

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

Celio M. Lopes<sup>1</sup>, Flora Misaki<sup>1</sup>, Karina Santos<sup>2</sup>, Carlos A. P. Evangelista<sup>3</sup>, Tatiana T. Carrijo<sup>2</sup> and Mário L. Garbin<sup>1\*</sup>

Received: December 13, 2016

Accepted: January 23, 2017

## 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 m<sup>2</sup>) 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

<sup>1</sup> Programa de Pós-Graduação em Ecologia de Ecossistemas, Laboratório de Ecologia Vegetal, Universidade Vila Velha, Rua Comissário José Dantas de Melo, s/n, Boa Vista, 29102-770, Vila Velha, ES, Brazil

<sup>2</sup> Laboratório de Botânica, Centro de Ciências Exatas, Naturais e da Saúde, Universidade Federal do Espírito Santo, Rua Alto Universitário, s/n, Guararema, 29500-000, Alegre, ES, Brazil

<sup>3</sup> Universidade Vila Velha, Rua Comissário José Dantas de Melo, s/n, Boa Vista, 29102-770, Vila Velha, ES, Brazil

\* Corresponding author: mlgarbin@gmail.com

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

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 (Percy 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 *restingas* (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* Schtdl. tree,

the main nurse plant in the *restingas* (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, Arecaceae, 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, Ronkonhoma, 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 (Bjørnstad 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](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*



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

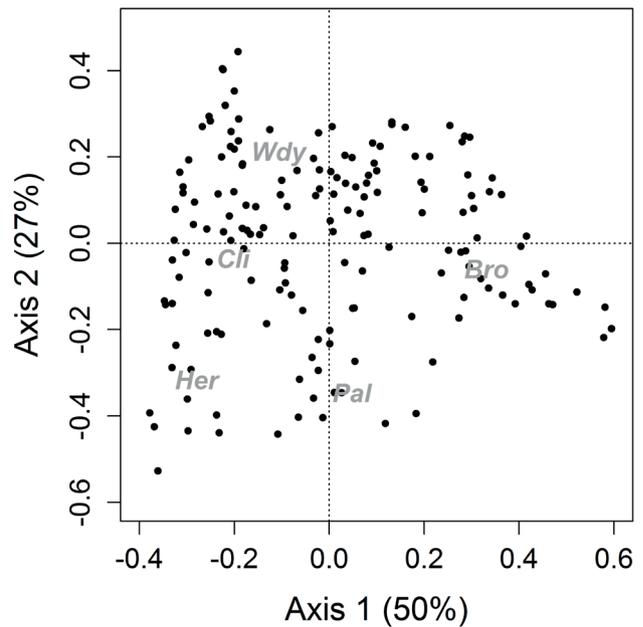
greater than expected Moran's  $I$ ) (Legendre & Legendre 2012), resulting in matrix  $M$ . The Moran's eigenvector mapping (MEM) approach (Griffith & Peres-Neto 2006; Dray *et al.* 2012) allowed us to model the relationship between life forms and environment while ensuring independence among sampling units, and modeling of more complex spatial structures in a context of canonical methods (Borcard *et al.* 2011; Legendre & Legendre 2012). Using this approach, spatial dependence is filtered out by detrending, but the information from these spatial structures can be exploited as they may reveal the presence of unmeasured processes (McIntire & Fajardo 2009; Dray *et al.* 2012).

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: *Vrisea procera*



**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.

(*Mart. ex Schult. & Schult.f.*) Wittm. and *Ananas saganaria (arruda)* Schult. & Schult.f.. The second axis distinguished the plots where herb species were more abundant than woody plants and bromeliads while abundance of climbers and palms was intermediate.

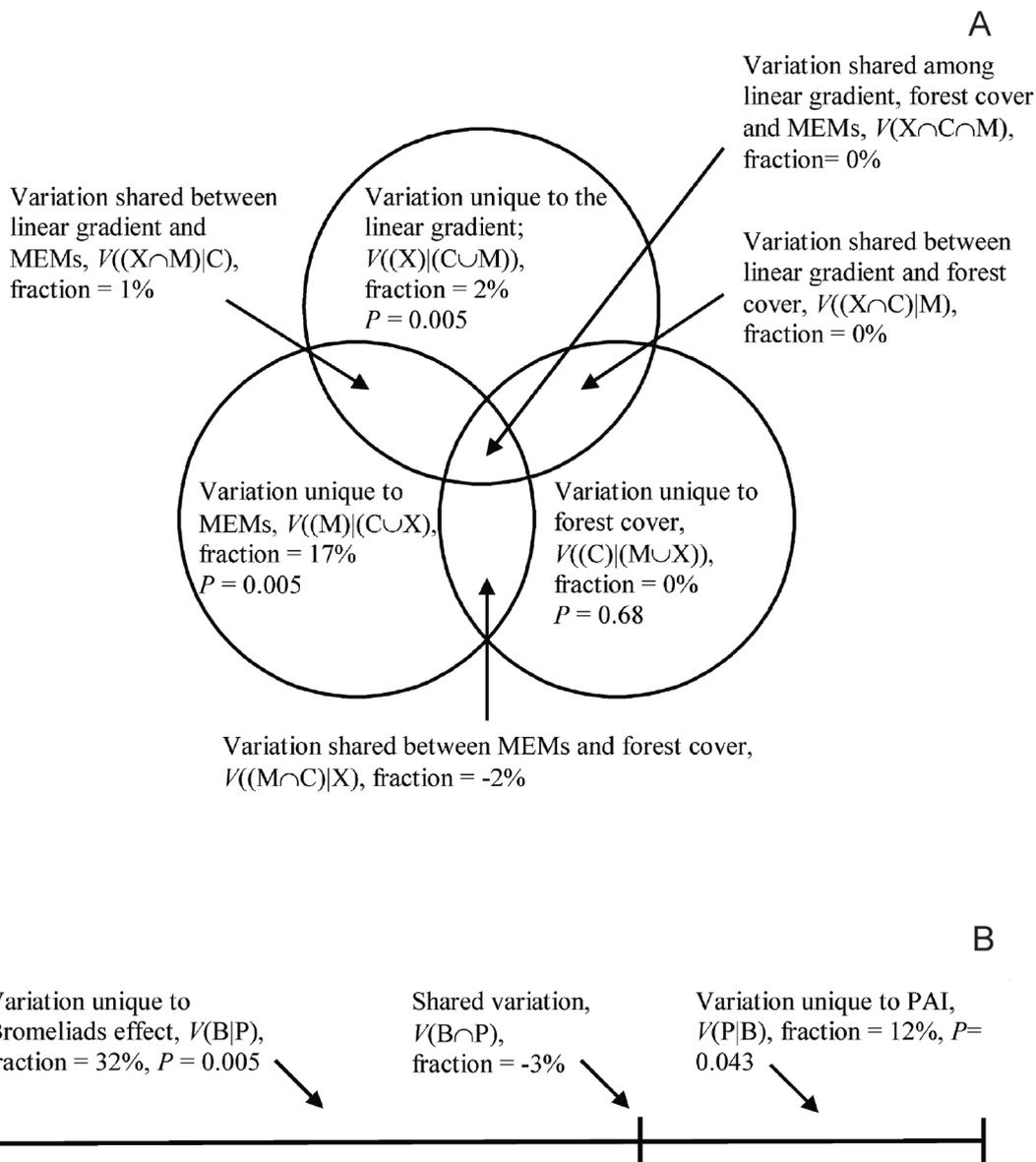
### *Variation partitioning*

Canopy cover (`fCover`) was unrelated to the variation in life form abundance between plots (including bromeliads). The linear gradient from seashore explained only a small fraction (2 %) while MEMs explained the largest fraction (17 %) of variation in life form abundance (Fig. 2A). When transects were used as sampling units, bromeliads (32 %) and PAI (12 %) were the most important factors (Figs. 2B, 3) in explaining patterns of life form abundance. The linear gradient had no significant relationship with life form abundance (with:  $P=0.81$ , without:  $P=0.39$ , bromeliads) and was not considered in the second partitioning procedure.

### *Univariate and bivariate spatial patterns*

`fCover` (Fig. 4A), bromeliads (Fig. 4B) and herbs (Fig. 4C) were positively aggregated in space at scales between zero and 10 meters. Bromeliads were negatively associated in space with climbing plants (Fig. 4D), herbs (Fig. 4E) and woody plants (Fig. 4F). See Table S1 in supplementary material for light environment parameters of each transect derived using CAN-EYE.





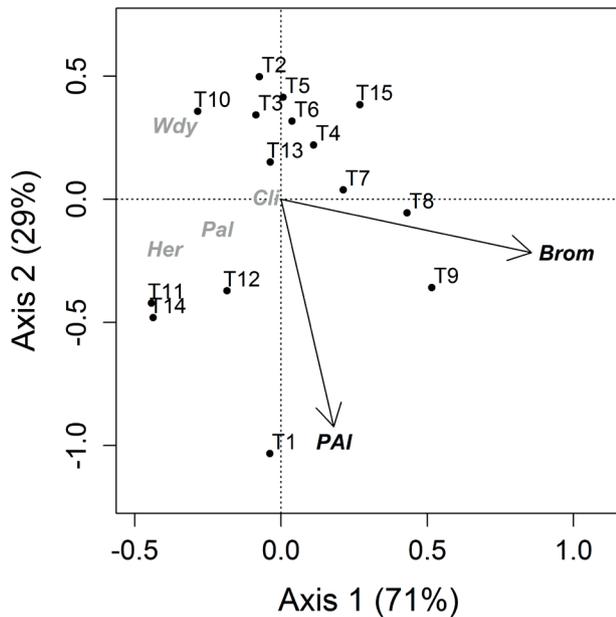
**Figure 2.** A) Venn diagram for the partitioning of life form abundance related to the linear gradient (**X**), fCover (**C**) and MEMs (**M**) as explanatory data sets. Total variation explained (**XUCUM**) was 18 % ( $P = 0.005$ ). B) Partition of the variation of life form abundance (after removing bromeliads) into two sources: bromeliads (**B**) and light environment (**P**). Total variation explained (**BP**) was of 41 % ( $P = 0.075$ ). U, combined variation.  $\cap$ , shared variation. See Økland (2003) for a detailed formulation of the variation partitioning procedures. Negative fractions should be interpreted as zeroes (Legendre 2008). See text for details.

## Discussion

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

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



**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 restingas (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

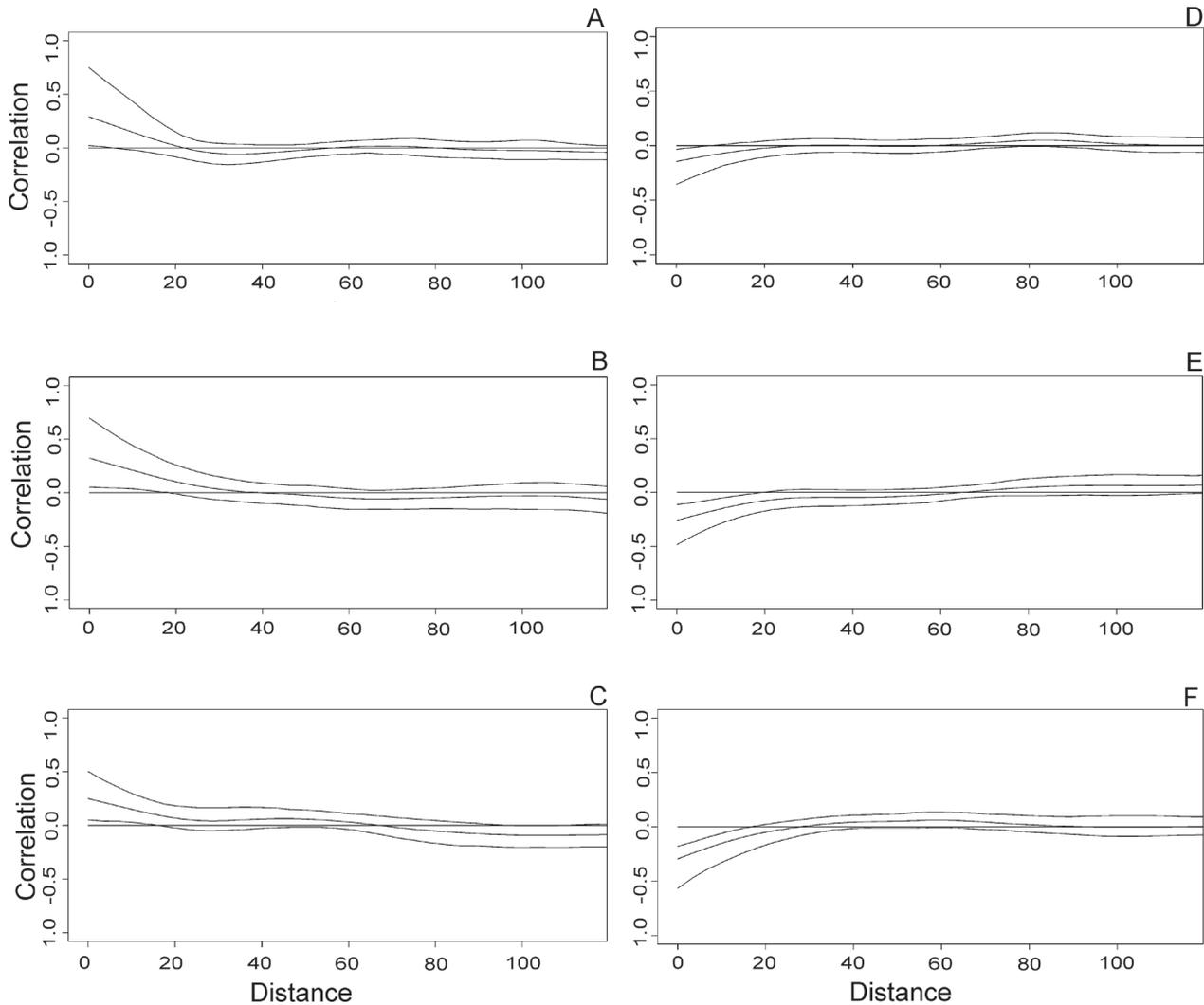
*et al.* 2007). Overall, our data suggest a limited role of abiotic stress associated with increasing proximity to seashore. We did not observe discernable effects of stress gradients on the organization of forest understory communities in this coastal system. Likewise, Castanho *et al.* (2012) found 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





**Figure 4.** Univariate spline correlograms of A) fCover, B) bromeliads, and C) herbs in 1.75 ha of a restinga forest. Spline cross-correlograms between bromeliads and: D) climbing plants, E) herbs, and F) woody plants. Upper and lower lines represent 95 % envelopes. Envelopes below or above zero in splines depict negative and positive significant spatial structures, respectively. In univariate splines (A, B and C), there was a positive association at scales between zero and 10 meters as envelope is above the zero line at these scales. For the cross-correlograms (D, E and F), there was a negative association at scales between zero and 10 meters as envelope is below the zero line at these scales.

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



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

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 regenerants.

### Acknowledgements

We thank FAPES and Capes (Espírito Santo State Research Agency/Brazilian Research Agency), which granted fellowships to M.L. Garbin, F. Misaki, C. Lopes, and K. Santos. We thank FAPES for funding (grant n°69329524/2015). We thank K. Gregório-Martins for building the map and P.C. Cavatte and A.C.S. Araujo for helpful suggestions. We are also grateful to IEMA (Espírito Santo Environmental Agency) for collection licenses.

### References

- Araujo DSD. 1992. Vegetation types of sandy coastal plains of tropical Brazil: A first approximation. In: Seeliger U. (ed.) Coastal plant communities of Latin America. San Diego, Academic Press. p. 337-347.
- Araujo DSD, Pereira MCA. 2004. Sandy coastal vegetation. In: Encyclopedia of Life Support Systems. Oxford, UNESCO, Eolss Publishers.
- Assis AM, Pereira OJ, Thomaz LD. 2004a. Fitossociologia de uma floresta de restinga no Parque Estadual Paulo César Vinha, Setiba, município de Guarapari (ES). *Revista Brasileira de Botânica* 27: 349-361.
- Assis AM, Thomaz LD, Pereira OJ. 2004b. Florística de um trecho de floresta de restinga no município de Guarapari, Espírito Santo, Brasil. *Acta Botanica Brasílica* 18: 191-201.
- Barberis IM, Batista WB, Pire EF, Lewis JP, León RJC. 2002. Woody population distribution and environmental heterogeneity in a Chaco forest, Argentina. *Journal of Vegetation Science* 13: 607-614.
- Barberis IM, Lewis JP. 2005. Heterogeneity of terrestrial bromeliad colonies and regeneration of *Acacia praecox* (Fabaceae) in a humid-subtropical-Chaco forest, Argentina. *Revista de Biología Tropical* 53: 377-385.
- Barberis IM, Torres PS, Batista WB, Magra G, Galetti L, Lewis JP. 2014. Two bromeliad species with contrasting functional traits partition the understory space in a South American xerophytic forest: Correlative evidence of environmental control and limited dispersal. *Plant Ecology* 215: 143-153.
- Beaudet M, Messier C. 2002. Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: An assessment based on hemispherical photographs. *Agricultural and Forest Meteorology* 110: 217-228.
- Bertness MD, Hacker SD. 1994. Physical stress and positive associations among marsh plants. *The American Naturalist* 144: 363.
- Bjørnstad ON. 2015. ncf: Spatial Nonparametric Covariance Functions. R package version 1.1-6. <https://CRAN.R-project.org/package=ncf>.
- Bjørnstad ON, Falck W. 2001. Nonparametric spatial covariance functions: Estimation and Testing. *Environmental Ecology Stat* 8: 53-70.
- Borcard D, Gillet F, Legendre P. 2011. *Numerical Ecology with R*. New York, Springer.
- Brançalion PHS, Gabriel VDA, Gómez JM. 2009. Do terrestrial tank bromeliads in Brazil create safe sites for palm establishment or act as natural traps for its dispersed seeds? *Biotropica* 41: 3-6.
- Braz MIG, Mattos EA. 2010. Seed dispersal phenology and germination characteristics of a drought-prone vegetation in southeastern Brazil. *Biotropica* 42: 327-335.
- Brokaw N. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by *Aechmea magdalenae* (Bromeliaceae) in a tropical forest. *Tropical Ecology* 24: 194-200.
- Brooker RW, Maestre FT, Callaway RM, *et al.* 2007. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96: 18-34.
- Callaway RM, Brooker RW, Choler P, *et al.* 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-848.
- Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20: 620-631.
- Castanho CT, Oliveira AA, Prado PI. 2012. The importance of plant life form on spatial associations along a subtropical coastal dune gradient. *Journal of Vegetation Science* 23: 952-961.
- Castanho CT, Prado PI. 2014. Benefit of shading by nurse plant does not change along a stress gradient in a coastal dune. *PLoS One* 9: e105082. doi: 10.1371/journal.pone.0105082.
- Chianucci F, Cutini A. 2012. Digital hemispherical photography for estimating forest canopy properties: current controversies and opportunities. *iForest - Biogeosciences and Forestry* 5: 290-295.
- Church JA, Clark PU, Cazenave A, *et al.* 2013. Sea level change. In: Stocker TF, Qin D, Plattner G-K, *et al.* (eds.) *Climate Change 2013: The physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge, New York, Cambridge University Press. p. 1137-1216.
- Clark DB. 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research* 26: 747-757.
- Clark DB, Clark DA, Rich PM, Weiss S, Oberbauer SF. 1996. Landscape-scale evaluation of understory light and canopy structures: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research* 26: 747-757.
- Correia C, Dias A, Scarano F. 2010. Plant-plant associations and population structure of four woody plant species in a patchy coastal vegetation of Southeastern Brazil. *Brazilian Journal of Botany* 33: 607-613.
- Crawford RMM. 2008. *Plants at the margin: Ecological limits and climate change*. Cambridge, Cambridge University Press.
- Denslow JS, Schultz JC, Vitousek PM, Strain BR. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71: 165-179.
- Dias ATC, Scarano FR. 2007. *Clusia* as nurse plant. In: Lüttge U. (ed.) *Clusia: A woody neotropical genus of remarkable plasticity and diversity*. Berlin, Heidelberg, Springer Berlin Heidelberg. p. 55-71.
- Dias ATC, Teixeira Zaluar HL, Ganade G, Scarano FR. 2005. Canopy composition influencing plant patch dynamics in a Brazilian sandy coastal plain. *Journal of Tropical Ecology* 21: 343-347.
- Dray S, Legendre P, Peres-Neto PR. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483-493.
- Dray S, Pélissier R, Couteron P, *et al.* 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82: 257-275.
- Duarte HM, Rocas G, Barreto SMB, *et al.* 2002. Acclimation or stress symptom? An integrated study of intraspecific variation in the clonal plant *Aechmea bromeliifolia*, a widespread CAM tank-bromeliad. *Botanical Journal of the Linnean Society* 140: 391-401.
- Ewel JJ, Hiremath AJ. 2005. Plant-plant interactions in tropical forests. In: Burslem DFRP, Pinard MA, Hartley SE. (eds.) *Biotic Interactions in the tropics: their role in the maintenance of species diversity*. Cambridge, Cambridge University Press. p. 3-34.
- Garbin ML, Carrijo TT, Sansevero JBB, Sánchez-Tapia A, Scarano FR. 2012. Subordinate, not dominant, woody species promote the diversity of climbing plants. *Perspectives in Plant Ecology Evolution and Systematics* 14: 257-265.
- Garbin ML, Guidoni-Martins KG, Hollunder RK, Mariotte P, Scarano FR, Carrijo TT. 2016. Spatial segregation of subordinate species is not controlled by the dominant species in a tropical coastal plant community. *Perspectives in Plant Ecology Evolution and Systematics* 18: 23-32.
- Griffith DA, Peres-Neto P. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87: 2603-2613.
- Jelaska SD. 2004. Analysis of canopy closure in the dinaric silver fir - Beech Forests (*Omphalodo fagetum*) in Croatia using hemispherical photography. *Hacquetia* 3: 43-49.



- Jonckheere I, Fleck S, Nackaerts K, *et al.* 2004. Review of methods for in situ leaf area index determination Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology* 121: 19-35.
- Kabakoff RP, Chazdon RL. 1996. Effects of canopy species dominance on understorey light availability in low-elevation secondary forest stands in Costa Rica. *Journal of Tropical Ecology* 12: 779-788.
- Kitajima K, Mulkey SS, Wright SJ. 2005. Variation in crown light utilization characteristics among tropical canopy trees. *Annals of Botany* 95: 535-547.
- Legendre P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology* 1: 3-8.
- Legendre P, Borcard D, Blanchet FG, Dray S. 2013. PCNM: MEM spatial eigenfunction and principal coordinate analyses [R package version 2.1-2/r109].
- Legendre P, Gallagher E. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.
- Legendre P, Legendre L. 2012. *Numerical Ecology*, Third. Amsterdam, Elsevier.
- Lima RAF, Gandolfi S. 2009. Structure of the herb stratum under different light regimes in the Submontane Atlantic Rain Forest. *Brazilian Journal of Biology* 69: 289-296.
- McGarigal K, Cushman S, Stafford S. 2000. *Multivariate Statistics for wildlife and ecology research*. New York, Springer.
- McIntire EJB, Fajardo A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90: 46-56.
- Melo ACG, Miranda DLC, Durigan G. 2007. Cobertura de copas como indicador de desenvolvimento estrutural de reflorestamentos de restauração de matas ciliares no Médio Vale do Paranapanema, SP, Brasil. *Árvore* 31: 321-328.
- Michalet R, Brooker RW, Caviers LA, *et al.* 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters* 9: 767-773.
- Montgomery RA. 2004. Effects of understorey foliage on patterns of light attenuation near the forest floor. *Biotropica* 36: 33-39.
- Montgomery RA, Chazdon RL. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82: 2707-2718.
- Nicotra AB, Chazdon RL, Iriarte SVB. 1999. Spatial Heterogeneity of Light and Woody Seedling Regeneration in Tropical Wet Forests. *Ecology* 80: 1908-1926.
- Økland RH. 2003. Partitioning the variation in a plot-by-species data matrix that is related to n sets of explanatory variables. *Journal of Vegetation Science* 14: 693-700.
- Oksanen J, Blanchet FG, Kindt R, *et al.* 2015. *Vegan: community ecology package*. R package version 2.3-2. <http://CRAN.R-project.org/package=vegan>. 15 Jul. 2016.
- Pearcy RW. 2007. Responses of Plants to Heterogeneous Light Environments. In: Pugnaire FI, Valladares F. (eds.) *Functional Plant Ecology*, 2nd. edn. Boca Raton, CRC Press. p. 724.
- Pearcy RW, Muraoka H, Valladares F. 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytologist* 166: 791-800.
- Pereira MCA, Cordeiro SZ, Araujo DSD. 2004. Estrutura do estrato herbáceo na formação aberta de Clusia do Parque Nacional da Restinga de Jurubatiba, RJ, Brasil. *Acta Botanica Brasílica* 18: 677-687.
- Peres-Neto PR, Legendre P, Dray S, Borcard D, *et al.* 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87: 2614-2625.
- Pérez-Harguindeguy N, Díaz S, Garnier E, *et al.* 2013. *New handbook for standardised measurement of plant functional traits worldwide*. *Australian Journal of Botany* 61: 167.
- Pimentel MCP, Barros MJ, Cirne P, *et al.* 2007. Spatial variation in the structure and floristic composition of “restinga” vegetation in southeastern Brazil. *Revista Brasileira Botânica* 30: 543-551.
- R Development Core Team. 2015. *A language and environment for statistical computing* R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>. 15 Jul. 2016.
- Scarano FR. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany* 90: 517-524.
- Scarano FR. 2006. Plant community structure and function in a swamp forest within the Atlantic rain forest complex: a synthesis. *Rodriguésia* 57: 491-502.
- Scarano FR. 2009. Plant communities at the periphery of the Atlantic rain forest: Rare-species bias and its risks for conservation. *Biology Conservation* 142: 1201-1208.
- Scarano FR, Rios RI, Esteves FA. 1998. Tree species richness, diversity and flooding regime: case studies of recuperation after anthropic impact in Brazilian flood-prone forests. *International Journal of Ecology and Environmental Sciences* 24: 223-235.
- Souza AF, Martins FR. 2005. Spatial variation and dynamics of flooding, canopy openness, and structure in a neotropical swamp forest. *Plant Ecology* 180: 161-173.
- Souza FFM, Gandolfi S, Rodrigues RRR. 2014. Deciduousness influences the understorey community in a semideciduous tropical. *Biotropica* 46: 512-515.
- Takeda H, Kawamura K. 2002. Light environment and crown architecture of two temperate *Vaccinium* species: Inherent growth rules versus degree of plasticity in light response. *Canadian Journal of Botany* 80: 1063-1077.
- Tateno R, Takeda H. 2003. Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. *Ecology Research* 18: 559-571.
- Théry M. 2001. Forest light and its influence on habitat selection. *Plant Ecology* 153: 251-261.
- Thomazi R, Rocha R, Oliveira M, Bruno AS, Silva AG. 2013. Um panorama da vegetação das restingas do Espírito Santo no contexto do litoral brasileiro. *Natureza On Line* 11: 1-6.
- Thomazi RD, Silva AG. 2014. Florística, diversidade e estrutura horizontal e vertical de uma área de vegetação arbustiva aberta numa planície arenosa costeira do Espírito Santo, sudeste do Brasil. *Natureza On Line* 12: 10-18.
- Townsend AR, Asner GP, Cleveland CC. 2008. The biogeochemical heterogeneity of tropical forests. *Trends in Ecology & Evolution* 23: 424-431.
- Uriarte M, Hubbell SP, John R, Condit R, Canham CD. 2005. Neighbourhood effects on sapling growth and survival in a neotropical forest and the ecological-equivalence hypothesis. In: Burslem DFRP, Pinard MA, Hartley SE. (eds.) *Biotic interactions in the tropics: Their role in the maintenance of species diversity*. Cambridge, Cambridge University Press. p. 89-106.
- Valladares F. 2003. Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. In: Esser K, Lüttge U, Beyschlag W, Hellwig F. (eds.) *Progress in botany: genetics physiology systematics ecology*. Berlin, Heidelberg, Springer. p. 439-471.
- Valladares F, Guzmán B. 2006. Canopy structure and spatial heterogeneity of understorey light in an abandoned Holm oak woodland. *Annals of Forest Science* 63: 749-761.
- Valladares F, Skillman JB, Pearcy RW. 2002. Convergence in light capture efficiencies among tropical forest understorey plants with contrasting crown architectures: A case of morphological compensation. *American Journal of Botany* 89: 1275-1284.
- Violle C, Enquist BJ, McGill BJ, *et al.* 2012. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27: 244-252.
- Wada N. 1993. Dwarf bamboos affect the regeneration of zoochorous trees by providing habitats to acorn-feeding rodents. *Oecologia* 94: 403-407.
- Weiss M, Baret F. 2014. *CAN-EYE V6.313 User Manual*. <https://www6.paca.inra.fr/can-eye/>
- Weiss M, Baret F, Smith GJ, Jonckheere I, Coppin P. 2004. Review of methods for in situ leaf area index (LAI) determination Part II. Estimation of LAI, errors and sampling. *Agricultural and Forest Meteorology* 121: 37-53.
- Wright SJ. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1-14.
- Yamada T, Yoshioka A, Hashim M, Liang N, Okuda T. 2014. Spatial and temporal variations in the light environment in a primary and selectively logged forest long after logging in Peninsular Malaysia. *Trees - Structure and Function* 28: 1355-1365.

