chance

	Trunk	Below	Away
Trunk	0	-	-
Below	0.24	0	-
Away	1	0.97	0

Table 5. Indicator species analysis showing which species are characteristic of habitat 1 (on trunk), 2 (below trunk) and 3 (away from trunk) and for combinations of habitats.

Group 1 - on trunk	
p-value	**Species**
0.001***	*Vriesea* sp.
0.015 *	*Erythroxylum amplifolium* (Mart.) O.E.Schulz
0.008 **	*Clethra scabra* Pers.
0.024 *	*Mikania glomerata* Spreng.
Group 2 - below trunk	
0.001 ***	*Anthurium* sp.
0.001 ***	*Myrcia pulchra* (O.Berg) Kiaersk.
0.013 *	*Cyperus* sp.
0.027 *	*Neomarica candida* (Hassl.) Sprague
0.045 *	*Scleria* sp.
Group 3 - away from trunk	
0.001 ***	*Calyptranthes concinna* DC.
0.001 ***	*Myrcia splendens* (Sw.) DC.
0.001 ***	*Coccocypselum lanceolatum* (Ruiz & Pav.) Pers.
0.001 ***	*Miconia* sp.
0.001 ***	*Myrcia hebepetala* DC.
0.001 ***	*Geonoma schottiana* Mart.
0.003 **	*Guatteria australis* A.St.-Hil.
0.002 **	*Alchornea triplinervia* (Spreng.) Müll.Arg.
0.014 *	*Euterpe edulis* Mart.
0.010 **	*Ilex pseudobuxus* Reissek
0.014 *	*Maytenus gonoclada* Mart.
0.044 *	*Pera glabrata* (Schott) Poepp. ex Baill.
Group 1+2	
0.021 *	*Myrcia ilheosensis* Kiaersk.
Group1+3	
0.005 **	*Clusia criuva* Cambess.
0.003 **	*Ocotea pulchella* (Nees & Mart.) Mez
0.049 *	*Ternstroemia brasiliensis* Cambess.
Group 2+3	
0.001 ***	*Ilex dumosa* Reissek

0.001 ***	*Calophyllum brasiliense* Cambess.
0.034 *	*Myrsine venosa* A.DC.