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PROGRAMA DE PÓS GRADUAÇÃO EM ECOLOGIA DE ECOSSISTEMAS

ARBUSTOS SUBORDINADOS DE DIFERENTES ESPÉCIES PROMOVEM A DIVERSIDADE E ABUNDÂNCIA DE PLANTAS TREPADEIRAS

FLORA MISAKI RODRIGUES

VILA VELHA

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Dissertação apresentada a Universidade Vila Velha, como pré-requisito do Programa de Pós Graduação em Ecologia de Ecossistemas para a obtenção do grau de Mestra em Ecologia.

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ARBUSTOS SUBORDINADOS DE DIFERENTES ESPÉCIES PROMOVEM A DIVERSIDADE E ABUNDÂNCIA DE PLANTAS TREPADEIRAS

Dissertação de Mestrado apresentada à Universidade Vila Velha, como um dos pré-requisitos do Programa de Pós Graduação em Ecologia de Ecossistemas para a obtenção do título de Mestre em Ecologia.

Aprovada em 17 de fevereiro de 2017,

Banca Examinadora:

Dr. Felipe Zamborlini Saiter - IFES

Dr. Walace P. Kiffer Jr – UVV

Dr. Mário Luís Garbin – UVV

Orientador

Dedico esse trabalho à minha mãezinha querida, que é a fonte de inspiração em tudo na minha vida.

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SUMÁRIO

RESUMO

RODRIGUES, Flora Misaki, M.Sc., Universidade Vila Velha - ES, fevereiro de 2017. **Arbustos subordinados de diferentes espéceis promovem a diversidade e abundância de plantas trepadeiras**. Orientador: Mário Luís Garbin.

A principal pergunta do trabalho foi: Qual o papel das espécies subordinadas em promover abundância e diversidade de plantas trepadeiras? Este foi realizado em uma comunidade vegetal costeira, localmente chamada de *Restinga*, Guarapari, sudeste do Brasil. Foram amostradas 65 moitas de vegetação em dois hectares de uma comunidade de *Restinga* aberta. Análise de redundância parcial (pRDA) foi usada para decompor hierarquicamente a abundância de plantas trepadeiras em diferentes fatores. Os fatores foram: abundância de plantas lenhosas dominantes e subordinadas, abundância de ervas, espaço (Moran's Eigenvectors Maps, MEM's), e qualidade da moita. Modelos lineares foram usados para acessar os descritores da qualidade da moita e das plantas lenhosas. Nossos resultados mostraram que diferentes plantas lenhosas subordinadas são responsáveis pela abundância e diversidade de plantas trepadeiras. Enquanto *Calyptranthes brasiliensis* Spreng. (Myrtaceae) promoveu a abundância de trepadeiras, *Chaetocarpus myrsinites* Baill. (Peraceae) e a árvore dominante *Clusia hilariana* Schltdl. (Clusiaceae) estavam fortemente associadas com a diversidade de trepadeiras. Apesar da identidade das espécies lenhosas subordinadas mudarem em diferentes comunidades, seu efeito de promover a abundância e a diversidade de plantas trepadeiras é mantido. Esses resultados aumentam o poder de generalizações a respeito do papel das espécies subordinadas em estruturar comunidades.

Palavras chave: facilitação, coexistência de espécies, estrutura de comunidade, plantas trepadeiras, Restinga.

ABSTRACT

RODRIGUES, Flora Misaki, M.Sc., University of Vila Velha - ES, february de 2017. **Different subordinate woody species promote diversity and abundance of climbing plants**. Advisor: Mário Luís Garbin.

The principal question of study was: What is the role of subordinate species in promoting the abundance and diversity of climbing plants? This was sampled in a sandy coastal plant community, locally called *Restinga*, Guarapari, southeastern Brazil. We sampled 65 vegetation patches in two hectares of an open *Restinga* community. Partial constrained redundancy analysis (pRDA) was used to hierarchically decompose the relative abundances of climbing plants into the different factors. The factors were: abundance of dominant and subordinate woody plants, abundance of herb species, space (Moran's Eigenvectors Maps, MEM's), and patch quality. Linear models were used to assess the relationship between climber diversity and descriptors of patch quality. Our results showed that different subordinate woody species are responsible for the abundance and diversity of climbing plants. While *Calyptranthes brasiliensis* Spreng. (Myrtaceae) promoted the abundance of climbers, *Chaetocarpus myrsinites* Baill. (Peraceae) and dominant tree *Clusia hilariana* Schltdl. (Clusiaceae) were strongly associated with climber diversity. Even though the identity of subordinate woody species changes in different plant communities, their effect in promoting the abundance and diversity of climbing plants is maintained. This finding increases the power for good generalizations regarding the role of subordinate species in community assembly.

Keiwords: climbing plants, community assembly, facilitation, species coexistence, Restinga.

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Capítulo 1

Different subordinate woody species promote diversity and abundance of climbing plants

Flora Misaki[1], Karlo G. Guidoni-Martins[2], Patryck Gouvea[1], Amélia Tuler[2], Pierre Mariotte[3], Tatiana T. Carrijo[2], Mário L. Garbin[1*]

[1] Universidade Vila Velha, Programa de Pós-Graduação em Ecologia de Ecossistemas, Laboratory of Vegetal Ecology, Rua Comissário José Dantas de Melo, s/n, Boa Vista, 29102-770, Vila Velha, Espírito Santo, Brazil

[2] Universidade Federal do Espírito Santo, Centro Universitário Norte do Espírito Santo, Rodovia BR 101 Norte, Km 60, Bairro Litorâneo, 29932-540, São Mateus, ES, Brazil

[3] Ecole Polytechnique Fédérale de Lausanne EPFL, School of Architecture, Civil and Environmental Engineering (ENAC), Laboratory of Ecological Systems (ECOS), Station 2, 1015 Lausanne, Switzerland.

[*] Corresponding author: M. Garbin; mlgarbin@gmail.com

Co-authors: F. Misaki; floramrbio@gmail.com
T. Carrijo; tcarrijo@gmail.com
K. Guidoni-Martins; karlogregorio@gmail.com
P. Gouvea; patrickgouvea@hotmail.com
P. Mariotte; Pierre.mariotte@hotmail.com

Abstract

Question(s): What is the role of subordinate species in promoting the abundance and diversity of climbing plants?

Location: a sandy coastal plant community, locally called *Restinga*, Guarapari, southeastern Brazil.

Methods: We sampled 65 vegetation patches in two hectares of an open *Restinga* community. Partial constrained redundancy analysis (pRDA) was used to hierarchically decompose the relative abundances of climbing plants into the different factors. The factors were: abundance of dominant and subordinate woody plants, abundance of herb species, space (Moran's Eigenvectors Maps, MEM's), and patch quality. Linear models were used to assess the relationship between climber diversity and descriptors of patch quality.

Results: Our results showed that different subordinate woody species are responsible for the abundance and diversity of climbing plants. While *Calyptranthes brasiliensis* Spreng. (Myrtaceae) promoted the abundance of climbers, *Chaetocarpus myrsinites* Baill. (Peraceae) and dominant tree *Clusia hilariana* Schltdl. (Clusiaceae) were strongly associated with climber diversity.

Conclusions: Even though the identity of subordinate woody species changes in different plant communities, their effect in promoting the abundance and diversity of climbing plants is maintained. This finding increases the power for good generalizations regarding the role of subordinate species in community assembly.

Keywords: climbing plants, community assembly, facilitation, species coexistence, Restinga

Nomenclature: The Brazilian Catalogue of Plants (http://floradobrasil.jbrj.gov.br; accessed on 03 Feb 2017).

Running head: Effects of subordinate woody species on climbers

Author contributions:

FM: conceived the study, designed the sampling procedures, collected and analyzed, wrote the manuscript

KGG-M: analyzed the data

PG: collected data

PM: wrote the manuscript

TTC: identified plant materials, wrote the manuscript

MLG: conceived the study, designed the sampling procedures, collected and analyzed, wrote the manuscript

Introduction

Subordinate species are an emergent research topic in community ecology (Mariotte 2014). This is in contrast with the attention given to dominant species in the last decades. This is mostly due their major role in ecosystem processes and the habitat delimitation for subordinate species (Grime 1998). Moreover, these species can be important in promoting the diversity of climbing plants in tropical communities (Garbin et al. 2012). The scarcity of studies, however, severely limits the power for good generalizations regarding the role of subordinate species in explaining diversity patterns. We need to know whether these findings configure a general pattern in sandy coastal plant community tropical systems, or if they are a special case in few plant communities.

Several morphological and functional features distinguish subordinate from dominant species (Peltzer et al. 2009; Doherty et al. 2011; Mariotte et al. 2013a; Garbin et al. 2014; 2016). These traits may reflect different strategies of resource acquisition or conservation between these two species groups (Grime et al. 1997; Diaz et al. 2004; Mariotte et al. 2013a). Besides being smaller in stature and more numerous than dominants, subordinate species tend to occupy the space delimited by dominants and they also filter newer dominants after disturbance events (Whittaker 1965; Grime 1998). Subordinate species can increase plant productivity (Mariotte et al. 2013b) and litter decomposition (Wardle & Zackrisson 2005) through positive associations with soil microbiota. Recent findings suggest that subordinate species have an important role in stimulating the resistance of plant communities to climate change (Mariotte 2014). Biomass production of subordinates may be enhanced during drought, thus increasing community stability (Kardol et al. 2010; Mariotte et al. 2013b). Besides this role in ecosystem processes, subordinate species can have important effects in promoting diversity in tropical systems. For instance, *Erythroxylum subsessile* (Mart.) O.E.Schulz, a subordinate woody shrub, promote diversity of climbing plants in a coastal plant community dominated by the nurse tree *Clusia hilariana* Schltdl. (Garbin et al. 2014).

This subordinate species seems to positively affect a subset of the climbers, which, together with *E. subsessile*, are also facilitated by this dominant tree.

Climbing plants (woody or not, using tendrils or stem twiners) are an important component in the regeneration of tropical forests (Schnitzer et al. 2000; Dewalt et al. 2000). When compared to trees and grass species, studies with climbers are more recent, with important implications for ecological theory (Schnitzer & Bongers 2002; Gerwing et al. 2006). This lower number of studies may be related to the increased difficulty in sampling climbing plants, especially in tropical forests, due to its growth form and intense vegetative reproduction (Putz 1984; Gentry 1991; Schnitzer & Bongers 2002; Gerwing et al. 2006). Climbers are a good model to understand how tropical plant communities assemble, given that they depend on other plants for their growth. Moreover, understanding the mechanisms that affect the diversity of climbers may indicate ways to understand overall plant diversity (Schnitzer & Bongers 2002). Climbers compete with trees for light and space, water and nutrients, and space for foliage development (Putz & Chai 1987). They can also cause mechanical injuries due to their weight and increase the effects of the mechanical strain (torque) caused by winds (Putz 1984; Gentry 1991). Nevertheless, the structural support offered by trees allows numerous species of climbers and epiphytes to persist through novel habitat creation (Mcintire & Fajardo 2014). Subordinate shrubs can positively affect climbing plants, especially stem twiners (Garbin et al. 2012; 2014). However, the understanding of what role subordinate species can have in shaping plant communities through positive effects demands a larger number of evidences from different systems to increase our power for better generalizations.

Our study site, a sandy coastal plant community locally called *Restinga*, comprise an ecosystem associated with the Atlantic Forest complex (Scarano 2002). The term refers to the Quaternary sandy coastal plains in Brazil including geomorphological characteristics, due to the deposition of sandy sediments from marine and fluvial-marine origins, and the plant communities covering these plains (Araujo & Pereira 2004; Zamith & Scarano 2006). The vegetation of Restingas comprise distinct physiognomies (herbaceous, shrubby and tree formations), arranged in mosaics and with high biodiversity (Araujo & Pereira 2004). Drought, salinity, high temperatures, and low soil nutrient contents are the most important limiting factors for plant establishment in these plains (Scarano 2002; 2009). The severity under extreme environmental conditions raises the potential for positive interactions (Hunter & Aarssen 1988; Callaway & Walker 1997; Brooker et al. 2008), even though the role of facilitation is diminished when stress is maximum (Castanho et al. 2015). The positive effect of subordinate shrubs on the diversity and abundance of climbing plants is related to the identity of the subordinate species (Garbin et al. 2012), the traits of climbing species (Garbin et al. 2014), and the spatial organization of the subordinate shrubs (Garbin et al. 2016). The problem is that it is not known if these results are generalizable. The understanding of how subordinate shrubs can promote diversity in such high diversity, extreme, peripheral systems demands the collection of evidences from other plant communities.

Considering the findings presented in Garbin et al. (2012), this study aimed to increase the knowledge about the identity and effects of subordinate species in promoting the diversity of climbing plants in tropical systems. We also aimed to quantify the role of different factors in explaining abundance and diversity of climbing plants. We tested the hypothesis that subordinate woody species are the main factor explaining the abundance and diversity of climbing plants.

Methods

Study site

The study was conducted in the Paulo César Vinha State Park (PCV) (20.59 °S, 40.41°W, sea level), municipality of Guarapari, Espirito Santo state, Southeastern Brazil (Fig.

S1). Temperatures vary between 18ºC and 24ºC, and the annual average rainfall is approximately 1,270 mm. The vegetation present in the PEPCV is characterized as *Restinga* and the studied physiognomy was the open *Clusia* shrub vegetation (Fig. 1). In the same way as in the coastal plains of the Rio de Janeiro state (Scarano 2002), the vegetation is characterized by patches of vegetation scattered in a matrix of white sand, which provides an aspect of mosaic due to the distribution of the vegetation in discontinuous "clumps" in the landscape (Pimentel et al. 2007). Each clump, or patch, provides a good model to understand how changes in subordinate woody species composition affect climbing plants composition and structure (Garbin et al. 2012, 2014, 2016). Each patch can be viewed as a community model and the set of patches as a metacommunity. In the studied site *C. hilariana* was the nucleating tree species at comunity.

Sampling design

We used the same sampling approach used by Garbin et al. (2012). Sampling was carried out systematically in a 2 ha plot of 300 m x 66.6 m (Fig. 2 and Fig. S2). The sampling unit was the clump characterized by the dominance of the *C. hilariana* tree. Only patches with a minimum diameter of 5 meters were sampled. Whether two patches were too much close to each other, although making their boundaries undistinguishable, we considered these as two patches if the distance between the trunks of *C. hilariana* was greater or equal to 5 m. If not, they were considered as a single patch.

Clumps usually can form larger patches of vegetation (Fig. S2), that is, they do not have well-defined natural borders. Withineach sampling unit, a 1 m x 2 m plot was installed in the side of each *C. hilariana* trunk. In each plot, the vegetation data was obtained by an adapted cover pin frame method (Dias et al. 2005) in 15 points or pins (distant every 0.5 m). Each pin had 3 to 5 height strata (of 90 cm each) depending on the height of *Clusia*. This method consists of estimating vegetation density using the number of touches of each species with a thin stick (0.8 cm in diameter) subdivided into 90 cm sections (the strata). This stick was positioned vertically at each point within a plot to record: 1) number of touches of eachplant, 2) touch height section, and 3) the identity of each species that touched the stick. The 15 points were composed to obtain the measure of vegetation density (total number of touches per height interval). For each vegetation clump, the following patch quality characteristics were obtained: the total number of touches of all species at each height interval (one measure of the architecture of the clump, *i.e.*, trellis availability), the area of the clump, and the height of the clump (Dias et al. 2005; Garbin et al. 2012). The spatial coordinates of each clump were registered in the central *Clusia* clump with a Garmin Etrex GPS (Garmin International Inc., Kansas City, USA). The botanical material was collected and later identified with the assistance of specialized botanical literature, comparison with herbarium collections and consultation with specialists. The nomenclature followed the suggestions of APG IV (Chase et al. 2016) and the species were reviewed according to Flora do Brasil (2020 *in construction*).

Data analysis

Partial constrained redundancy analysis (pRDA; Legendre & Legendre 2012) was used to decompose the relative abundances of climbing plants into four components (Økland 2003): association with herbs, association with trees and shrubs, space (MEM's) and patch quality. Thus, five sets of data, one response and four explanatory, were used in the analysis. The space was filtered using Moran Eigenvector Mapping (MEM, Griffith & Peres-Neto 2006; Dray et al. 2012). Variation partitioning was performed hierarchically using the method proposed by (McGarigal & Cushman 2002). Such method separates the partitioning into two tiers. The first tier is the traditional partitioning of response data into the three causal components, while the second-tier further partitioned the response data into subgroups of variables from the first-tier components. These second-tier fractions were obtained through marginal and conditional partitionings. The difference between marginal and conditional partitions in the second-tier procedures is that the first-tier causal components are used as covariables in the conditional partitions (McGarigal & Cushman 2002). In addition, the relationships between patch quality variables and Rényi diversity parameter scales were investigated through the selection of linear models using the Akaike Information Criterion (AIC) as an adjustment measure (Crawley 2002; Venables & Ripley 2002; Crawley 2007). The same was done using woody species (W) as predictors. All the statistical analyzes were performed in the R (R Development Core Team, 2015) program with the vegan version 1.17-1 (Oksanen et al. 2016), PCNM (Legendre et al. 2013) and BiodiversityR packages (Kindt & Coe 2005).

For each sampling unit, the relative abundances (RA) for each group of plants (woodys, herbs, climbers) were calculated separately. For this, the RA of each species was calculated as the number of touches of a species in the stick divided by the total number of touches of all other species of its group. This resulted in three RA matrices of species per sampling unit: matrix C, for climbing plants; matrix W, for woody plants (shrubs and trees); and matrix H, for herb species. Two clumps that did not show any climbing plant were removed. In total, mwe used data from 63 sampling units. In addition, all species with less than five occurrences were removed to minimize analysis noise and improve regression parameters (Borcard et al. 1992; Wagner 2003; Garbin et al. 2012). Relative abundances were normalized (Legendre & Legendre 2012). Species were ranked based on their abundances within each plant group (Magurran 2004).

Eight habitat variables (patch quality) composed matrix P: area of the clumps (calculated as [π (d1/2) (d2/2)], where d1 and d2 are the smallest and largest diameter in meters, respectively); clump height and six architectural variables (trellis availability, calculated as the total number of tree and shrub touches by height class interval, 90 cm each, six height classes, Te1 to Te6) in each sampling unit. The spatial component was included in the analyzes using a matrix (S) composed of the *x* and *y* coordinates. Moran's Eigenvector Mapping (MEM, Griffith & Peres-Neto 2006; Dray et al. 2012) was used to model the relationship between species and the environment and, ensuring the independence between sampling units and the modeling of more complex spatial structures in a context of canonical methods (Borcard et al. 2011; Legendre & Legendre 2012). In this way, spatial dependence is filtered out by *detrending*, but information can be explored from these spatial structures, as they may indicate the effects of unmeasured explanatory variables (McIntire & Fajardo 2009; Dray et al. 2012). Matrix P was standardized prior to analyses (see Legendre & Legendre 2012).

For variation partitioning, partial Redundancy Analysis (pRDA; Legendre & Legendre 2012) was performed using the matrix C as response and matrices W, P, H and S as explanatory datasets. Before partitioning procedures, variables maximally related to the response dataset within each explanatory matrix were selected using vegan's ordistep function with the forward direction. After that, the H matrix was not included in the further analyses because no herb species was selected. The conceptual model of the hierarchical variation decomposition used can be visualized using a Venn Diagram (Fig. 3). The first level of decomposition was composed by three datasets: woody species, space (MEMs), and patch quality variables. The second level of climber community variation used the variables selected in the first level. The first level partition had seven discrete components of explained climber community variation (Fig. 3a). The numbers refer to the components, after variable selection, described in Fig. 3a, these are: (1) pure effect of woody species W (*i.e.*, community variation of climbers explained by W variables, which is also not explained by any P and S); (2) pure P effect; (3) pure S effect; (4) combined effect of W and S variables (*i.e.*, community variation that is explained jointly by W and S factors, but independent of the measured variables of P; (5) combined effect of W and S variables; (6) combined effect of P and S variables; (7) shared effect between W, P and S variables (*i.e.*, community variation that is simultaneously explained by W, P and S variables).

The variables (species) in matrix W were classified into dominant species (D), subordinate species (U) and transient species (T). Thus, in the second level (tier) of decomposition (McGarigal & Cushman 2002), W variables resulted in six variant components (8-10 and 14-16; Fig. 3b$_1$ and Fig. 3b$_2$). No variables in T were significantly related to the response matrix and they were not included in the second-tier decomposition. b$_1$ refers to the effect of the marginal components of the variables W (*i.e.*, variance explained by pure effects of D and U, shared effect of D and U, without taking the variation of first tier components P and S into account). The figure b$_2$ refers to the effect of the conditional components of the W variables (*i.e.*, variation explained only by the pure D and S effect and their shared fractions, but considering first tier components P and S as covariables). In addition, in the second level of the decomposition, the P variables resulted in further six variant components (11-13 and 17-19; Fig. 3c$_1$ and Fig. 3c$_2$), in which the variables in matrix P were classified in patch size variables (I, patch area and height) and trellis availability variables (T, the total number of touches in the stick of woody plants in each stratum, Te1 to Te6). c$_1$ refers to the marginal effects of the variant components of P (*i.e.*, variance explained by pure effects of I and T, shared effect of I and T, without taking the first tier components W and S into account). c$_2$ refers to the effect of the conditional components of the variables I and T, *i.e.*, variation explained only by the pure effect of I and T and their shared fraction. In all partitions, the RsquareAdj function was used in *vegan* to obtain unbiased estimates of the fractions (Griffith & Peres-Neto 2006; Borcard et al. 2011).

To investigate the relationships between environmental variables and diversity, the Rényi scales of diversity (Rényi 1961; Hill 1973; Tóthmérész 1995; Anand & Orlóci 1996) were used. An array containing α parameters of Rényi 0, 1, 2, 3, 5, 10 and 12 (see Oksanen et al. 2016 for details of calculations) per sampling unit (clump) was calculated using all sampled climbing species. The response variables are, in this case, vectors describing diversity. Linear models were used to relate the habitat variables and woody species to each

Rényi diversity vector. The set of explanatory variables comprised the eight variables of matrix P after standardization. The step function was used with the specified *forward* and *backward* directions and AIC as the selection criterion (Crawley 2002; Venables & Ripley 2002). The selected models were tested against a null intercept model, using the anova function with F tests.

Results

Thirteen species of climbing plants, 26 herb species and 63 species of shrubs and trees were identified (Table S1). Considering trees and shrubs, the dominant species was *Clusia hilariana* Schldtl, whereas subordinate species were (Table S2): *Chaetocarpus myrsinites* Baill., *Protium icicariba* (DC.) Marchand, *Calyptranthes brasiliensis* Spreng. *Ocotea notata* (Nees & Mart.) Mez, *Schoepfia brasiliensis* A. D.C, *Pera glabrata* (Schott) Poepp. ex Baill., and *Coccoloba arborescens* (Vell.) R.A.Howard. The other species were classified as transients (Table S2). The most common climbing species was *Smilax rufescens* Grineb. (Fig. S3). Apocynaceae was the richer climber family with six species, while Passifloraceae was represented by two species (Table S1). We observed three species with tendrils (*S. rufescens*, *Passiflora* sp., and *Passiflora galbana* Mast.), while all other species were stem twiners.

For the first-tier partitions, patch height was selected from the P matrix, the filters V5, V8, V4 were selected from the S matrix, and the species *C. brasiliensis* and *Guapira pernambucensis* were selected from the W matrix. No herb species was selected and the H matrix was not used in the further analyses. Variable selection for the second-tier partitions only selected components of W as significant. Thus, W was decomposed into dominant, subordinate, and transient species components in the second-tier partitioning procedures. However, no species of the transient species matrix was selected, and this component was not used in the further partitions. Figure 4 shows the final model used for the first- and second-tier partitions.

Tree species of woody shrubs were responsible for the largest significant fraction of the variation in explaining the relative abundances of climbers in the first-tier partition (Table 1). The spatial fraction had no explanatory power. For the second-tier partitions, the selected subordinate species were *C. brasiliensis*, *P. icicariba* and *C. arborescens*. These species were responsible for the largest fraction of the variation accounting for climbing plants abundances for the marginal partitions. For conditional partitions, we used D and U matrices with the same species of the marginal partition adding matrices of P and S as covariables. Subordinate species (U) were again responsible for the largest fraction of variation (Table 2). The total variation explained by patch size datasets (I and T) was not significant in the second-tier partitions.

The selection of the Rényi diversity parameters showed that trellis availability in the fourth stratum was associated with greater species richness and diversity of climbers (Table 3). However, these final models were not significant. The model based on woody species selected the species *Chaetocarpus myrsinites* and *Clusia hilariana* of all Rényi's diversity parameters tested (Table 3)Discussion

Our results showed that subordinate woody species accounted for the largest fraction of explanation of climbing plants abundances in this coastal system. Moreover, different species of subordinate shrubs favored the abundance and diversity of climbing species. While *Calyptranthes brasiliensis* (Myrtaceae), *Guapira pernambucensis* (Nyctaginaceae), *P. icicariba* and *C. arborecens* seemed to be associated with climber abundance, *Chaetocarpus myrsinites* (Peraceae) and the dominant nurse plant *Clusia hilariana* (Clusiaceae) were more related with climber diversity. Thus, we expanded the knowledge the effects of subordinate woody species in promoting climbing species abundances and diversity. However, the identity of the subordinate species changed. While *Erythroxylum subsessile* was the most important subordinate shrub favoring climbing plants in (Garbin et al. 2012) study, two subordinate species were associated for different aspects of climber presence in our study system

(*Calyptranthes brasiliensis and Chaetocarpus myrsinites)*. Thus, changes in the identity of subordinate species do not affect their effects as promoters of climbing plants abundance and diversity of climbing plants in regional scale, comparing two *Restingas* of tropical system.

The classification of species into dominants, subordinates, and transients, based on their abundances or productivity (biomass), is functional because it expresses the biological activity and the complementarity in resource use (Whittaker 1965; Grime, 1998; Mariotte 2014). However, the knowledge about their functional effects on maintaining diversity was less well-understood and restricted to a single site in southeast Brazil (Garbin et al. 2012; 2014). Our findings expand the knowledge about the role of subordinate species as a functional effect group in promoting and maintaining abundance and diversity of other life forms, in our case, climbing plants.

Subordinate species seem to be functionally redundant in their effects on climbing plants. Functional redundancy is an important component of the resilience of plant communities and it points to the degree of biological simplification a system can pass through without having a significant loss in its structure and function (Walker 1992). If functional redundancy is high, the processes that structure the plant community would remain the same regardless of changes in composition or abundance or species losses. Species with similar roles in a community could be considered as redundant and species losses from different functional groups are more dangerous than losses within a given group (Walker 1992; Fonseca & Ganade 2001). Species could then be replaceable without causing prejudices to ecosystem functioning (Lawton 1994). For a functional group containing many species, these species would be more likely to show functional redundancy (Kang et al. 2015). Our results point to the presence of species redundancy when comparing subordinate species from different restinga sites. The change in subordinate species composition did not affected their effect in promoting climber abundance and diversity.

The understanding about how diversity is organized within discrete functional groups in different communities is crucial for better decisions regarding management in face of functional redundancy (Rosenfeld 2002). This could help anticipate different scenarios to manage communities and ecosystems (Castellanos-castro & Argenis Bonilla 2009). Thus, it is suggested that subordinate shrub species are important for the growth of climbing plants and have a primary role in structuring restinga communities, despite changes in the identity of these subordinate species.

Previous studies showed that subordinate shrub species segregate in space, *i.e.*, they tend to be more abundant in different vegetation patches, when one is presented the other is not (Garbin et al. 2016). Myrtaceae was the family more adundant in our study. Allelopathy was suggested to account for such segregation because Myrtaceae species, well-known for their allelopathic effects (Nishimura et al. 1984; May & Ash 1990; Espinosa-García et al. 2008), were abundant in patches where other subordinate species were less abundant (Garbin et al. 2016). This was more conspicuous for the genus *Myrcia*, which is also known to produce allelopathic effects (Imatomi et al. 2013a, 2013b). In our site, the Myrtaceae species *Calyptranthes brasiliensis* was associated with higher abundance of climbing plants. We suggest that the species redundancy of subordinate species when comparing different resting communities is not generalizable within the restinga studies here. The positive effect of subordinate species over climbing plants was dependent on the identity of the subordinate shrub species: while one species favored abundance, the other was more related to diversity. We suggest that the Myrtaceae species *C. brasiliensis* can favor the abundance of the dominant climbers, especially *Smilax rufescens*, but restricts other climbers probably through allelopathic compounds. This is in opposition to the positive association of the Peraceae species *C. myrsinites* with higher richness and diversity of climbers. Thus, identity matters for the positive effects of subordinate species on diversity and abundance of climbing plants in our site study .

The role of the dominant species, *C. hilariana*, on subordinate shrubs and climbers in our site seems to be similar to its effects in other restingas. In the Jurubatiba National Park, Rio de Janeiro State, this species is well-known for its role as a nurse-plant for other plant species growing under its canopy and by inhibiting their growth as succession proceeds mainly through shadowing understory species (Zaluar & Scarano 2000). *C. hilariana* also nucleates vegetation patches in the Paulo Cesar Vinha Park. Our results point to conjunct role of this species with *C. myrsinites* in favoring the richness and diversity of climbing plants through higher availability of trellis support. Given that higher climber richness was found at the fourth stratum, it is suggested that climbers use subordinate species as initial support, and then use higher availability of trellis *C. hilariana* as an upper canopy support. Moreover, a single climbing individual may reach the canopy trough a single patch, and then grows using several different patches only through the canopy. This can lead to a high number of species in a patch, without association to local patch attributes other than trellis availability at the upper canopy, mainly through *C. hilariana*. Therefore, trellis availability produced by subordinate shrubs and *C. hilariana* would be the main causes acting over climber abundance and diversity in this site. Our initial hypothesis that subordinate shrubs would be responsible for the larger fraction of the causes acting over climber abundance and diversity was confirmed. The results suggest, as proposed by (Garbin et al. 2012), that subordinate species account for the maintenance of abundance and diversity of climbers in this fisionomy of restinga.

Conclusions

Our results corroborate the findings from Garbin et al. (2012) showing that subordinate shrubs are the main structuring agents of climber plant community in the restinga. Moreover, it suggests, that different subordinate shrubs drive diversity and abundance of climbers. We also demonstrate that the dominant nurse, *Clusia hilariana*, along with one subordinate shrub, was associated with higher climber diversity at the upper canopy of the patch. Future studies should made use of a functional approach to understand how subordinate shrubs relate to climbers, and test whether allelopathic effects can affect the climbing plants. Subordinate shrubs should also be used in restoration programs in order to increase species diversity in degraded restingas.

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Figures' captions

Figure 1. Two examples of the vegetation patches of the Paulo Cesar Vinha State Park: an isolated patch surrounded by white sand (a), and a vegetation patch with its borders in contact with nearby patches (b). Photo credit: Flora Misaki, 2016.

Figure 2. Spatial configuration of the sampled vegetation patches. The size of the bubbles corresponds to the size area (m^2) of every sampled patch.

Figure 3. Conceptual model showing first- and second-tier decompositions to understand how woody plants, patch quality, and space affect climbing plants. Circles correspond to the total species variance accounted for by each individual variable subset. The numbered areas correspond to the individual variance components. There are five different decompositions and a total of 19 separate variance components considering the two tiers: 7 at the first tier (a), and 12 at the second tier associated with four different partitionings (b_1, b_2, c_1, c_2). Solid arrows depict the second-tier marginal decompositions from first-tier circles. Dotted arrows are second-tier conditional decompositions from first-tier independent effects (gray area). A, first-tier decomposition of climber community variation into three components: woody species, patch quality and space (MEMs). b1, second tier decomposition of marginal woody species-level factors into two components: dominant (D) and subordinate (U) species. b2, second-tier decomposition of conditional woody species-level factors into dominant and subordinate species. c1, second-tier decomposition of marginal patch quality-level factors into patch size (I, area and height) and trellis availability (T, Te1 to Te6). c2, second-tier decomposition of conditional patch quality-level factors.

Figure 4 - Selected model showing the first- and second-tier decompositions. Circles correspond to the total species variance accounted for by each individual variable subset. The numbered areas correspond to the individual variance components. In this two tiered partitioning, we derive a total of 13 separate variance components, 7 at the first tier (depicted by the inner three overlapping circles), and 6 at the second tier associated with three different partitionings (depicted by the three sets of overlapping circles on the periphery). In the figure, the solid arrows are from first-tier circles to second-tier marginal decompositions, while dotted arrows are from first-tier independent effects, to second-tier conditional decompositions corresponding to the hatching area. The three different decompositions are labeled as follows: A. first-tier decomposition of woody species, patch quality and space (MEMs) level factors; Bm. Second tier decomposition of marginal species dominants and subordinates-level factors; Bc. Second-tier decomposition of conditional species dominants

and subordinates -level factors. It is observed that the variables of space and patch quality were not significatives, so they did not enter on the second level of partitions.

Tables' captions

Table 1. Summary of calculation and results of partial constrained redundancy analysis (pRDA) of the first tier (Fig. 3). Climbing plants abundances were used as response and woody species abundances, space (MEMs) and patch quality (size and trellis availability) as explanatory datasets. Steps 1a–1c are the first order partial terms; 2a–2f, second order partial unions; 3, third order partial unions, ∪ combined variation, ∩ shared variation. See text for details.

Table 2. Summary of calculation and results of second tier partial constrained redundancy analysis (pRDA) using (b1) species subordinates and dominants and (b2) patch quality and space added to subordinates and dominants (see Fig. 3). In Marginal partition relative abundances of climbers were used as response matrix to two sources of variation: D (species dominants) and U (species subordinates). In Conditional partition, relative abundances of climbers were used as response matrix to four sources of variation: P (patch quality variables), S (spatial variables) added to D and U. Steps and calculations follow Økland (2003). Steps 4a–4b and 6a-6d are the first order partial terms; 5, second order partial unions; 7, second order partial intersections; ∪ combined variation, ∩ shared variation. See text for analytical details. Negative fractions were interpreted as zeros (see Legendre, 2012).

Table 3. Final models of Rényi scale parameters of climber species diversity in function of the environmental variables (patch area, height, and six architectural variables describing trellis availability) and woods species as variables selected by lowest AIC. Abbreviations: 4th stratum, total number of touches of all trees/shrubs at the fourst stratum (271–360 cm); Adj. R2 is the adjusted R2; RSS, the residual sum of squares of the final model; Res. DF, the residual degrees of freedom; Res. SE, the residual sum of squares; AIC, Akaike's Criterion of Information for null (intercept) and final models (f.m.), F-statistic and Pr(>F), p-value..

Supplementary material

Figure S1. Location map of the Paulo César Vinha State Park in the municipality of Guarapari, state of Espírito Santo, southeastern.

Figure S2. Satellite image of study site.

Figure S3. Species abundance distribution for climbers in 2 ha of a Restinga vegetation. Values in *y* axis are the percent log of mean relative abundances of the vegetation patches.

Table S1. List of surveyed species in the Paulo César Vinha State Park, Southest Brazil. See Methods for sampling details. At the family level, there were 16 unidentified plant materials for woody plants; 3 for herbs; and 2 for climbers.

Table S2. Woody shrub and tree species in 2 ha of Restinga vegetation followed by the species, code, relative abundance, cumulative relative abundance and frequency.

Figure 1

a)

b)

Figure 2

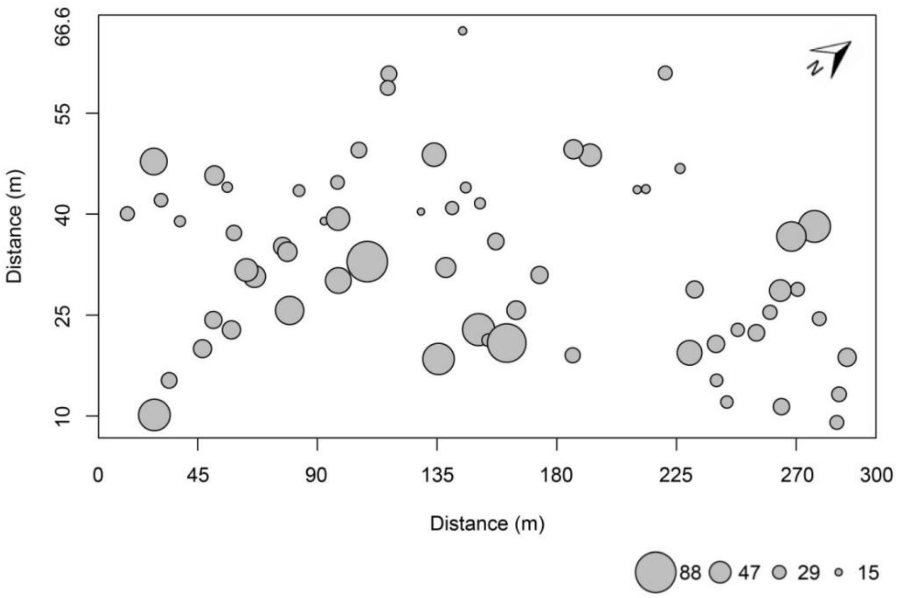
66.6
55
40
25
10
Distance (m)
0
45
90
135
180
225
270
300
Distance (m)
N
88
47
29
15

Figure 3

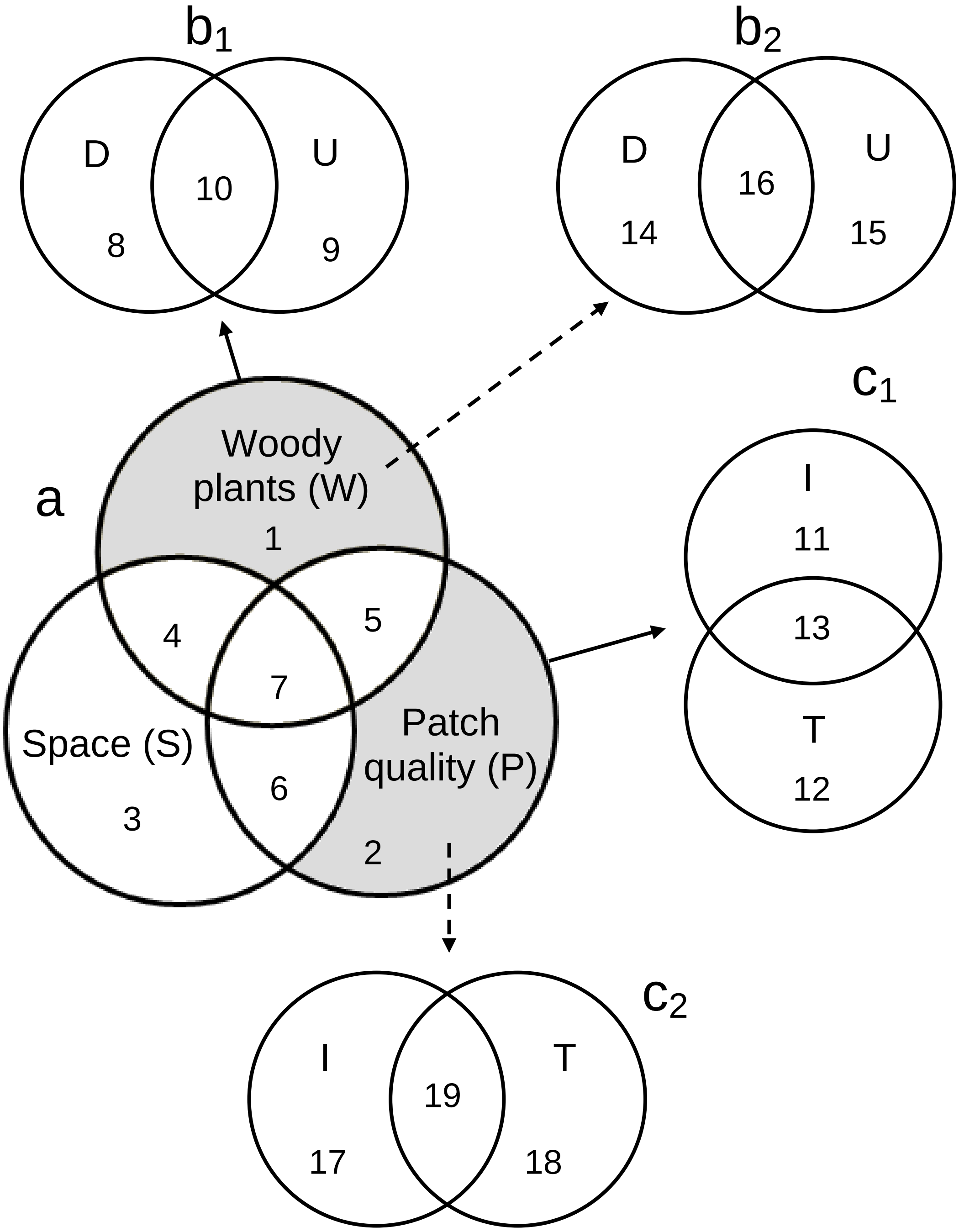
b1
D
10
U
8
9
b2
D
16
U
14
15
c1
a
Woody plants (W)
1
I
11
4
5
13
7
Space (S)
Patch quality (P)
T
6
12
3
2
c2
I
T
19
17
18

Figure 4

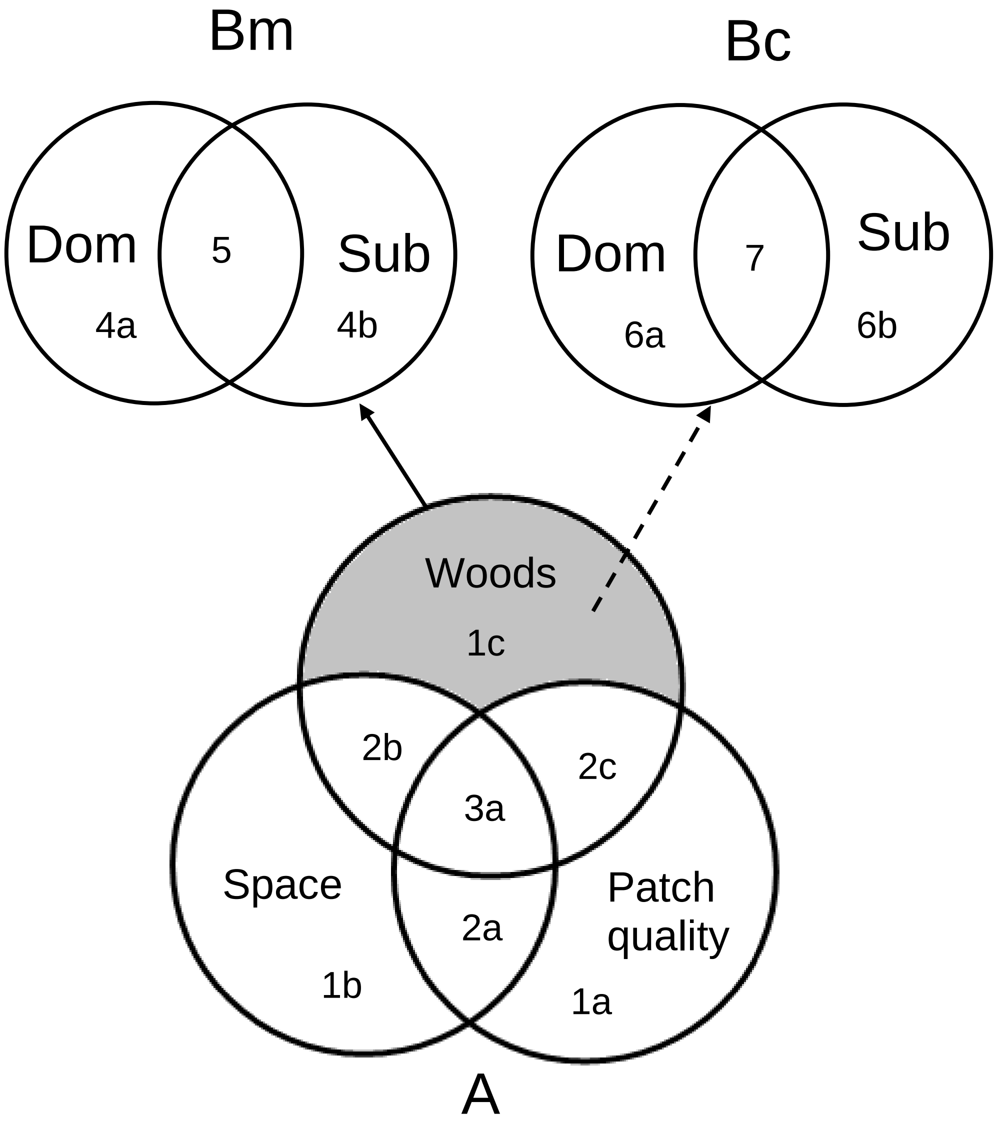
Bm
Bc
Dom
5
Sub
4a
4b
Dom
7
Sub
6a
6b
Woods
1c
2b
2c
3a
Space
2a
Patch quality
1b
1a
A

Figure S1

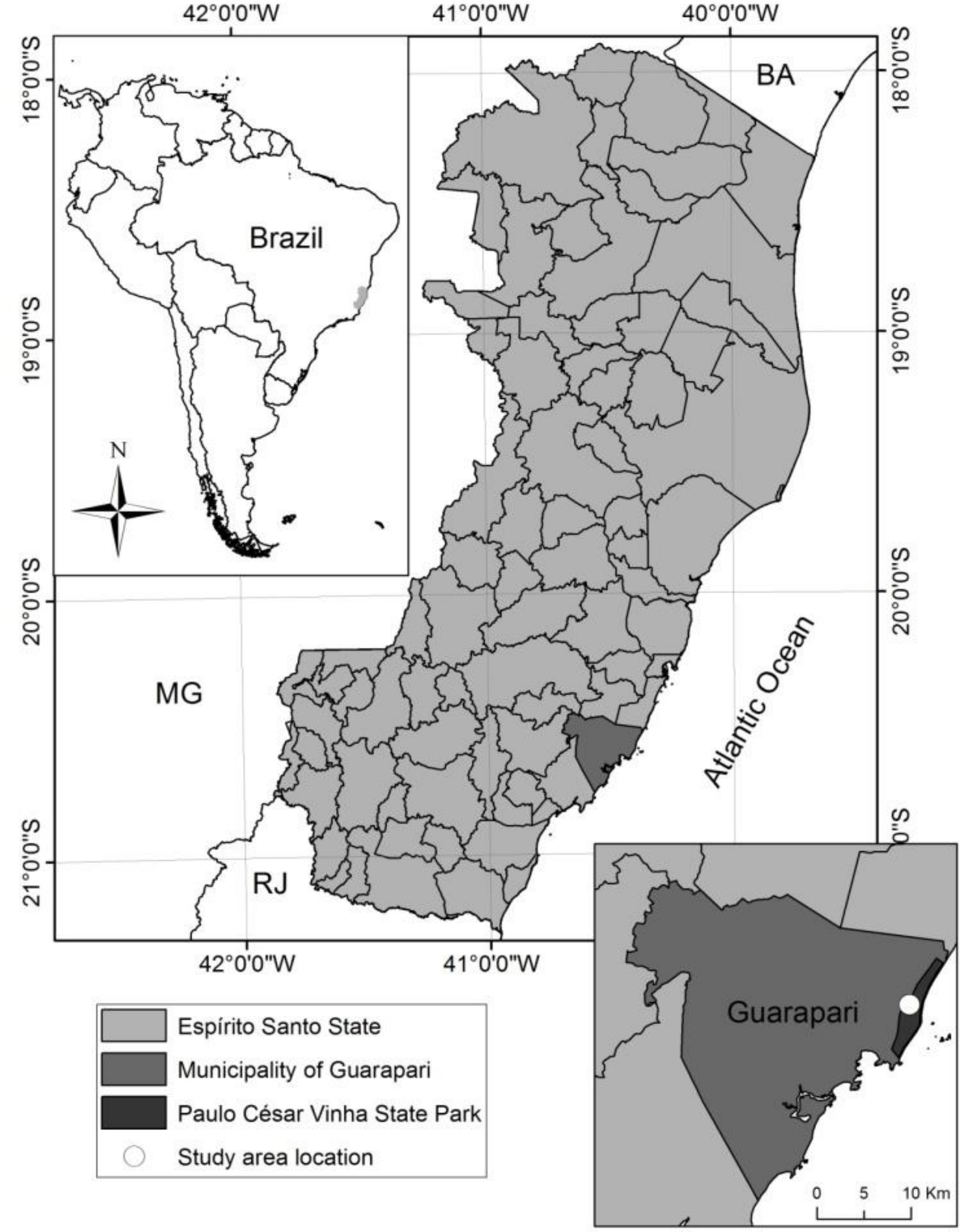
42°0'0"W
41°0'0"W
40°0'0"W
18°0'0"S
19°0'0"S
20°0'0"S
21°0'0"S
Brazil
N
BA
MG
RJ
Atlantic Ocean
Guarapari
0 5 10 Km
Espírito Santo State
Municipality of Guarapari
Paulo César Vinha State Park
Study area location

Figure S2

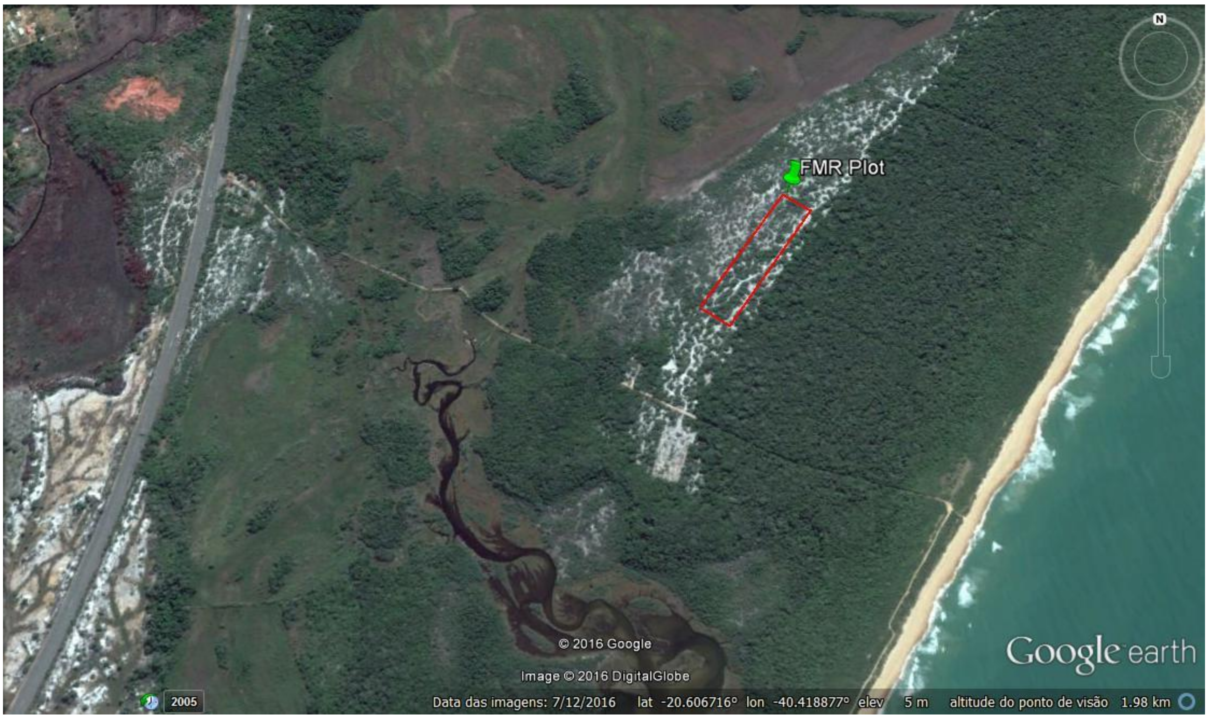
N
FMR Plot
© 2016 Google
Image © 2016 DigitalGlobe
Google earth
2005
Data das imagens: 7/12/2016 lat -20.606716° lon -40.418877° elev 5 m altitude do ponto de visão 1.98 km

Table 1.

Step	Component of variation	Calculation	% Explained variation (adjusted)	*P* value
0	Total variation explained (TVE)	C(W ∪ P ∪ S)	**33.39 (12.11)**	**0.039**
1a	Patch quality (P) Pure	C((P)| W ∪ S)	14.86 (0.75)	0.413
1b	Space (S) Pure	C((S)| W ∪ P)	3.05 (-1.49)	0.655
1c	Woody species (W) Pure	C((W)| S ∪ P)	**8.77 (7.51)**	**0.012**
2a	S ∪ P	C((S ∪ P)| W)	18.39 (-0.04)	0.479
2b	W ∪ P	C((W ∪ P)| S)	29.95 (13.59)	0.030
2c	W ∪ S	C((W ∪ S)| P)	11.76 (5.57)	0.089
2d	P ∩ S	2a − (1a + 1b)	0.47 (0.70)	
2e	P ∩ W	2b – (1a + 1c)	6.31 (5.33)	
2f	S ∩ W	2c – (1b + 1c)	-0.07 (-0.46)	
3	P ∩ S ∩ W	TVE – (1a+1b+1c+2a+2b+2c)	-0.02 (-0.24)	
	Unexplained variation (UV)	(UV / TVE) * 100	66.61 (87.89)	

Table 2

Step	Component of variation	Calculation	% Explained variation biased and (adjusted)	P value
Second-tier (b1): Marginal factors				
0	Total variation explained (TVE)	C (D ∪ U)	**14.20 (9.83)**	**0.005**
4a	Dominants Pure (D)	C((D)| U)	1.18 (-0.28)	0.477
4b	Subordinates Pure (U)	C((U)| D)	**13.07 (10.33)**	**0.001**
5	D ∩ U	0 – (4a +4b)	0 (-0.21)	
	Unexplained variation (UV)	UV / TVE *100	85.80 (90.17)	
Second-tier (b2): Conditional factors				
0	Total variation explained (TVE)	C (D ∪ U | P ∪ S)	**13.75 (10.17)**	**0.002**
6a	D Pure	C ((D) | U ∪ P ∪ S)	1.47 (0.06)	0.361
6b	U Pure	C ((U) | P ∪ S ∪ D)	**12.17 (10.16)**	**0.006**
7	D ∩ U	0 – (6a + 6b)	0.11 (-0.06)	
	Conditional (covariables)		8.59	
	Unexplained variation (UV)	UV / TVE *100	77.66 (89.83)	

Table 3

Rényi scale parameter	Final model	Adj. R2	RSS f.m.	Res. DF	Res. SE	AIC null	AIC f.m.	F	Pr (>F)
Patch quality									
0	4th stratum	0.030	13.537	61	0.471	-91.96	-92.87	2.887	0.094
5	4th stratum	0.025	7.489	61	0.350	-129.56	-130.17	2.578	0.114
12	4th stratum	0.031	6.453	61	0.325	-138.52	-139.55	3.004	0.089
Woody species abundances									
0	*C. myrsinites* + *C. hilariana*	0.096	12.401	60	0.455	-91.96	-96.40	4.299	0.018
1	*C. myrsinites* + *C. hilariana*	0.095	9.847	60	0.405	-106.57	-110.93	4.258	0.019
2	*C. myrsinites* + *C. hilariana*	0.087	8.583	60	0.378	-115.67	-119.58	4.017	0.024
5	*C. myrsinites* + *C. hilariana*	0.083	6.930	60	0.340	-129.56	-133.06	3.792	0.028
12	*C. myrsinites* + *C. hilariana*	0.080	6.030	60	0.317	-138.52	-141.82	3.685	0.031

Table S1

Family	Taxon	Habit
Annonaceae	Annonaceae sp.	woody
Apocynaceae	*Oxypetalum alpinum* (Vell.) Fontella	climber
	Peplonia asteria (Vell.) Fontella & A. Schwasz	climber
	Temnadenia odorifera (Vell.) J.F. Morales	climber
	Apocynaceae sp.1	climber
	Apocynaceae sp.2	climber
	Apocynaceae sp.3	climber
Araceae	*Anthurium parasiticum* (Vell.) SteIIfeld	herb
Arecaceae	*Allagoptera arenaria* (Gomes) Kuntze	herb
Bromeliaceae	*Aechmea nudicaulis* (L.) Griseb.	herb
	Aechmea bromeliifolia (Rudge) Baker	herb
	Aechmea lingulata (L.) Baker	herb
	Vriesea neoglutinosa Mez	herb
	Vriesea procera (Mart. ex Schult. & Schult.f.) Wittm.	herb
	Tillandsia sp.	herb
Burseraceae	*Protium icicariba* (DC.) Marchand	woody
Cactaceae	*Hylocereus setaceus* (Salm-Dyck) R.Bauer	herb
	Cereus sp.	herb
Calophyllaceae	*Kielmeyera albopunctata* Saddi	woody
Celastraceae	*Maytenus obtusifolia* Mart.	woody
	Maytenus sp.1	woody
	Maytenus sp.2	woody
	Maytenus sp.3	woody
Commelinaceae	*Dichorisandra* sp.	herb
Clusiaceae	*Clusia hilariana* Schltdl.	woody
	Clusia criuva Cambess.	woody
	Garcinia brasiliensis Mart.	woody
Chrysobalanaceae	*Couepia ovalifolia* (Schott) Benth. ex Hook.f.	woody
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn	herb
Ericaceae	*Agarista revoluta* (Spreng.) J. D. Hook. ex Nied.	woody
	Ericaceae sp.	herb
Eriocaulaceae	*Paepalanthus klotzschianus* Körn.	herb
Erythroxylaceae	*Erythroxylum subsessile* (Mart.) O.E. Schulz	woody
	Erythroxylum sp. 1	woody
	Erythroxylum sp. 2	woody
	Erythroxylum sp. 3	woody
Fabaceae	Fabaceae sp.	woody
Fabaceae	*Andira fraxinifolia* Benth.	woody
Lauraceae	*Ocotea notata* (Nees & Mart.) Mez	woody
	Nectandra sp.	woody
Liliaceae	Liliaceae sp.	herb

Malpighiaceae	*Stigmaphyllon paralias* A.Juss.	woody
Melastomataceae	Melastomataceae sp.	woody
Moraceae	*Ficus tomentella* (Miq.) Miq.	woody
Myrtaceae	*Campomanesia* sp.	woody
	Eugenia astringens Cambess.	woody
	Eugenia ilhensis O.Berg	woody
	Eugenia punicifolia (Kunth) DC.	woody
	Eugenia sulcata Spring ex Mart.	woody
	Eugenia pisiformis Cambess.	woody
	Myrcia bergiana O.Berg	woody
	Myrciaria floribunda (H.West ex Willd.)O.Berg	woody
	Neomitranthes obtusa Sobral & Zambom	woody
	Psidium brownianum Mart. ex DC.	woody
	Psidium cattleianum Sabine	woody
	Calyptranthes brasiliensis Spreng.	woody
	Myrtaceae sp.	woody
	Marlierea neuwiediana (O.Berg) Nied.	woody
Nyctaginaceae	*Guapira pernambucensis* (Casar). Lundell	woody
	Guapira obtusata (Jacq.) Little	woody
Ochnaceae	*Ouratea cuspidata* (A. St.-Hil.) Engl.	woody
Olacaceae	*Heisteria* sp.	woody
Opiliaceae	*Schoepfia brasiliensis* A.DC.	woody
	Schoepfia sp.	woody
Orchidaceae	*Cattleya* sp.1	herb
	Cattleya sp.2	herb
	Cattleya guttata Lindl.	herb
	Cyrtopodium holstii L.C.Menezes	herb
	Vanilla sp.	herb
Passifloraceae	*Passiflora alata* Aiton	climber
	Passiflora sp.	climber
Peraceae	*Pera glabrata* (Schott)Poepp. ex Baill.	woody
	Chaetocarpus echinocarpus (Baill.) Ducke	woody
	Chaetocarpus myrsinites Baill.	woody
Polipodiaceae	*Microgramma* sp.	herb
Polipodiaceae	*Polypodium* sp.1	herb
Polipodiaceae	*Polypodium* sp.2	herb
Polygonaceae	*Coccoloba arborescens* (Vell.) R.A.Howard	woody
Primulaceae	*Myrsine guianensis* (Aubl.) Kuntze	woody
	Myrsine parvifolia A.DC.	woody
Rubiaceae	*Chiococca alba* (L.) Hitchc.	woody
	Emmeorhiza umbellata (Spreng.) K. Schum.	climber
	Rudgea sp.	woody
	Melanopsidium nigrum Colla	woody
Sapindaceae	*Paullinia weinmanniifolia* Mart.	climber
	Dodonaea viscosa Jacq.	woody
	Smilax rufescens Grineb.	climber

Unidentified family	Sixteen materials	woody
	Three materials	herb
	Two materials	climber

Table S2

Taxon	Code	Abundance	Cumulative relative abundance (%)	Frequency
Clusia hilariana	chi	33.79	100.00	63
Protium icicariba	pic	5.92	46.37	38
Calyptrantes brasiliensis	mcfo	5.80	36.98	44
Schoepfia brasiliensis	sbr	1.85	27.77	20
Ocotea notata	ono	1.49	24.84	24
Coccoloba arborescens	car	1.47	22.48	12
Chiococca alba	cal	1.41	20.15	10
Calyptranthes brasiliensis	cbr	1.29	17.92	34
Myrciaria floribunda	mfl	1.23	15.87	5
Pera glabrata	pgl	0.92	13.92	17
Myrcia bergiana	mbe	0.70	12.47	5
Eugenia astringens	eas	0.56	11.35	3
Fabaceae ou Leguminosae sp2	flsp2	0.54	10.46	10
Psidium brownianum	pbr	0.50	9.61	3
Heisteria sp.	hcfp	0.47	8.82	6
Andira fraxinifolia	afr	0.47	8.08	8
Garcinia brasiliensis	bgr	0.45	7.33	1
Myrsine parvifolia	mpa	0.40	6.62	4
Guapira pernambucensis	gpe	0.30	6.00	6
Ouratea cuspidata	ocu	0.28	5.51	5
Nectandra sp.	ncfp	0.27	5.07	7
Unidentified 8	i8	0.24	4.65	1
Melanopsidium nigrum	mni	0.21	4.27	2
Clusia criuva	ccr	0.19	3.94	2
Neomitranthes obtusa	nob	0.18	3.64	1
Annonaceae sp.	ansp	0.17	3.35	1
Ficus tomentella	fto	0.17	3.08	1
Stigmaphyllon paralias	spa	0.16	2.81	7
Unidentified 72	i72	0.16	2.55	4
Chaetocarpus myrsinites	cmy	0.15	2.29	1
Unidentified 24	i24	0.15	2.05	1
Eugenia sulcata	seu	0.10	1.82	2
Maytenus sp.	msp	0.10	1.67	2
Dodonaea viscosa	dvi	0.09	1.51	3
Chaetocarpus echinocarpus	cec	0.08	1.37	1
Unidentified 143	i143	0.07	1.25	2
Myrtaceae sp.	myr	0.06	1.13	1
Unidentified 153	i153	0.05	1.05	1
Eugenia pisiformis	epi	0.05	0.96	3
Unidentified 4	i4	0.05	0.87	1
Erythroxylum sp.	esp	0.05	0.79	1
Campomanesia sp.	ccfg	0.05	0.71	2

Unidentified 7	i7	0.05	0.63	1
Erythroxilum subsessile	esu	0.03	0.56	2
Eugenia ilhensis	eil	0.03	0.50	1
Unidentified 3	i3	0.03	0.45	1
Erythroxilum sp. 1	ecfs	0.02	0.41	1
Unidentified 11	i11	0.02	0.38	1
Unidentified 16	i16	0.02	0.34	1
Melastomataceae sp.	mesp	0.02	0.31	1
Rudgea sp.	rcfu	0.02	0.28	1
Myrsine guianensis	mgu	0.02	0.25	1
Couepia ovalifolia	cov	0.02	0.22	1
Marlierea neuwiediana	mne	0.02	0.19	1
Maytenus obtusifolia	mob	0.02	0.17	1
Psidium cattleianum	pca	0.02	0.14	1
Unidentified 55	i55	0.02	0.11	1
Unidentified 56	i56	0.02	0.09	1
Kielmeyera albopunctata	kal	0.02	0.07	1
Maytenus sp.	mcf	0.01	0.04	1
Guapira obtusata	gob	0.01	0.02	1
Erythroxilum sp. 2	ecfn	0.00	0.00	1
Schoepfia sp.	ssp	0.00	0.00	1