The role of terrestrial bromeliads in determining the spatial organization of plant life forms in a tropical coastal forest

Celio M. Lopes, Flora Misaki, Karina Santos, Carlos A. P. Evangelista, Tatiana T. Carrijo and Mário L. Garbin

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ABSTRACT

The interplay between plant-plant interactions and light heterogeneity in the understory of tropical forests has rarely been examined. We aimed to identify the relative importance of the understory light environment and terrestrial bromeliads in explaining the abundance and spatial organization of different plant life forms along a coastal forest gradient from seashore inland in southeastern Brazil. We estimated the abundance of various life forms (herbs, woody plants, bromeliads, climbers, and palms) and the degree of light availability using hemispherical photographs in 165 plots (1 m²) within a 1.75 ha site. We used ordination methods, partial redundancy analysis (pRDA), spatial filtering using Moran’s eigenvector mapping, and Moran’s I splines. Forest cover was highly heterogeneous, but did not explain variation in abundance of life forms. Spatially, bromeliads were negatively associated with woody saplings, herbs and climbing plants at scales between 5-20 m, while the distance to seashore was found to be unrelated to these patterns. Our findings revealed that terrestrial bromeliads play an important role in the spatial organization of various life forms near the forest floor. Overall, the presence of terrestrial bromeliads and the plant area index better explained the understory vegetation than forest cover and distance to seashore.

Keywords: community assembly, hemispherical photographs, herb layer, shrub layer, spatial patterns

Introduction

Light is commonly viewed as the most important resource determining establishment, reproduction and growth of plants within forests and, not surprisingly, it is also the most heterogeneous in time and space (Pearcy 2007). The understory light environment is both cause and result of forest dynamics (Nicotra et al. 1999). Variations in light availability are expected to affect structure and composition of herb layer vegetation within tropical forests (Lima & Gandolfi 2009). Nevertheless, only a few studies ever quantified the patchiness of forest light conditions (Clark 1996; Nicotra et al. 1999; Valladares & Guzmán 2006) or examined how spatial variation in light conditions relates to the spatial organization of herb layers in tropical forests (Montgomery 2004), especially in coastal systems (Souza & Martins 2005).

The light environment is mainly determined by canopy structure, which directly affects growth and survival of seedlings and saplings (Kabakoff & Chazdon 1996; Nicotra et al. 1999; Montgomery & Chazdon 2001; Melo et al. 2007). This is because light availability has strong effects on the physiological processes of forest plants (Denslow et al. 1990). Spatial patchiness of light availability within...
forests is mainly caused by canopy gaps due to treefall (Denslow et al. 1990), selective logging (Nicotra et al. 1999; Beaudet & Messier 2002) and crown architecture (Takeda & Kawamura 2002; Kitajima et al. 2005; Pearcy et al. 2005). The role that canopy gaps play in forest regeneration is a central research topic (Pearcy 2007). Nevertheless, there is a multitude of other processes affecting the patterns of shrub layer vegetation within forests. These include plant-plant interactions (Ewel & Hiremath 2005; Garbin et al. 2016), deciduousness of trees (Souza et al. 2014), soil heterogeneity (Tateno & Takeda 2003; Townsend et al. 2008) and plant dispersal (Braz & Mattos 2010), all of which may interact with light heterogeneity. Thus, even though light can have a strong filtering effect on the organization of understory vegetation, the spatial organization of plant communities is a result of many different processes. Because these competing hypotheses are not mutually exclusive (Uriarte et al. 2005), quantitative data are needed to understand the relative contribution of factors that determine spatial patterns of the shrub layer.

Regardless of the importance of variation in light availability in explaining plant growth and distribution patterns, few studies made use of spatially explicit analytical tools to measure heterogeneity in forests (but see Valladares & Guzmán 2006). Most studies compared different vegetation types (e.g. Montgomery 2004) or estimated the effects of gap creation on regeneration patterns (e.g. Nicotra et al. 1999). Many replicates are required to reliably estimate spatially explicit patterns of canopy openness or light availability, which may explain the lack of studies in this regard. Using spatially explicit mapping approaches would allow the quantification of patch size and magnitude (contrast) of the light environment in tropical forests. Patch size (spatial autocorrelation) varies between 1 and 20 meters (Clark et al. 1996; Nicotra et al. 1999; Pearcy 2007) to about 50 meters (Yamada et al. 2014), or even 125 meters (Souza & Martins 2005) when canopy openness is considered. However, the complex nature of the interplay between plant-plant interactions and spatial light heterogeneity in the understory of tropical forests has hardly been assessed.

Our study site, a coastal plain in Brazil (hereafter, restinga), has a marked zonation pattern in plant physiognomies from seashore to inland shaped by wind and sea level oscillations (Araujo & Pereira 2004). Coastal systems represent a great challenge to plants that are constantly stressed by wind, salt, flooding and the threat of losing habitat due to sea level variation (Crawford 2008), requiring a continuous adjustment to changing climate conditions (Church et al. 2013). Although negative interactions can also occur among subordinate species (Garbin et al. 2016), positive interactions are an important structuring mechanism in restingsas (Scarano 2002; Dias & Scarano 2007). Terrestrial bromeliads are an important component of these systems (Araujo 1992; Pereira et al. 2004), known for nursing the Clusia hilariana Schldtl. tree, the main nurse plant in the restingsas (Correia et al. 2010) and for trapping palm seeds while negatively affecting palm seedlings (Brancalion et al. 2009).

These conflicting observations may be related to the strong effect of stress conditions on plant interactions (Bertness & Hacker 1994; Callaway et al. 2002; Michalet et al. 2006; Brooker et al. 2007). The benefit from nurse plants may not change with increasing distance from seashore (Castanho & Prado 2014). Moreover, distance from seashore did not affect the outcome of associations between different life forms, such as trees, herbs, climbers or shrubs (Castanho et al. 2012). Brancalion et al. (2009) found that terrestrial bromeliads were mainly present in open canopy areas, where they negatively affected palm seedlings. Knowledge on how terrestrial bromeliads organize in space in response to canopy cover with increasing distance from seashore (a proxy for stress conditions, sensu Castanho et al. 2012) and how they associate with other life forms can provide a better understanding of the interplay between plant associations and light environment in restinga forests. This has not yet been quantitatively tested under a spatially explicit approach.

We aimed to identify the relative importance of the understory light environment and terrestrial bromeliads in explaining the abundance of different life forms along a coastal forest gradient from seashore towards inland in southeast Brazil. Our objectives were twofold. First, we aimed to identify patterns of association among different life-forms (bromeliads, palms, woody plants, climbing plants, and herbs), and the role of space (in the form of patches), forest cover and distance from seashore in explaining such patterns. We hypothesized that forest cover and distance from seashore are the main structuring factors that determine the abundance of the various life forms. Second, we sought to understand how canopy cover and bromeliads relate to other plant life forms by quantifying patterns of spatial covariation among these components, hypothesizing that terrestrial bromeliads, by preferentially occupying canopy gaps, negatively affect the abundance of other life forms in space due to their spatially aggregated growth patterns.

Materials and methods

Study site

The study was conducted in the Paulo César Vinha State Park (1,574.85 ha) in the municipality of Guarapari (20°33’-20°38’S and 40° 26’-40° 23’W, sea level). The plant communities in the park are located on quaternary sandy coastal plains in southeast Brazil (Scarano 2002; Araujo & Pereira 2004). There is a wide variety of vegetation types including forests, shrubs and herbaceous plant communities delimited by sharp boundaries as a result of
the geomorphological diversity caused by changes in sea level (Araujo & Pereira 2004; Pimentel et al. 2007). The climate is characterized as Aw (Köppen), with an average annual temperature of 23.3 °C, annual average rainfall of 1,307 mm and annual relative humidity of 80 % (Assis et al. 2004a). Our study was conducted in the non-flooded coastal plain forest formation (Assis et al. 2004a) on a spatial gradient (about 350 meters) between the inland limits of the beach vegetation and the open shrub C. hilariana Schltdl. vegetation (Araujo & Pereira 2004; Thomazi et al. 2013). This restinga forest has a continuous canopy of about 8 meters height and a herb layer vegetation that varies in composition and includes bromeliads, Arecales, Piperaceae, and Rubiaceae (Assis et al. 2004b). These forests are termed dry forests, sandy forests, non-flooded forests, or simply restinga forests (Assis et al. 2004a; Thomazi & Silva 2014). The most abundant plant families in these forests are Myrtaceae, Bromeliaceae, Orchidaceae, Sapotaceae, Lauraceae, and Rubiaceae (Assis et al. 2004a). Details on the study location are available in Figure S1 in supplementary material.

Sampling and image acquisition

Field work was conducted between December 2015 and January 2016. We established 15 transects parallel to seashore (oriented in azimuth angle of 30 degrees). Each transect was 50 m long and the distance between them was 25 m. We installed 11 sampling units (1 m x 1 m plots) at every 5 m interval in each transect, resulting in 165 plots (15 transects x 11 plots) within 1.75 hectares (350 m x 50 m). Details on the study plot and sampling scheme are available in Figure S2 in supplementary material. In each sampling unit, we surveyed the vegetation and acquired hemispherical photographs. We sampled seven different life forms: woody plants (tree saplings), climbing plants (woody or herbaceous), cacti, herbaceous plants, palms, bromeliads, and pteridophytes. However, cacti and pteridophytes were removed from the analyses due to their very low abundance and frequency in the plots. Sampling was conducted using an adapted cover pin frame approach (Dias et al. 2005; Garbin et al. 2012): at every 0.5 m interval of the plot, a thin stick (0.8 cm diameter) was positioned vertically, and the identity and the number of times each life form touched the stick was recorded up to a height of 1.5 m. The nine pin assessments were pooled to obtain a measure of life form abundance (number of times each life form touched the stick).

Light environment was assessed indirectly using hemispherical photographs (Jonckheere et al. 2004; Weiss et al. 2004; Chianucci & Cutini 2012). We used a digital camera model (Canon 1200D, resolution of 5184 x 3456, and 72 dpi), with a fish eye lens (180 degrees field of view, 4.5 mm; Sigma Corp. of America, Ronkonkoma, NY, EUA), resulting in circular images. The camera was mounted on a tripod of 1.7 m height. Images were obtained in summer (growing season) when leaves are at their maximum expansion (Pérez-Harguindeguy et al. 2013). All photographs were taken before sunrise, just after sunset or under an evenly overcast sky to ensure optimal backlight conditions (Jelaska 2004).

Data analysis

We used ordination methods, partial redundancy analysis (pRDA), spatial filtering using Moran’s eigenvector mapping (MEM; see Dray et al. 2006 and Griffith & Peres-Neto 2006), and Moran’s I splines. The objectives were: 1) to describe the main patterns of variation in life form abundance, 2) to partition this variation into spatial components (linear, gradient from seashore, and MEMs) and 3) to quantify univariate and bivariate spatial patterns for the different life forms and forest cover. All analyses were carried out in the R environment (R Development Core Team 2015): simple and constrained ordinations were run in the vegan package (Oksanen et al. 2015). MEMs were run in the PCNM package (Legendre et al. 2013), Moran’s I spline univariate and cross-correlograms were run in the ncf package (Bjornstad 2015).

Images were processed using CAN-EYE version 6.313 (2014, INRA, France, available at http://www6.paca.inra.fr/can-eye). The camera fish-eye system was calibrated using the method described in http://www.avignon.inra.fr/can_eye to compute the optical center and the projection function (Weiss & Baret 2014). For each single image, the cover fraction (fCover) was computed. A set of 11 images of each transect was used to derive plant area index (PAI, at three different zenith angles, 38, 53, and 68 degrees, which correspond to the LAI2000 rings 3, 4, and 5, see Weiss et al. 2004), the fraction of absorbed photosynthetically active radiation (fAPAR, modeled and measured for white and black sky), gap fraction and modeled fCover. We adopted the term PAI, instead of LAI (leaf area index) because some leaves may be behind trunks, branches, and stems. Therefore, we followed Weiss & Baret (2014) in that CAN-EYE provide estimates of PAI, but not LAI. Thus, nine light environment variables were used in the analyses.

Relative abundances of life forms were calculated for each sampling unit by dividing the total number of touches of each life form by the total number of touches of all life forms, with the resulting matrix (L) of sampling units per life form abundance. Matrix C comprised fCover per plot. A third matrix (X) was constructed using the local spatial coordinates (x and y) of each sampling unit. Another set of matrices was built considering each transect as a sampling unit. Raw abundance data (number of touches) for plots within a transect were pooled. Light environment data was composed by the nine variables generated in CAN-EYE (matrix P). Abundance matrices were normalized prior to the analyses (see Legendre & Gallagher 2001). Environmental data (C and P) were standardized (McGarigal et al. 2000). Then, matrix X was expanded into Moran’s Eigenvector predictors with positive Moran’s I (calculated Moran’s I
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Figure 1. Principal coordinates analysis (PCoA) of different life forms (grey) in 165 plots in 1.75 hectares of a restinga forest understory. Bro, bromeliads; Pal, palms; Her, herbs; Cli, climbing plants; Wdy, woody saplings. The analysis revealed a pattern of segregation between bromeliads and other life forms.

The first axis of the PCoA analysis showed that where bromeliads were abundant, other life forms were less present (Fig. 1). Two bromeliad species were dominant: *Vriesea procera* and *Ananas sagenaria* (Mart. ex Schult. & Schult.f.) Wittm. and *Ananas sagenaria* (Martiex Schult. & Schult.f.) Wittm. & *Ananas sagenaria* (Mart. ex Schult. & Schult.f.) Wittm. and *Ananas sagenaria* (Mart. ex Schult. & Schult.f.) Wittm. and *Ananas sagenaria* (Mart. ex Schult. & Schult.f.) Wittm.

First, we ran a Principal Coordinates Analysis (Legendre & Legendre 2012) on matrix L, using the Bray-Curtis dissimilarity on the raw relative abundances matrix, in order to reveal the main trends of variation of life form abundance in the forest understory. Second, a partial redundancy analysis (pRDA; Økland 2003) was run using matrix L as response and matrices M, X, and C as explanatory variables. Thus, we considered the gradient from seashore to inland as an explanatory linear spatial structure, and the MEMs as the more complex (patchy) structures (see Borcard et al. 2011). A forward selection of variables was run on the explanatory matrices using the ordistep function of the package vegan. Thus, partial constrained ordination (pRDA) was used to partition the variation of life form abundance into three sources: fCover, MEMs, and the linear gradient from seashore. Third, a second pRDA was run using the transects as sampling units. The response matrix was composed by the pooled life form abundance in each plot within a transect after standardization by total (relative abundance) and normalization (Legendre & Legendre 2012). Explanatory datasets were the linear distances from seashore of each transect, matrix P, and the abundance of bromeliads. These were extracted from the raw abundance matrix, which comprised the remaining life forms. This pRDA determined the bromeliads as an external cause over the other life forms within the forest. In all partitioning procedures, we used the RsquareAdj function in vegan to obtain unbiased estimates of fractions (Peres-Neto et al. 2006; Borcard et al. 2011). Lastly, spatial univariate and cross-correlation functions were estimated between bromeliads, fCover and the other life forms using spline (cross) correlograms (Bjørnstad and Falck 2001). Correlograms were built at a distance of 115 m, roughly one third of the maximum amplitude. Uncertainty for spline (cross) correlograms was estimated by bootstrapping (10,000 iterations) and used to construct 95% envelopes.

Results

Patterns of variation in life form abundance

The first axis of the PCoA analysis showed that where bromeliads were abundant, other life forms were less present (Fig. 1). Two bromeliad species were dominant: *Vriesea procera*.
We found that bromeliads have a stronger impact on structuring the shrub layer vegetation than canopy cover or distance from seashore in this tropical coastal forest. Despite the expected predominant role of light and stress tolerance in filtering understory vegetation, bromeliads were able to occupy the shadier parts of the forest (with high PAI) and, due to their aggregated spatial organization, other life forms were excluded from these sites. Bromeliads have been shown before to affect the presence and density of other plant groups within forests (Brokaw 1983; Wada 1993; Barberis et al. 2002; Barberis & Lewis 2005). Nevertheless, in these studies, bromeliads had different effects on understory vegetation by either promoting regeneration or inhibiting other plant groups. In restingas and swamp forests, bromeliads are especially...
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Figure 3. Axis 1 and 2 of a constrained ordination (RDA) of life form abundance constrained by light environment (PAI, plant area index) and bromeliads (Brom). Total variation explained by the model was 41%. See Fig. 2B for fractions. T, transect; numbering from 1 to 15 depicts the position of the transect in relation to seashore, the higher the number, the closer the transect is to seashore.

known to nurse tree species (Scarano et al. 1998; Scarano 2006; Scarano 2009; Correia et al. 2010). When acting as a trap for seeds, they can competitively exclude palm seedlings (Brancalion et al. 2009). These authors found that bromeliads were negatively associated with shaded conditions and that conditions for palms were better where bromeliads were absent. In summary, our results suggest that bromeliads adjust to shaded conditions, establish dense colonies, and then inhibit woody, herbaceous and climbing plants, regardless of distance from seashore.

The role of forest cover and distance from seashore

In coastal systems, distance from seashore is a good proxy for abiotic stress (Castanho et al. 2012). In our study, the distance from seashore to the nearest transect was about 170 meters. It seems that the restinga forest and the beach vegetation (Araujo & Pereira 2004) are capable to buffer the effects of wind and salt spray. Distance from seashore did not affect spatial associations and nurse effects in restings (Castanho et al. 2012; Castanho & Prado 2014). Moreover, in open shrub formations of the restinga, distance from seashore was not associated with floristic composition or structural parameters of the vegetation. In contrast, vegetation differed among plots parallel to the sea (Pimentel et al. 2007). Overall, our data suggest a limited role of abiotic stress associated with increasing proximity to seashore. We did not observe discernable effects of stress gradients on the organization of forest understory communities in this coastal system. Likewise, Castanho et al. (2012) found no evidence that spatial life form associations change with increasing distance from seashore. Our study showed that the findings for sand dunes (Castanho et al. 2012) and shrub vegetation (Pimentel et al. 2007) also apply to the forest formations in the restinga. Canopy cover, PAI, FAPAR and gap fraction were not related to distance from seashore, and the same was true for life form abundance of the shrub layer vegetation. Thus, it seems that the understory vegetation of these forests is buffered against the potentially harmful effects caused by the proximity to the seashore.

Understory plant species are affected by competition with canopy trees and lianas, and by low levels of light reaching the forest floor (Wright 2002). Low levels (less than 2.5% of the above canopy) and temporal heterogeneity of light reaching the floor (e.g. Canham et al. 1990) drive a wide variation in morphology and physiological plasticity of the understory species, directly affecting the observed patterns of diversity and species coexistence (Théry 2001; Valladares 2003). The vertical leaf orientation of bromeliads that would impair their capacity to harvest light, may be compensated by their high photosynthetic capacity and biomass allocation to leaf tissue (Valladares et al. 2002). Restinga bromeliads acclimate poorly to high levels of light under exposed conditions, while they seem to perform better and acclimate to more shaded conditions in forests (Duarte et al. 2002). In our study site, bromeliads appear to cope with high shade conditions (indicated by PAI) creating dense patches (as indicated by the large space fraction explained by MEMs), but the physiological mechanisms behind these patterns require further study. Moreover, the large fraction explained by MEMs indicated a highly-aggregated pattern of bromeliads unrelated to canopy cover. The patchy pattern of bromeliads and their dissociation in space with other plant life forms was evident in the spline and cross-correlogram outputs.

Spatial patterns

Terrestrial bromeliads seem to partition space with other groups of plant life forms. It is noteworthy that canopy cover and distance from seashore had no effect on the abundance of the different life forms studied. Understory light conditions are expected to affect shrub layer vegetation (Montgomery 2004). The patterns of spatial segregation between bromeliads and the other life forms, and the limited role of canopy cover and gradient stress in determining these patterns, point to an important role of competition for space and of dispersal limitation (see Barberis et al. 2014) in the spatial organization of the shrub layer of the restinga forest. Our results indicate that terrestrial bromeliads may have a...
strong influence on structure and spatial organization of an understory plant community. Future studies should evaluate the physiological plasticity of bromeliads allowing them to cope with the different light environments of the restinga forest, and to measure patterns of tree seed germination and abundance of tree seedlings in sites with and without bromeliad colonies.

Conclusions

We showed that the assembly of the herb layer vegetation in this restinga forest is independent of canopy cover and distance from seashore. Importantly, terrestrial bromeliads tend to occupy the shadiest portions of the gradient (as indicated by PAI), and they seem to play a crucial role in determining the spatial organization of different life forms in this forest. Thus, these internal filters (sensu Violle et al. 2012) of the community (the local environmental conditions driven by PAI) and the density-dependent processes are more important than the external filters, such as distance from seashore (as a proxy for the stress gradient). The nonrandom co-occurrence patterns between terrestrial bromeliads and other life forms detected here (the negative cross-correlation spatial structure) provides evidence that biotic internal filters can be more important than external filters in the assembly of the herb layer vegetation in these forests. Future
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studies should assess the plasticity of bromeliads in coping with changes in light conditions, and address the question if different bromeliad species have different effects on other plant life forms, especially on seedlings and saplings of tree species regenerators.

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