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Effects of climate and forest structure on palms, bromeliads and bamboos in Atlantic Forest fragments of Northeastern Brazil

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Abstract

Palms, bromeliads and bamboos are key elements of tropical forests and understanding the effects of climate, anthropogenic pressure and forest structure on these groups is crucial to forecast structural changes in tropical forests. Therefore, we investigated the effects of these factors on the abundance of these groups in 22 Atlantic forest fragments of Northeastern Brazil. Abundance of bromeliads and bamboos were assessed through indexes. Palms were counted within a radius of 20 m. We also obtained measures of vegetation structure, fragment size, annual precipitation, precipitation seasonality and human population density. We tested the effects of these predictors on plant groups using path analysis. Palm abundance was higher in taller forests with larger trees, closed canopy and sparse understory, which may be a result of the presence of seed dispersers and specific attributes of local palm species. Bromeliads were negatively affected by both annual precipitation and precipitation seasonality, what may reflect adaptations of these plants to use water efficiently, but also the need to capture water in a regular basis. Bamboos were not related to any predictor variable. As climate and forest structure affected the abundance of bromeliads and palms, human-induced climatic changes and disturbances in forest structure may modify the abundance of these groups. In addition, soil properties and direct measurements of human disturbance should be used in future studies in order to improve the predictability of models about plant groups in Northeastern Atlantic Forest.

Keywords: Arecaceae, Bambusoideae, Bromeliaceae, disturbance, rainfall, secondary forest fragments.

Efeitos do clima e da estrutura da vegetação em palmeiras, bromélias e bambus em fragmentos de Mata Atlântica no nordeste brasileiro

Resumo

Palmeiras, bromélias e bambus são importantes elementos das florestas tropicais e, entender os efeitos do clima, pressão antrópica e estrutura da floresta nesses grupos é crucial para prever alterações estruturais em florestas tropicais. Portanto, nós investigamos os efeitos desses fatores na abundância desses grupos vegetais em 22 fragmentos de Mata Atlântica no nordeste brasileiro. Abundâncias de bromélias e bambus foram registradas através de índices. Palmeiras foram contadas em um raio de 20 m. Nós também obtemos medidas da estrutura da vegetação, tamanho de fragmento, precipitação anual, sazonalidade na precipitação e densidade populacional humana. Nós testamos os efeitos desses preditores nos grupos vegetais através de análises de caminhos. A abundância de palmeiras foi maior em florestas mais altas, com árvores mais grossas, dossel fechado e sub-bosque aberto, o que deve refletir a presença de dispersores de sementes e atributos específicos das espécies de palmeiras locais. Bromélias foram negativamente afetadas pela precipitação anual e pela sazonalidade na precipitação, o que deve refletir adaptações dessas plantas para o uso eficiente da água, mas também a necessidade de captar água regularmente. Bambus não estiveram relacionados com nenhum dos preditores avaliados. Dado que clima e estrutura florestal afetaram a abundância de bromélias e palmeiras, as mudanças climáticas e distúrbios na estrutura das matas causados por ações antrópicas podem alterar a abundância desses grupos. Adicionalmente, propriedades do solo e medidas diretas de distúrbios antrópicos devem ser usadas em estudos futuros para melhorar o poder preditivo dos modelos sobre a abundância de plantas na Mata Atlântica do nordeste brasileiro.

Palavras-chave: Arecaceae, Bambusoideae, Bromeliaceae, distúrbios, precipitação, fragmentos de mata secundária.

1. Introduction

Tropical forests are complex and heterogeneous environments that hold most of the World's biodiversity (Köhler, 2000; Dirzo and Raven, 2003). These forests share higher resemblance in structure than in species composition (Grubb et al., 1963) and identifying structural patterns is a primary goal in plant ecology. Many studies addressed how forest structure varies along successional gradients (Saldarriaga et al., 1988; Brown, 1991; Terborgh and Petren, 1991; Montgomery and Chazdon, 2001; Guariguata and Ostertag, 2001; DeWalt et al., 2003) and how structure is shaped by factors such as topography, soil, water availability, disturbances and previous land use (Grubb et al., 1963; Lieberman et al., 1996; Guariguata and Ostertag, 2001; Thompson et al., 2002; Hietz et al., 2006; Nepstad et al., 2007; Santos et al., 2008; Costa et al., 2010; Emilio et al., 2014; Rodrigues et al., 2014).

Palms, bamboos and bromeliads are commonly found in tropical forests, where they interplay with other vegetation components and with the fauna. These plants can influence animals either directly, providing resources, or indirectly by influencing other organisms. Bromeliads can be valuable resources for forest dwelling animals, providing fruits, nectar, water, shelter and adequate conditions for reproduction (Richardson et al., 2000; Craynet al., 2004; Alves-Silva and Silva, 2009; Amora et al., 2013; Ferrari and Hilário, 2012). Palms can modify forest structure and composition due to their morphological characteristics, large amount of litter formation and leaf dropping, which may damage seedlings and hamper the recruitment of new trees (Farris-Lopez et al., 2004; Aguiar and Tabarelli, 2010). Furthermore, palms are key species in tropical forests because they provide important food resources for several species of mammals and birds (Snow, 1981; Eiserhardt et al., 2011). Large bamboo stands can shape forest structure by competing with herbs and trees, and increasing fuel for wildfires (Gagnon and Platt, 2008). Indeed, bamboos may arrest forest succession by shading and physically damaging the seedlings (Griscom and Ashton, 2003). Therefore, high bamboo density may indicate high frequency of disturbances (Tabarelli and Mantovani, 2000) and, in fact, there is a positive feedback between bamboos and disturbances, since these plants can take advantage under forest degradation going through rapid clonal reproduction and providing conditions for new disturbances (Gagnonet al., 2007; Gagnon and Platt, 2008; Smith and Nelson, 2011). Nevertheless, some bamboo species follow a consolidator strategy, growing slowly after disturbances and being hampered by such events (Franklin et al., 2010).

Climatic factors may affect forest structure and limit the occurrence of some plant groups in a global scale (Parsons and Moldenke, 1975; Kucharik et al., 2000; Walther et al., 2007; Eiserhardt et al., 2011). Although abrupt shifts in climatic conditions may modify vegetation physiognomy on a scale of tens of kilometers, as observed at the ecotone between the Atlantic Forest and the Brazilian xerophytic biome known as Caatinga (Ab'Sáber, 2003), climatic factors generally operate on the scale of hundreds of kilometers (Levin, 1992; Woodward et al., 2004; Eiserhardt et al., 2011). The recent increase in human population and the growing demand for natural resources have impacted tropical forests worldwide (Mittermeier et al., 2005). Thus, in densely populated regions, both climate variation and anthropogenic disturbances may drive shifts in forest structure and composition.

Northeastern Brazil presents high human population densities and the process of forest degradation in this region goes back to the 16th century. Most Atlantic Forest in the region was extirpated and today less than 16% (including secondary forests) of the original vegetation is left (Ribeiro et al., 2009). Further, the Atlantic Forest at this region encompasses a wide range of precipitation, from ~1000 to 2500 mm annually (Rodal et al., 2008, 2013). This scenario provides an opportunity to investigate the effect of climatic variation and anthropogenic pressure on the abundance of key vegetation groups – palms, bromeliads and bamboos – in Atlantic Forest fragments in Northeastern Brazil. We hypothesize that the abundances of these plant groups are affected by forest structure, anthropogenic pressure or climatic conditions, and that the groups are differently impacted by these factors.

2. Material and Methods

2.1. Study area

The study encompasses about 15,000 km^2 of the Atlantic Forest domain in the biogeographical sub-region of Bahia (Silva and Casteleti, 2003), between the São Francisco and Paraguaçu rivers, in the Northeastern Brazilian states of Sergipe and Bahia (Figure 1). This region presents a humid tropical climate, and the majority of the study area can be classified as As in the Köppen system, except for the southern portion, which is Af due to its less seasonal precipitation pattern (Peel et al., 2007). Annual rainfall ranges from 1,100 mm to 1,800 mm and is concentrated between April and September. Daily mean temperature averages 24 °C with a tendency to be slightly lower during the rainy season (WorldClim – Hijmans et al., 2005). The topography is lightly hilly, with maximum elevation of 250 m.a.s.l..

The study area is highly relevant because it is part of one of the world's 25 biodiversity hotspots (Myers et al., 2000; Mittermeier et al., 2005), and presents high levels of endemism for plants and vertebrates (Thomas et al., 1998; Silva et al., 2004). Furthermore, the habitat is highly fragmented, increasing the expectancy of loss of many species (Silva and Tabarelli, 2000). Nevertheless, the fragments of the study area are still important refuge to many regionally threatened animals, such as the collared peccary (*Pecari tajacu* Linnaeus), the yellow-breasted capuchin monkey (*Cebus xanthosternos* Wied-Neuwied), the puma (*Puma concolor* Linnaeus) and the maned three-toed sloth (*Bradypus torquatus* Illiger). Moreover, the study area coincides with the geographic range of

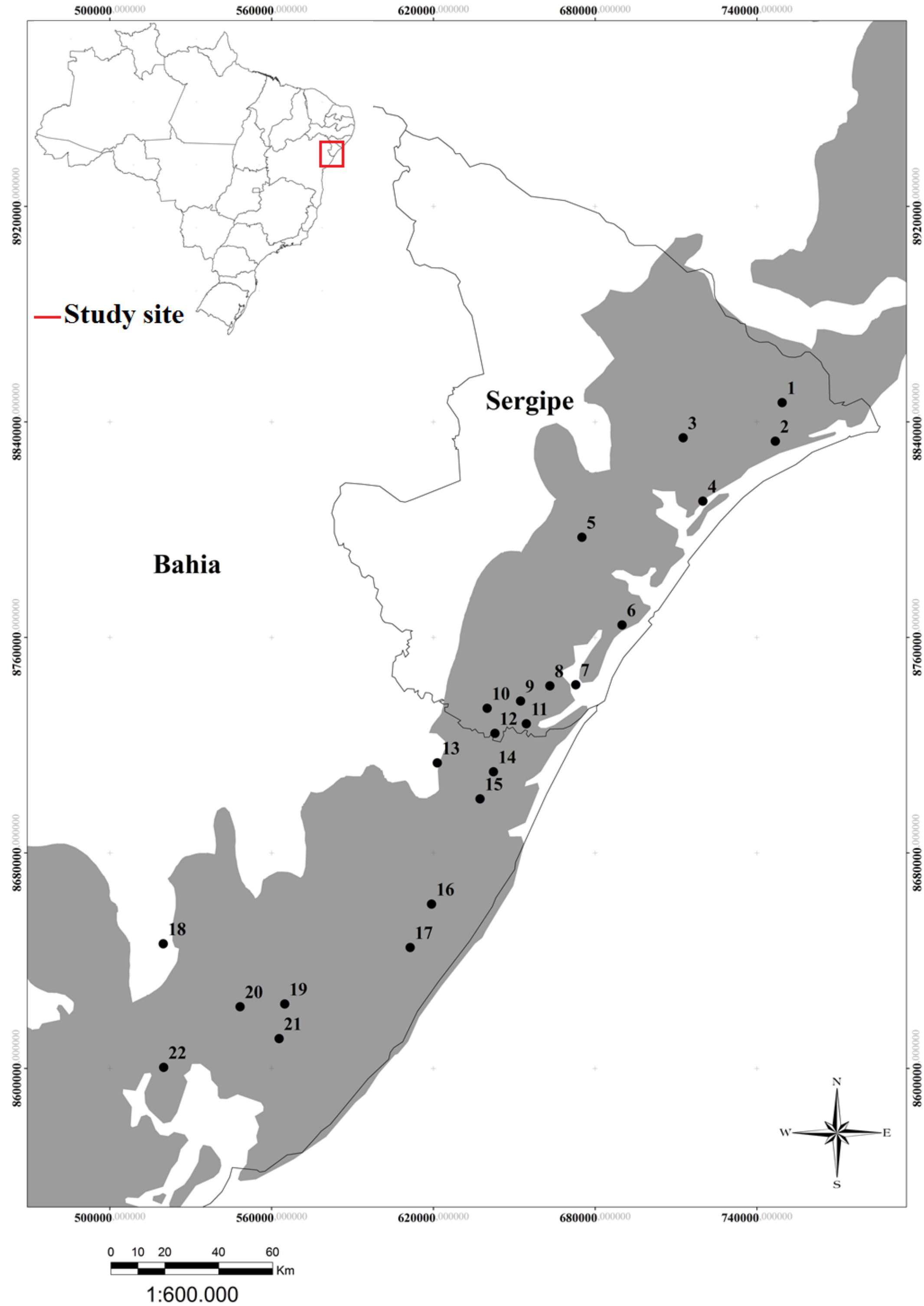

Figure 1. Location of the 22 sites surveyed within the study area in northeastern Brazil. The shaded area represents the Atlantic Forest biome.

two endangered animal species: the Coimbra-Filho's titi monkey (*Callicebus coimbrai* Kobayashi & Langguth) and the fringe-backed fire-eye (*Pyriglena atra* Swainson).

2.2. Vegetation sampling

Twenty two forest fragments (Figure 1) were surveyed between May 2011 and December 2012. Vegetation surveys were based on the point-centered quarter method (Cottam and Curtis, 1956), with five points being sampled at intervals of 50 meters along randomly-selected transects. Each transect was separated by a distance of at least 300 m from each other. The number of transects per fragment varied from five to 23 depending on fragment size. These transects were distributed throughout the fragments, except in those larger than 1,000 ha, in which the sampling was concentrated in a portion of the forest. At each point, the nearest tree with a Diameter at Breast Height (DBH) of at least 5 cm in each quadrant was sampled and the following measurements were taken: distance from the tree to the central point, stem height up to the first branch, and DBH. At each point, we also measured the understory density, canopy height, canopy openness and the abundance of bromeliads, palms and bamboos. Understory density was assessed using a sighting target adapted from McIntyre (1995) and Barlow et al. (2002), consisting of a 20 cm × 20 cm red plastic card, which was hung around the neck of the principal investigator, who moved backwards away from the field assistant standing at the sampling point until no part of the card could be visualized. The distance between the sampling point and the final position of the target was measured with a surveyor's tape.

Canopy openness was assessed using a 30 cm × 30 cm PVC pipe frame divided into 100 squares of equal size using nylon lines. The frame was held at arm's length above the head of the principal investigator at each sampling point, and the number of squares in which the sky was visible was counted.

The abundance of bromeliads within a radius of 10 m of each sampling point was estimated using an index ranging from 0 to 3, where zero corresponds to the complete absence of these plants, a score of 1 represents up to 10 rosettes (genets), 2 corresponds to 11-20 rosettes and 3 to more than 20 rosettes. The abundance of bamboos was also estimated with an index ranging from 0 to 3. In this case, zero corresponds to complete absence of bamboos, 1 corresponds to points where these plants were difficult to notice, 2 represents areas where bamboos were easily detectable, and 3 corresponds to areas where bamboos were the dominant plant form in the understory. The abundance of palms was recorded through the counting of all individuals with height > 2 m within a radius of 20 m. For all variables, the mean values for the set of sampling points were considered to be representative of the fragment as a whole for the analysis of the data.

2.3. Anthropogenic variables

The size of each fragment was measured from satellite images using Global Mapper version 7.01 (BLUE MARBLE GEOGRAPHICS, 2005). In two cases, it was not possible to acquire adequate satellite images, and then fragment size was obtained from Sousa et al. (2008). Fragment size was log-transformed before running the analyses.

We used human population density in the year 2000 within a radius of 10 km around each fragment as a proxy for anthropogenic pressure. These data were obtained with a 30 arc-second resolution from the American Socioeconomic Data and Applications Center (SEDAC, 2013).

2.4. Climatic variables

The total annual precipitation and the coefficient of variation in monthly precipitation (hereafter: precipitation seasonality) were obtained for each of the surveyed fragments through WorldClim. WorldClim presents interpolated data on climatic variables on a 30 arc-second resolution (Hijmans et al., 2005). Annual mean temperature does not vary considerably through the study area (range: 23.0-25.4 °C) and therefore it was not included in our analyses.

2.5. Data analysis

We used Principal Component Analysis (PCA) to reduce the dimensionality of the six vegetation variables. The first PCA axis was used to represent forest structure (a predictor variable) in subsequent analyses. We used path analysis to test a hypothesized model, which describes how predictor variables – forest structure (first PCA axis), annual precipitation, precipitation seasonality, human population density and fragment size – affect direct and indirectly the abundance of palms, bromeliads and bamboos in forest fragments. These analyses were performed in the R statistical platform (version 3.1.0) using the packages stats (R CORE TEAM, 2014) and lavaan (Rosseel, 2012). We tested for the presence of spatial autocorrelation in the dependent variables through Moran's I index in the software SAM (Rangel et al., 2010). Moran's I were invariably small, especially in the first classes of distance, and thus did not represent any problem to the analyses (see Legendre et al., 2002).

3. Results

We surveyed fragments ranging from 115 to 3,497 ha (mean ± standard deviation: 932.0 ± 976.8 ha). Annual precipitation also varied largely across the study area (range: 1,027-1,795 mm, 1,432.7 ± 200.4 mm), and decreased northward and westward. Precipitation seasonality varied by a factor of two (29-64%, 50.3 ± 8.8%), and decreased southward and westward. Human population density varied considerably within the study site (65.4-248.0 individuals·km^{-2}, 132.5 ± 63.4 ind.·Km^{-2}) and was greatest in its southernmost portion.

The six variables used to describe forest structure also varied considerably throughout the study site (Table 1). Particularly, canopy openness and basal area showed the widest ranges, varying by a factor of 5 and 3, respectively. The PCA revealed two main forest structure gradients for the 22 fragments (Table 1). The first axis captured 49.8% of the total variation and was positively related to canopy height, stem height, basal area and understory density, and

Table 1. Descriptive statistics, variance explained and loadings of the six forest structure variables on the first two axes produced by a Principal Component Analysis.

Forest structure variables	Mean ± SD	Min	Max	Axis 1	Axis 2
Canopy height (m)	10.2 ± 1.4	7.3	13.2	0.91	0.02
Canopy openess (%)	7.2 ± 4.0	3.7	17.6	–0.81	0.17
Distance from trees to the center point (cm)	251.4 ± 23.3	225.0	304.1	–0.26	–0.91
Stem height (m)	4.51 ± 0.75	3.4	6.0	0.90	–0.08
Basal area (cm^2)	137.4 ± 44.6	84.5	268.5	0.58	–0.75
Understory density (m)	22.4 ± 3.4	16.6	29.0	0.55	0.71
Variance Explained (%)				49.8	32.4

negatively related to canopy openness. High values for this axis are associated to taller forests, larger trees, closed canopy and sparse understory. The second axis captured 32.4% of the variation and was positively related to understory density, and negatively related to basal area and average distance from trees to the center point. High values for this axis represent forests with small, close-spaced trees and sparse understory. As the first axis captured most of the variation in the original data, we used only this axis on the subsequent analyses. The first axis of the PCA did not show any clear spatial pattern.

Palm abundance had an 87.3-fold increase from the smallest (0.3 palms per point) to the largest abundance (26.2) with an average of 8.1 ± 8.0 palms per point across the 22 fragments. Palm abundance did not show any clear spatial pattern. The abundance index of bromeliads varied from 0.00 to 1.53, averaging 0.45 ± 0.43. Bromeliads tended to be more abundant in more continental sites. For bamboos, the index varied from 0.15 to 2.52 and averaged 1.26 ± 0.73. Bamboo abundance was higher in two regions: the middle portion of the study area and in its southernmost part.

The whole picture about the direct and indirect effects of forest structure, precipitation, human population density and fragment size on plant groups is shown through path analyses (Figure 2). None of the predictor variables affected forest structure significantly, but palm abundance was directly and positively ($b_{stand.}$ = 0.47, P = 0.009) affected by forest structure (Figure 2A), indicating higher density of palms in taller forests with larger trees, closed canopy and sparse understory. Bromeliads abundance was directly and negatively affected by both annual precipitation ($b_{stand.}$= –0.59, P = 0.002) and precipitation seasonality ($b_{stand.}$= –0.42, P = 0.015; Figure 2B), pointing to higher abundance of these plants in sites with lower annual precipitation and more equally distributed humidity along the year. Bamboo abundance was neither directly nor indirectly related to any of the predictor variables in the analysis (Figure 2C). Fragment size was positively related to human population density ($b_{stand.}$= 0.39, P = 0.047), which is an indicative that past deforestation rates were higher on countryside instead of areas adjacent to urban centers. However, human population density and fragment size did not affect significantly any of the plant groups.

4. Discussion

This study encompassed an area of more than 15,000 km^2 of the Atlantic Forest domain and showed that different plant groups are affected differently by climate and forest structure. Bromeliads' abundance was negatively related to annual precipitation and precipitation seasonality. Differently to our results, bromeliads are expected to be more abundant in humid sites (Gentry and Dodson, 1987; Richardson et al., 2000). Nevertheless, this taxon has developed morphological and physiological adaptations to survive in dry environments. The phylotelmata formed by tank-like leaves allows water and nutrient impounding, and the water-conserving type of photosynthesis called Crassulaceum Acidic Metabolism (CAM) avoids excessive water losses by absorbing CO_2 at night (Cushman, 2001; Zotz and Hietz, 2001; Crayn et al., 2004). Although about half of the species of bromeliads are epiphytic, terrestrial species are often found on stony soils and on bare rocks (Cogliatti-Carvalho and Rocha, 2001). In the studied fragments, most bromeliads were observed on the ground, where they are probably less impacted by water stress than the epiphytic life-form. Particularly, the group of terrestrial bromeliads with thorn-bearing leaves (locally called *gravatá*) was observed in high abundance in more continental fragments, resulting in higher abundance indexes for areas where precipitation is lower. Less precipitation leads to a more open vegetation, where plants may experience increased light availability (DeWalt et al., 2010). Bromeliads probably benefit from this increase in light availability since they have mechanisms to tolerate water shortage. The negative relationship of the abundance of bromeliads with precipitation seasonality is probably due to the absence of deep roots for uptaking water from deeper soil layers. Therefore, although bromeliads have specialized mechanisms to use water efficiently, these plants need to capture water in a regular basis to maintain their metabolism. In regions with long dry season, the bromeliads may benefit from dew as water supply to survive (Gentry and Dodson, 1987), but their abundance may not be as high as in sites with constant rain water supply.

A number of studies have shown predictable changes in vegetation structure during ecological succession in tropical forests (Saldarriaga et al., 1988; Terborgh and Petren, 1991; Finegan, 1996; Denslow and Guzman, 2000; Montgomery and Chazdon, 2001; Kennard et al., 2002; DeWalt et al.,

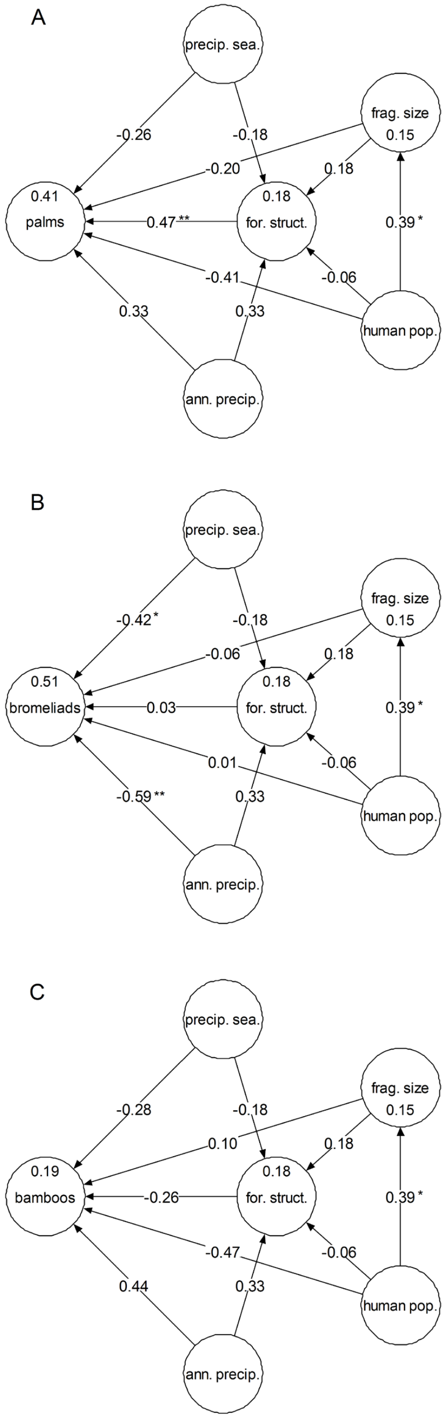

Figure 2. Path diagrams of direct and indirect effects of forest structure (first PCA axis), annual precipitation, precipitation seasonality, fragment size and human population density on the abundance of (A) palms, (B) bromeliads and (C) bamboos for 22 Northeastern Atlantic Forest fragments. Standardized regression coefficients are shown on the lines. R^2 values for each dependent variable are given inside the circles. Significant relationships are indicated with asterisks (* *P*<0.05; ** *P*<0.01).

2003; Chazdon et al., 2007). Overall, the forest increases in height, trees become larger, tree density decreases, and the canopy becomes denser, shadowing the understory, which becomes sparser. On the other hand, frequent human or natural induced disturbances have a degenerating effect on forest structure (Hietzet al., 2006). Nonetheless, forest may differ regarding structural patterns achieved through the successional process. In some forests the basal area peaks at intermediate stages of succession and not in the later stages (Denslow and Guzman, 2000). Also, studies have pointed out lowest tree densities at intermediate successional stages (Terborgh and Petren, 1991; Denslow and Guzman, 2000). These different patterns are probably associated to local characteristics of study site, such as soil, species composition, site history, and also linked to the study design.

Our results revealed that taller forests, with larger trees, closed canopy and open understory bear higher palm abundance. A number of factors affect palm community at local and regional scale in tropical forests, such as soil physical and chemical characteristics, topography (slope and altitude), climate, hydrology and components of forest structure (Cintra et al., 2005; Costa et al., 2009; Eiserhardt et al., 2011; Emilio et al., 2014; Rodrigues et al., 2014; Schietti et al., 2014). The greater abundance of palms in forests with a given structure can be a result of specific preferences of the local species (Eiserhardt et al., 2011). This assumption is limited by the fact that we did not identify the palm species in this study. However, in accordance to our results, other studies found smaller abundance of some palm species in more degraded forests (Arroyo-Rodríguez et al., 2007a; Baez and Balslev, 2007). Forest structure may also influence the occurrence and abundance of seed dispersers (Balcomb et al., 2000; Arroyo-Rodríguez et al., 2007b). Taller forests, with larger trees and closed canopy resemble forests in a later stage of succession, which could retain a larger fraction of the original frugivore guild. Functional extinction of bird populations in Atlantic Forest remnants has led to a reduction in seed size of *Euterpe edulis* Martius, which may have negative effects on seed survival in dry conditions and seedling size, consequently decreasing palm population fitness (Galetti et al., 2013).

Fragment size has long been recognized as an effective predictor of alteration in community structure for a great number of taxa (Tabarelli et al., 1999; Pardini et al., 2005; Martensen et al., 2008; Laurance et al., 2011). Edge effect is higher in smaller fragments and are strongly associated with changes in forest structure, increasing tree mortality, especially over the large ones (Laurance et al., 2000, 2001), and decreasing substantially the forest biomass (Laurance et al., 1997; Nascimento and Laurance, 2004). In fact, plant community and stand structure differed markedly between edge and interior plots in Northeastern Brazil (Santos et al., 2008). However, we commonly observed evidence of human impacts at the interior of forest fragments, what could have blurred any relation between fragment size and forest structure.

We also found that human population density was not a good predictor of forest structure in Northeastern Brazil. In other tropical forests, such as Amazonia, there is a positive relation of forest degradation (deforestation) with population density, distance from commercial markets, accessibility through roads and rivers and government-subsidized development projects (Pfaff, 1999; Laurance et al., 2001, 2002; Barniet al., 2012). However, the relationship between degradation and human demographic density may become saturated at certain point, when every forest site becomes accessible for at least some local residents. Since Northeastern Brazil is densely populated, all forest fragments were invariably close to human settlements in our study site. Some fragments were near large cities while others were close to farms or small towns. People from large cities often consume resources that are produced at distant places. Conversely, rural populations frequently rely on natural resources such as fiber, firewood and bush meat. Perhaps this reasoning may also explain why we did not find any relationship between the abundance of bamboos and any of the predictor variables. Although numerous studies associate bamboos with disturbed areas (e.g. Tabarelli and Mantovani, 2000; Gagnon and Platt, 2008; Smith and Nelson, 2011; McMichael et al., 2013), there is a lack of linkage between human population density and the frequency of disturbances. In addition, some bamboo species do not respond positively to disturbances (Franklin et al., 2010). Besides anthropogenic disturbance, other factors can also affect bamboo abundance, such as slope, soil attributes, light availability, canopy openness and deciduousness of trees (Suzaki et al., 2005; Wang et al., 2009; Lima et al., 2012). Therefore, such unmeasured factors could be responsible for the regulation of the abundance of bamboos in the studied fragments. More studies including other variables and more direct approaches to measure disturbances are needed to clarify what affect bamboo abundance in the study area.

5. Conclusions

In summary, our study showed that higher palm abundance was associated with late successional forests (larger trees and closed canopy), possibly as a result of maintenance of ecological functionality (reproduction, dispersion) in these fragments and the preference of locally abundant palm species for taller forests. Bromeliads abundance was negatively affected by annual precipitation and precipitation seasonality, underlying habitat selection toward sites with increased light availability and well distributed rain along the year. Forest structure was not affected by annual precipitation, precipitation seasonality, human population density or fragment size, probably because long-term human disturbances on the fragments disrupted the relationships between these variables. The lack of relationship between bamboos and the predictor variables may be related to the lack of linkage between human population density and the intensity of disturbance within the fragment sand/or the lack of other predictor variables in our analysis.

These findings underlie that different factors may affect the abundance of plant groups at a regional scale in the Northeastern Atlantic forest fragments. Changes in environmental factors and forest structure may influence directly the abundance and probably the composition of such plant groups. Therefore, human-induced climatic changes and disturbances that alter forest structure may alter the abundance of plant groups into these forest remnants.

Future studies may apply this regional approach including species composition in the analysis in order to refine our understanding about the direct and indirect effects on plant groups. Also, predictors such as soil texture and fertility, soil water availability and direct measures of human disturbance should be taken into account to improve our knowledge about the factors which determine plant group abundance and distribution in Northeastern Atlantic Forest.

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