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Padrões de Variação da Diversidade Funcional e de  
Espécies em Comunidades Arbóreas na Floresta  
Atlântica do Sul do Brasil

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# Padrões de Variação da Diversidade Funcional e de Espécies em Comunidades Arbóreas na Floresta Atlântica do Sul do Brasil

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*Dedico meu trabalho aos que se emocionam  
com os perfis das encostas e seus tons de verde  
ao amanhecer.*

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## RESUMO

O conhecimento sobre o funcionamento e a diversidade das florestas tropicais vem crescendo nos últimos anos. Formas de quantificar as causas da diversidade beta funcional estão sendo desenvolvidas e perguntas sobre quais fatores determinam essa variação da diversidade em comunidades permanecem em aberto, sobretudo em uma escala regional. Nosso objetivo foi identificar as causas da variação da diversidade (i.e. diversidade beta) de espécies e da diversidade funcional de uma metacomunidade de árvores na Floresta Ombrófila Densa Submontana do sul do Brasil, extremo sul de seu limite de distribuição. Nossa hipótese é de que as causas da diversidade beta funcional e de espécies são distintas. A diversidade beta funcional seria explicada por fatores ambientais e a diversidade beta de espécies por fatores históricos. Para testar nossa hipótese utilizamos a análise de partição da variação através da análise de redundância canônica (RDA). Assim, quantificamos a porção da diversidade beta de espécies e funcional entre comunidades explicada pela variação de variáveis explanatórias ambientais (variáveis bioclimáticas e topológicas) ou espaciais (PCNMs). Também tivemos acesso à porção não explicada por nenhum destes fatores, possivelmente relacionada a variáveis não mensuradas ou fatores internos da comunidade como interações biológicas. Compilamos a informação da composição de espécies arbóreas de 12 sítios ao longo da metacomunidade e coletamos atributos de 104 espécies para compor a informação funcional. Como variáveis resposta utilizamos a matriz de composição de espécies, para a abordagem taxonômica, e duas matrizes para a abordagem funcional, uma de atributos médios ponderados pela abundância das espécies na metacomunidade e outra de abundâncias das espécies ponderada pelas relações difusas definidas pelas suas similaridades funcionais. Os resultados indicaram que 82% da diversidade beta de espécies não foi explicada pelas variáveis explanatórias, enquanto que para as matrizes de diversidade funcional essa fração diminuiu para 43 e 37%. A fração puramente ambiental representou 5% da explicação da diversidade beta de espécies, e para a diversidade funcional ela não foi significativa. Porém, o ambiente estruturado no espaço explicou 17 e 21% da variação da diversidade beta funcional e 8% da variação de espécies, e a fração espacial foi significativa para ambas as abordagens (5% na taxonômica e 42 e 44% na funcional). Diagramas de dispersão mostraram as comunidades latitudinalmente estruturadas quanto à composição de espécies, enquanto na abordagem funcional comunidades geograficamente distantes resultaram ser semelhantes. A diversidade beta de espécies é causada por uma variação latitudinal fortemente relacionada às variáveis ambientais. Fatores históricos, como a migração da floresta no sentido norte-sul podem ser os principais determinantes deste padrão. A diversidade-beta funcional, também determinada por fatores espaciais, está relacionada a escalas mais finas de variação espacial podendo estar ligada a centros de endemismo e rotas de migração regionais. Os diferentes padrões detectados analisando a diversidade funcional e de espécies mostram a importância das duas abordagens para o entendimento da metacomunidade.

*Palavras-chave:* diversidade-beta, gradientes ambientais, atributos funcionais, Floresta Atlântica, metacomunidades de plantas.

## **ABSTRACT**

In the last years, knowledge about the functionality of tropical forest has grown. Ways of quantifying beta-diversity causes are still under developing and questions about what factors determine diversity variation, especially on a regional scale, have not been answered yet. Our aim was to identify the drivers that are defining variation of functional and species diversity (i.e. functional and species beta-diversity) in a Southern Brazilian Atlantic rainforest tree metacommunity, located along the coast of Paraná, Santa Catarina and northeast Rio Grande do Sul states. We hypothesize that different drivers explain functional and species diversity variation within the metacommunity. Specifically, environmental variables, representing niche processes, may define functional diversity patterns along the gradient whereas species diversity should be explained by metacommunity history, represented by the spatial variables. To test this we partitioned the variation of each variable set through redundancy analyses (RDA). So we used a matrix of space, represented by eight PCNM variables, and other of environment, represented by climatic and topologic variables, as explanatory matrices. The unexplained fraction of variation was further quantified, which is often related to unmeasured variables or internal community factors such as biotic interactions. We compiled tree species composition data from 12 sites and to assess functional information we sampled traits of 104 species representing plant ecological strategies. We used the species composition matrix and two functional diversity matrices, a community-weighted mean trait matrix and a functional fuzzy-weighted matrix, as response variables. A large unexplained fraction (82%) was found for species beta-diversity data, whereas this fraction had lower values for functional beta-diversity (43 and 37%). A pure environmental fraction represented 5% of species beta-diversity explanation and it was not significant for functional beta-diversity. Spatially structured environmental fraction explains a large amount of both functional (17 and 21%) and species (8.4%) beta-diversity, and the pure spatial fraction was significant for both (5% to species and 42 and 44% to functional). Scatter diagrams showed that species composition data is latitudinally structured, whereas functional information can be similar despite of geographical distance. Species beta-diversity was mainly caused by latitudinal variation (large spatial scale) related with climatic environmental variables. Historical factors as the north-south forest migration may be determining this pattern. Functional beta-diversity was related to this spatial variation as well, but finer spatial scale related with local endemism centers and species migration routes are also influencing. Different patterns detected by species and functional beta-diversities showed the importance of both approaches to understand tree metacommunity patterns.

*Key words:* beta-diversity, environmental gradients, functional traits, Brazilian Atlantic Forest, plant metacommunity.

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## INTRODUÇÃO GERAL

O verde do mar de morros que acompanha o litoral brasileiro passa a ideia de uma floresta homogênea e intocada. Porém, aqueles que conhecem essas matas, ou a teoria sobre ecossistemas tropicais e sua complexidade, sabem que a realidade da floresta se aproxima mais de uma colcha de retalhos. Buscar padrões e tentar entender os processos que alinhavaram cada fragmento são verdadeiros enigmas que instigam a curiosidade de diversos pesquisadores. Com este trabalho buscamos encontrar pistas sobre como a Floresta Ombrófila Densa do Sul do Brasil está moldada. Nesta busca tentamos entender, utilizando partição da variação da diversidade funcional e de espécies, como os retalhos foram dispostos e o que gerou esta disposição.

A Floresta Ombrófila Densa é a formação mais característica do bioma Mata Atlântica sendo conhecida como Floresta Atlântica *sensu stricto* (Oliveira-Filho & Fontes 2000). Esta formação acompanha o litoral brasileiro tendo como barreira oeste as serras do Mar e Geral. Trata-se uma floresta tropical úmida com grande diversidade, sendo considerada um *hotspot* da biodiversidade (Myers *et al.* 2000). Por estar localizada justamente na região de maior concentração humana do país, as regiões de mais fácil acesso, baixadas e encostas pouco íngremes, deram lugar a centros urbanos ou lavouras. O corte seletivo realizado até 1988, quando a lei da Mata Atlântica entrou em vigor tornando o corte de madeira nativa crime, causou grandes danos à estrutura original da floresta. Um exemplo claro é o dano às populações de *Ocotea catharinensis* Mez, popularmente conhecida como canela-preta. Esta espécie considerada uma das mais abundantes em várias regiões da Floresta Ombrófila Densa do sul do Brasil

(Klein 1980) é rara nos levantamentos atuais realizados na região (Vibrans *et al.* 2010).

Seu fácil acesso e proximidade aos centros urbanos também fez com que a floresta fosse bem conhecida em termos florísticos. Mas, assim como para a maioria dos ecossistemas tropicais, pouco se sabe quanto aos seus padrões regionais de organização. No sul de seu limite de distribuição estes enigmas começaram a ser desvendados por botânicos e naturalistas que descreveram a região quanto a aspectos físicos e florísticos (Rambo 1942; Veloso & Klein 1968). Em muitos de seus trabalhos é possível encontrar hipóteses sobre a dinâmica deste ecossistema (Rambo 1951; Klein 1984b). Estes relatos incluem informações sobre possíveis rotas de migração de espécies, centros de endemismo e barreiras biogeográficas. Muitos levantamentos fitossociológicos e estudos florísticos têm sido realizados na região e, desde o início da última década, pesquisadores começaram a reunir esta informação para responder perguntas ecológicas na escala regional (Oliveira-Filho & Fontes 2000; Duarte, Carlucci & Pillar 2009; Marques, Swaine & Liebsch 2011).

Esse movimento tem ocorrido em todo o mundo e o entendimento das florestas tropicais, seus padrões e processos, tem se tornado um dos focos da ecologia. Métodos de ecologia funcional são comumente utilizados para esse propósito. Esta abordagem apresenta vantagens que complementam a maneira mais tradicional de se estudar as comunidades biológicas, como por exemplo: a possibilidade de acessar as regras que moldam a comunidade (Pillar *et al.* 2009), pensando que as características das espécies (i.e. seus atributos funcionais) revelam sua ligação com o ambiente e são a resposta das interações entre os indivíduos da comunidade; permitem ligar a informação biológica aos processos

ecossistêmicos (Diaz *et al.* 2007), com uma abordagem mecanicista da comunidade; e comparar padrões e processos encontrados em ecossistemas mesmo quando estes possuem espécies distintas, já que essa abordagem tenta desvincular do rótulo da espécie.

A ideia deste trabalho foi utilizar esta abordagem funcional para acessar a informação da dinâmica regional da metacomunidade de espécies arbóreas da Floresta Ombrófila Densa do sul do Brasil. Para isso aplicamos a técnica de partição de variância (Borcard, Legendre & Draupeau 1992) através de análises de redundância (RDA) a conjunto de dados de espécies e funcional. A utilização desta análise à abordagem funcional é recente na literatura e a forma com que foi realizada não foi explorada até então. Estes foram os principais motivadores da pesquisa gerando muita curiosidade tanto do ponto de vista teórico e metodológico como da informação que essa abordagem poderia gerar para o melhor entendimento deste ecossistema.

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## **CAPÍTULO 1<sup>1</sup>**

### **Different drivers of functional and species composition variation across a forest tree metacommunity in Southern Brazil**

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<sup>1</sup> O conteúdo deste capítulo encontra-se estruturado para submissão ao periódico *Functional Ecology*. Por esse motivo foi escrito na língua inglesa e não acompanha a estruturação do restante do documento. Autores do artigo a ser submetido: Adriane Esquivel Muelbert, Lúcia Sevegnani, Sandra Cristina Müller

## INTRODUCTION

The comprehension of the causes of biodiversity variation at the metacommunity<sup>2</sup> level is key to understanding ecosystems and giving support to conservation policy. Different origins of variation of species diversity require different conservation strategies (Legendre, Borcard & Peres-Neto 2005). However, there is a huge discussion about how to assess the processes that lead the variation of species composition in the metacommunity (Legendre, Borcard & Peres-Neto 2005; Tuomisto & Ruokolainen 2006; Legendre, Borcard & Peres-Neto 2008; Tuomisto & Ruokolainen 2008). On the other hand, any approach restricted to species composition may be limited to access information about ecosystem functions and services. A link between composition and ecosystem processes can be made through functional traits (Diaz *et al.* 2007), and with this information communities can be seen in a more mechanistic way. Thus important knowledge can also be obtained if we consider in metacommunity analysis not only the variation in community composition but also the differences between species, through functional traits. Methods to assess the origins of functional diversity variation in the metacommunity and its interpretations have just started being discussed (de Bello *et al.* 2010; Meynard *et al.* 2011; Stegen & Hurlbert 2011).

Species interactions, dispersion limitation and environmental control are the main hypotheses regarding the origin of species composition variation in metacommunities (Legendre, Borcard & Peres-Neto 2005). The lack of a relationship between species composition and environment or space, coupled with a uniform composition pattern over large areas, can indicate the influence of biological

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<sup>2</sup> We applied metacommunity *sensu* Hubbell (2001), in which it consists of all trophically similar individuals and species in a regional collection of local communities.



interactions in modelling metacommunities (Pitman *et al.* 2001), where species may differ in competitive abilities but individuals must be able to grow equally well in all sites (Tuomisto & Ruokolainen 2006). A random spatially autocorrelated pattern of species composition variation indicates a metacommunity modelled by neutral models (Bell 2001; Hubbell 2001); in this case species might be competitively equal and abundance may vary in a spatially autocorrelated way driven by dispersal limitation (Tuomisto & Ruokolainen 2006). When environmental variables explain composition variation this gives the idea of environmental filters selecting species by their niches (Whittaker 1957; Tuomisto *et al.* 1995), where species may not be competitively equal and competition ranking must change regarding environmental conditions (Tuomisto & Ruokolainen 2006).

Variation partition is the main method used to assess the explanation of the variation of composition data and to test the hypothesis that niche or neutral theories could be the origin of the variation (Legendre, Borcard & Peres-Neto 2005). Variation partition based on redundancy analysis (RDA), proposed by Borcard *et al.* (1992) has been used to find factors that can explain the variation in composition data. Despite some relevant arguments in the literature about the capacity of this method on test neutral models as a consequence of spatially structured communities (Tuomisto & Ruokolainen 2006; Legendre, Borcard & Peres-Neto 2008; Tuomisto & Ruokolainen 2008; Gilbert & Bennett 2010), it has been widely used with this purpose (Legendre *et al.* 2009; Li *et al.* 2011) and recent tests showed that it can be effectively applied (Diniz-Filho *et al.* 2012).

Species composition variation is a measure of beta diversity (Anderson *et al.* 2011), a metacommunity descriptor that quantifies differences between local communities based on their species composition. The concept of beta diversity plays

an important ecological role linking local (alpha) and regional (gamma) diversities (Whittaker 1957; Whittaker 1972) and must be considered in conservation strategies (Legendre, Borcard & Peres-Neto 2005). In a world of a vast number of techniques (Petchey & Gaston 2002; Pavoine, Dufour & Chessel 2004; Botta-Dukát & Wilson 2005; Ricotta 2005), ecologists have been trying to reach a consensus about the best ways to assess alpha, beta and gamma components of functional diversity and also phylogenetic diversity (Jost 2007; de Bello *et al.* 2010). Methods have also been developed to evaluate the relationship between metacommunity functional and phylogenetic structure throughout environmental gradients (Pillar *et al.* 2009; Pillar & Duarte 2010; Duarte 2011; Meynard *et al.* 2011; Stegen & Hurlbert 2011). Pillar and colleagues (2009) used functional information weighted by species abundance to evaluate trait assembly patterns, disentangling convergence and divergence patterns on a metacommunity level, across environmental gradients. As this technique uses Mantel correlation between functional and environmental distance matrices, we can infer that it also measures the turnover, *sensu* Tuomisto and Ruokolainen (2006; 2008), of functional diversity across environmental gradients. But turnover means the rate of beta diversity variation and not the origin of beta diversity assessed by partitioning of variation analysis.

In a recent study, Meynard *et al.* (2011) discriminated and compared the drivers of birds functional, phylogenetic and taxonomic metacommunity diversity components. However, even though the authors have partitioned the variation of functional and phylogenetic diversity vectors, their methodology can not explain the variation between communities (beta diversity) but just the variation of alpha diversity (Tuomisto & Ruokolainen 2008). Considering the phylogenetic approach, a recent method has been proposed by (Duarte 2011) to assess phylogenetic structure by

generating principal coordinate axes from a matrix describing the phylogeny-weighted species composition (PCPS – principal coordinates of phylogenetic structure). So, for metacommunity data, variation partitioning applied to such axes can reveal the drivers of beta phylogenetic diversity (Duarte, Prieto & Pillar 2012). However, functional diversity variation drivers have not yet been assessed and the theoretical background of this kind of analysis remains unclear (Stegen & Hurlbert 2011).

In the present study we are interested in assessing the drivers, spatial or environmental, of functional and species diversity variation in a metacommunity described by tree species in the Southern Brazilian Atlantic rainforest. For this purpose, we partitioned the variation and explored the patterns found using a species composition matrix for taxonomic approach, and a community-weighted mean trait values matrix (CWM, following Garnier *et al.* 2004 or matrix T following Pillar *et al.* 2009) and a functional fuzzy-weighted matrix (matrix X, Pillar *et al.* 2009) for the functional approach. We also discussed the ecological meanings and applications of both approaches.

Brazilian Atlantic rainforest, one of Brazilian Atlantic Forest's formations (Oliveira-Filho & Fontes 2000), is one of the most diverse forests in the world and an important endemism centre for many fauna and flora groups (Morellato & Haddad 2000; Carnaval *et al.* 2009; Werneck *et al.* 2011). However, there are few studies (e.g. Oliveira-Filho & Fontes 2000; Marques, Swaine & Liebsch 2011; Bergamin, Müller & Mello in press) concerning metacommunity patterns and processes on a regional scale. This lack of studies on forest regional dynamics is even more critical in the southernmost portion of its distribution range where some studies indicates forest expansion to higher altitudes (Bergamin 2010) and higher latitudes since about 3600

years ago (Jeske-Pieruschka, Pillar & Behling for reviewing). Along its distribution there are points of endemism and ecotone zones with different vegetation formations (i.e. *Araucaria* and Semi-deciduous forests) (Veloso & Klein 1968) that confer complexity to their assembly patterns. Taking this into account, we believe that history, i.e. neutral processes, might be the main cause of species composition variation in this forest. As forest physiognomy is maintained all over the metacommunity in spite of species changes (Veloso & Klein 1968), we can suppose that functional composition variation includes niche processes as its main cause of origin. We expect that by considering only species information, space should have a greater importance than when considering functional information. In other words, environmental variables that represent niche processes (Legendre, Borcard & Peres-Neto 2005) may be selecting some traits along the gradient whereas species variation is mostly explained by metacommunity history, i.e. neutral processes.

## **METHODS**

To evaluate the drivers of functional and taxonomic composition along Southern Brazilian Atlantic rainforest we partitioned their variation through redundancy analyses. Spatial and environmental matrices were used as explanatory variables, a species composition matrix and two matrices with functional composition information were used as response variables.

### **Data Collection**

We compiled tree species composition data from 12 studies in Southern Brazilian Atlantic rainforest, including coastal forest areas in the states of Paraná, Santa Catarina and Rio Grande do Sul (Figure 1; Table 1). Most of the study data

(eight areas) was provided by the recent Floristic and Forest Inventory of Santa Catarina State (IFFSC, Vibrans *et al.* 2010).

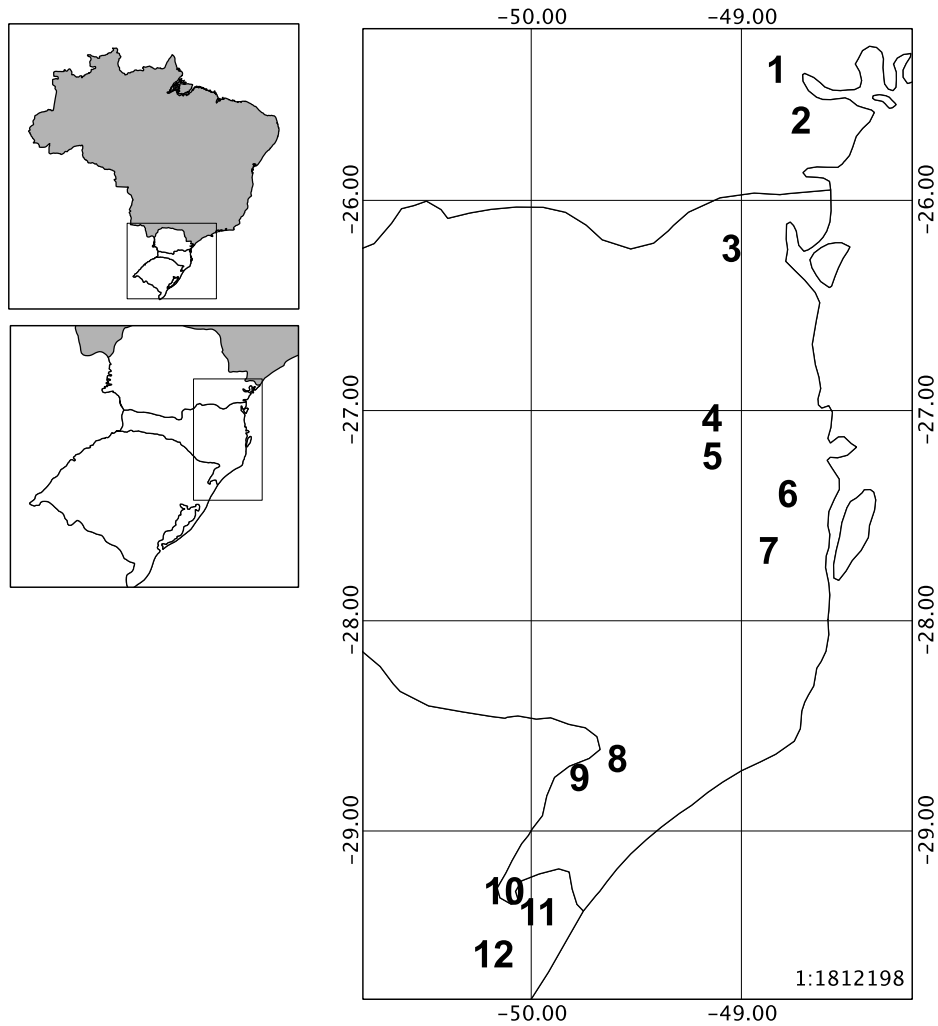


Figure 1 – Map of the study area. Numbers from 1 to 12 represent the studied sites.

Table 1 – Cities, codes, UTM Coordinates and references of sites that compound the evaluated communities.

Municipality	Code	Latitude	Longitude	Reference
Antonina	1	7195438.897	718016.8498	(Liebsch, Goldenberg & Marques 2007)
Morretes	2	7168483.957	729349.0498	(Blum 2006)
Joinville	3	7101530.43	695077.5071	(Vibrans <i>et al.</i> 2010)
Blumenau	4	7012173.63	684558.9861	(Vibrans <i>et al.</i> 2010)
Botuverá	5	6992261.327	684264.5092	(Vibrans <i>et al.</i> 2010)
Biguaçu	6	6971734.718	719583.9499	(Vibrans <i>et al.</i> 2010)
Águas Mornas	7	6941971.1	710165.7263	(Vibrans <i>et al.</i> 2010)
Siderópolis	8	6833301.419	637840.7596	(Vibrans <i>et al.</i> 2010)
Morro Grande	9	6764032.998	584562.1892	(Vibrans <i>et al.</i> 2010)
Praia Grande	10	6823523.675	620139.781	(Vibrans <i>et al.</i> 2010)
Morrinhos do Sul	11	6752792.988	600308.4862	(Jarenkow 1994)
Maquiné	12	6730794.257	579249.0862	(Zanini 2011)

#### *Taxonomic data*

All selected sites were located in preserved areas and the elevation of the sites ranged between 50 and 400 meters high. Our goal was to analyse only the arboreal vegetation, so ferns and plants with less than 10 cm DBH (Diameter Breast Height) were not include in the analysis. We organized tree species composition data in a species matrix according to their densities (number of individuals per hectare) in each community, from now on called matrix **W**.

We performed the analysis using a set of more representative species in the metacommunity. To select these species, we calculated the total species density in the metacommunity and selected only the species with more than 20 individuals per hectare of density in total. We called the matrix of selected species as matrix **W<sub>B</sub>**. As the same patterns were obtained when comparing matrix **W** and matrix **W<sub>B</sub>** through Principal Coordinate Analyses (PCoA) scatter diagrams, only matrix **W<sub>B</sub>** was used also for species composition analyses.

### Functional data

To assess functional information we sampled traits that represent plant's ecological strategies. We chose plant traits based on the ideas of plant ecology strategy schemes (PESS, Westoby 1998; Wilson, Thompson & Hodgson 1999; Westoby *et al.* 2002; Wright *et al.* 2007), which aim to describe species strategies by their morphological or physiological traits. Three axes are considered important to describe such strategies: competitive, dispersal and exploitation of resources capacity (Wilson, Thompson & Hodgson 1999). As there is no consensus on which traits can better describe each axis (Westoby 1998; Westoby *et al.* 2002; Wright *et al.* 2007), we opted for using more than one trait to represent each axis. The selected traits and some more details are in Table 2.

Table 2 – Plant traits measured and their functionality. Plant Ecology Strategy Schemes (PESS) axes: competitive (**C**), dispersal (**D**) and exploitation of resources capacity (**E**). Range of values column contains minimum and maximum trait values found in this study.

Trait	Way of calculation	Code	PESS axes	Range of values
Specific Leaf Area	Leaf area/oven-dry mass (m <sup>2</sup> kg <sup>-1</sup> )	SLA	<b>C E</b>	2.69 to 32.24
Leaf Dry Matter Content	Oven-dry mass (mg)/water-saturated fresh mass (g)	LDMC	<b>C E</b>	168.20 to 529.99
Potential Plant Height	Literature information (m)	Phe	<b>C D E</b>	3 to 45
Leaf Area	Area of leaf or leaflet's blade (mm <sup>2</sup> )	LA	<b>C E</b>	2.25 to 3563.46
Seed Mass	Oven-dry seed mass (g)	Sma	<b>C D</b>	2.7x10 <sup>-5</sup> to 4
Animal dispersion	Animal dispersed or not	AD	<b>D</b>	0 or 1
Leaf Nitrogen content	Total amount of N (mg)/per unit of dry leaf mass (g)	LNC	<b>E</b>	1.01 to 3.57
Leaf Phosphorus content	Total amount of P (mg)/per unit of dry leaf mass (g)	LPC	<b>E</b>	0.05 to 0.5
Relation LNC/LPC	LNC/LPC	NP	<b>E</b>	3.51 to 32.45
Reproduction System	Monoicus or Dioicus	RE	<b>D</b>	0 or 1

We adopted the term trait as used by Violle *et al.* (2007), so all the information was obtained on the individual level and scaled up to the species level using mean trait values per species. It is also known that traits have important variation between individuals of the same species (Cianciaruso *et al.* 2009; Carlucci *et al.* 2012); however, we decided not to consider this here because of sampling efforts and logistics issues. All trait information related to leaves was sampled along the gradient. Thus, for leaf traits – specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), leaf phosphorus content (LPC) and leaf area (LA) - we sampled six leaves of three to six individuals per species, following Cornelissen *et al.* (2003) for measure techniques. Information about the other traits, potential plant height, dispersion by animals and syndrome of pollination, were obtained from literature. Data of LDMC and potential plant height were log transformed to fit on a normal distribution. This data collection process originated a matrix of species described by functional traits averages, hereafter called matrix **B**.

Partitioning variation of diversity requires a raw data response matrix (Borcard, Legendre & Draupeau 1992). Even with the great amount of methods to quantify functional diversity (Petchey & Gaston 2002; Mason *et al.* 2003; Botta-Dukát & Wilson 2005) no one has proposed a raw data matrix that expresses functional composition in order to apply the same kind of analysis of the variation partitioning of species diversity. Thus, as an alternative to perform the analyses of partitioning variation of functional composition, we suggest using the following two data matrices:

- **Community-weighted mean trait matrix:** It consists in a post-multiplication of matrix  $\mathbf{W}_B$  of species per site by matrix  $\mathbf{B}'$  of traits per species, that results in a matrix of traits means per site weighted by



species density (Díaz, Acosta & Cabido 1992; Díaz & Cabido 1997). We called it matrix  $\mathbf{T}$  ( $\mathbf{T} = \mathbf{B}'\mathbf{W}_B$ ) *sensu* Pillar et al. (2009). The data in each row of this matrix holds averages of a certain trait in each community (Pillar *et al.* 2009; Pillar & Duarte 2010). Values of traits were standardized by the total value, so the values of each column of matrix  $\mathbf{T}$  range between zero and one.

- **Functional fuzzy-weighted matrix:** It is the result of the post-multiplication of matrix  $\mathbf{W}_B$  of species per site by matrix  $\mathbf{U}$  of functional similarities between species,  $\mathbf{X}$  ( $\mathbf{X} = \mathbf{U}'\mathbf{W}_B$ ) *sensu* Pillar et al. (2009). Matrix  $\mathbf{W}_B$  is previously standardized to the unit sum in each site. Matrix  $\mathbf{U}$  contains fuzzy degrees of belonging of every species to fuzzy sets defined by each species on the basis of the trait similarities. This means that with the traits information of each species (matrix  $\mathbf{B}$ ) we calculated how similar species are, in other words, how species belong to each other in terms of functional traits. Each cell of  $\mathbf{X}$  matrix is a probability of a species occurrence in the community based on the information on how similar a species is in comparison with the other species of that community.

Matrices  $\mathbf{T}$  and  $\mathbf{X}$  are regularly used in the analysis of assembly patterns, in a method that discriminates trait-convergence and trait-divergence assembly patterns, in the context of an environmental gradient of interest (Pillar *et al.* 2009). In the former study, matrix  $\mathbf{T}$  was used to express trait-convergence and matrix  $\mathbf{X}$  trait-divergence and convergence assembly patterns at the metacommunity level, through a series of Mantel correlations with an environmental matrix. Values of matrix  $\mathbf{T}$ , community-weighted mean trait values (CWM, Garnier *et al.* 2004), are also used to define the

dominant traits in a community (Diaz *et al.* 2007) and is related to Grime's (1998) mass ratio hypotheses.

### *Explanatory variables*

To assess the influence of space on species and functional composition, we generated continuous spatial variables from the  $x$  and  $y$  coordinates. We calculated principal coordinates neighbour matrices (PCNM, Borcard & Legendre 2002; Borcard *et al.* 2004) using  $x$  and  $y$  coordinates of each site. We calculated the PCNMs using the procedure described at Borcard *et al.* (2004) for irregular two-dimensional sampling, with a truncation distance of 130.53 km. We considered only vectors with the positive eigenvalues. Axes orders represent a gradient from a broader to a finer scale (Borcard *et al.* 2004). So, the first axes represent broader scales while finer scales are related with the last axes. These axes values per site integrate matrix **S** used in the following analyses to quantify the influence of space in variation of communities.

In order to generate matrix **E** of environmental variables per site for the following analyses, we used climatic variables with information of Rainfall and Temperature obtained by Geographical Information System techniques. All variables were obtained from WorldClim database (Hijmans *et al.* 2005). We extracted the data from files using the software Quantum GIS (Quantum GIS Development Team 2011).

### **Data Analysis**

To model the variation of species and functional composition in terms of environmental and spatial variables, we applied canonical redundancy analysis (RDA, Rao 1964) partitioning the amount of explanation for each set of variables (Variation partitioning analyses, Borcard, Legendre & Draupeau 1992; Peres-Neto *et al.* 2006). We tested the influence of explanatory variables, environment (matrix **E**) and space

(matrix **S**), on the variation of species composition (matrix **W<sub>B</sub>** after Hellinger transformation), and functional composition (matrices **X** and **T**).

This analysis allowed us to isolate and test the explanation of each variable set. We expressed the variation explained by **E** as fraction [a+b], the variation explained by **S** as fraction [b+c] and the unexplained variation as fraction [d]; fraction [b] corresponds to the explanation shared by spatial and environmental data. We isolated all the fractions [a], [b], [c], [d] and computed the amount of variance, also called adjusted  $R^2$  ( $R^2_{adj}$ ) (Peres-Neto *et al.* 2006), explained by each fraction and tested the significance of testable ones,  $\alpha$ -value ( $P < 0.1$ ), by permutation (999 random permutations) (Borcard, Legendre & Draupeau 1992).

To find the most parsimonious subset of exploratory variables, for spatial and environmental sets, we performed forward selection analyses. We did that by considering those explanatory variables that better explained the variation of composition for each response matrix (matrices **W<sub>B</sub>**, **T** and **X**). This procedure was performed using double stop criterion,  $R^2_{adj}$  and  $\alpha$ -value ( $P < 0.05$ , after 9999 random permutations), following Blanchet *et al.* (2008).

We plotted diagrams of the first axes of Principal Coordinates Analysis (PCoA) to display and discuss the main trends of the variation of response matrices (**W<sub>B</sub>**, **T** and **X**). For species data set we used chord distance as a resemblance measurement (Legendre & Legendre 1998) for functional matrices we used Euclidian distance. Square root scalar standardization was applied on matrix **W<sub>B</sub>** beforehand to resemblance measure this data.

We built matrices **T** and **X** with the software Syncca (Pillar 2010) following Pillar *et al.* (2009). We computed PCNM eigenvectors, the RDA analyses, variation partitioning and tests of significance of the fractions using the *vegan* package

(Oksanen *et al.* 2007) from R statistical language version 2.14.1 (R Development Core Team 2007). We performed forward selection analyses using the *packfor* library (Dray, Legendre & Blanchet 2007) from R version 2.15.0 under development.

## RESULTS

The results of the variation partitioning analyses of the three data matrices are presented in Table 3. Fraction [c], of spatial variables, showed significant explanation of variation of species and matrix **X**. The explanation of this fraction increased when we considered functional composition by using matrix **X** (Table 3). Total proportion of explained variation [a+b+c] was also significant to both former data sets and increased with the functional composition approach, followed by a decreasing in unexplained variation [d] (Table 3). Environment fraction [a] was a significant driver only for species composition.

Table 3 – Variation partitioning results of taxonomic and functional composition. Metacommunity data correspond to 12 areas in Southern Brazilian Atlantic Forest. Rainfall seasonality was used as an environmental variable for matrices **T** and **X** (functional composition), while both it and temperature seasonality composed the chosen set for the analysis applied to taxonomic composition (Matrix **W<sub>B</sub>**). Space variables: one PCNM axis (PCNM1) for taxonomic composition matrix (Matrix **W<sub>B</sub>**) and four PCNM axes (PCNM1, PCNM2, PCNM7 and PCNM8) for functional composition matrices (matrices **T** and **X**) of a total of eight PCNM axes. Values are referent to  $R^2_{adj}$  and those in bold represent P-value  $<0.05$ , after 9999 random permutations.

Font of variation	Data set	[a]	[b]	[c]	[a+b]	[b+c]	[a+b+c]	[d]
<i>Taxonomic</i>	matrix <b>W<sub>B</sub></b>	<b>5%</b>	8.4%	<b>5%</b>	<b>13%</b>	<b>14%</b>	<b>18%</b>	82%
<i>Functional</i>	matrix <b>T</b>	1%		21%	9%	<b>35%</b>	43%	78%
	matrix <b>X</b>	29%	44%	<b>65%</b>	<b>21%</b>	<b>8%</b>	<b>36%</b>	34%

Note: Table columns represent fractions that explain data variance: [a] only environment, [b] environment spatially structured, [c] only space, [a+b] environment, [b+c] space, [a+b+c] environment and space, [d] unexplained (Borcard, Legendre & Draupeau 1992). Significance of [b] and [d] fractions are not testable.

We obtained eight positive PCNM axes. PCNM axes 1, 2, 3, 6 and 7 were chosen for functional composition analyses after the forward selection. PCNM axis 1 was the only one selected as a spatial variable for taxonomic composition variation partitioning analysis. PCNM axis 3 was the only medium scale spatial variables selected. Rainfall seasonality and was selected by the double stop criteria forward selection analyses despite of the response matrix. Its values range from 8 to 44 and represent the coefficient of variation of annual rainfall values. For taxonomic level analyses, temperature seasonality and rainfall seasonality was the best environmental subset selected. Temperature seasonality values varied from 2.84 to 3.42 degrees Celsius and represent the coefficient of variation of annual temperature values. Figure 3 shows the distribution of values of selected environmental and spatial variables across the metacommunity.

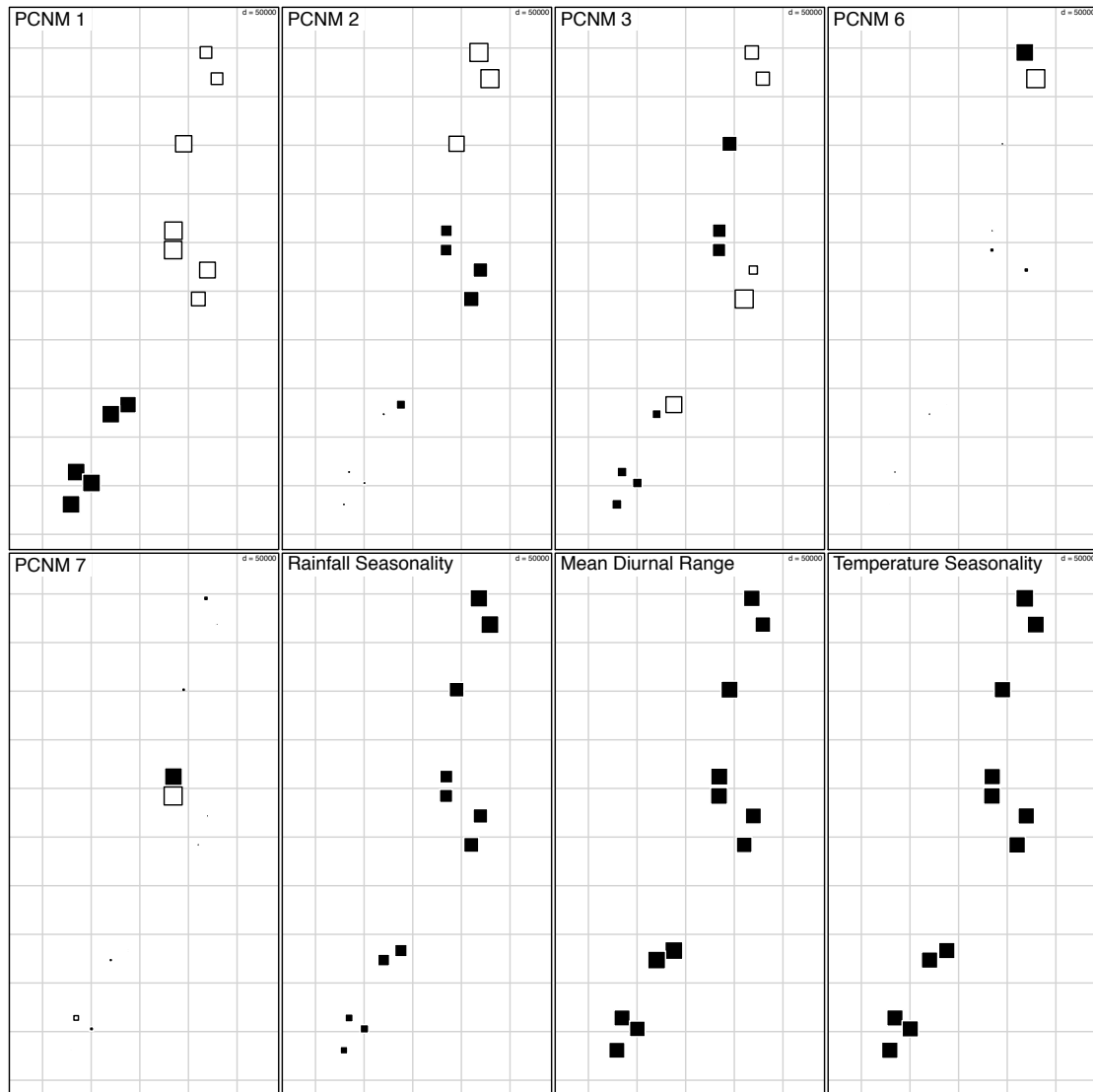


Figure 2 – Spatial distribution of values of variables chosen through forward selection in the metacommunity sites. The first five graphs correspond to spatial distribution of PCNM axis values. The last three graphs are Rainfall Seasonality (coefficient of variation of Rainfall), Mean Diurnal Range of Temperature and Temperature Seasonality (coefficient of variation of Temperature) values. Positive values are in black, negative values in white. Values are represented by the size of the squares.

On the taxonomic level (Figure 4a), the first and the second PCoA axes expressed the latitudinal gradient separating communities of north and south, shaped like a horseshoe. Functional composition matrices showed similar scatter diagram patterns (Figure 4b and 4c). Some communities of opposite extremes in the gradient expressed by species composition were located closer to each other, so the taxonomic latitudinal gradient was not so clear at the functional level of the studied

metacommunity. Both axes of the community-weighted mean trait matrix scatter diagram (Figure 4c) were strongly correlated with traits that represent all PESS axes. LDMC, SLA and Leaf Area were more strongly related with the second ordination axis (Figure 4c).

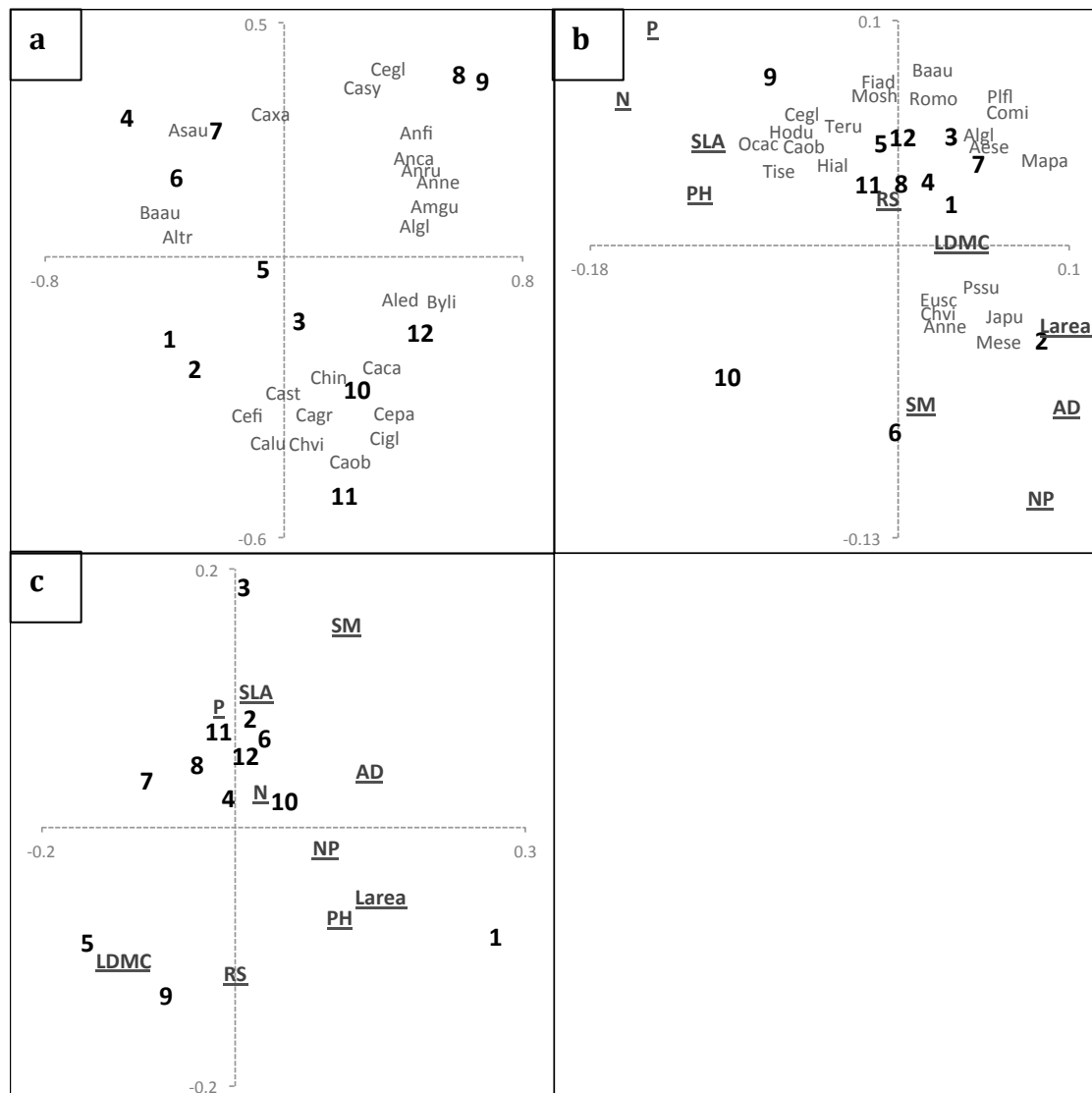


Figure 3 – Scatter diagrams of Principal Coordinate Analyses based on data matrices used in the variation partitioning analyses of functional and species composition in Southern Brazilian Atlantic Forest. (a) Square Root transformed data of tree species abundance (matrix  $W_B$ ). Percentage of explanation of the first axis is 26.06% and of the second axis is 13.71%. (b) Functional fuzzy-weighted matrix (matrix  $X$ ) and correlation of trait mean community value. Percentage of explanation of the first axis is 19.75% and of the second axis is 18.96%. (c) Community-weighted mean trait matrix (matrix  $T$ ). Percentage of explanation of the first axis is 39.99% and of the second axis is 29.64%.

The patterns of community-weighted mean trait values for each site did not follow the latitudinal gradient. Leaf area and seed mass were the traits with more variation among CWM values along the metacommunity (Figure 5). In both cases the variation did not follow the north-south gradient. Other traits had little average changes across communities (Figure 5). SLA, LNC and LPC had higher values in southern communities, whereas in the north animal dispersion CWM values were higher.

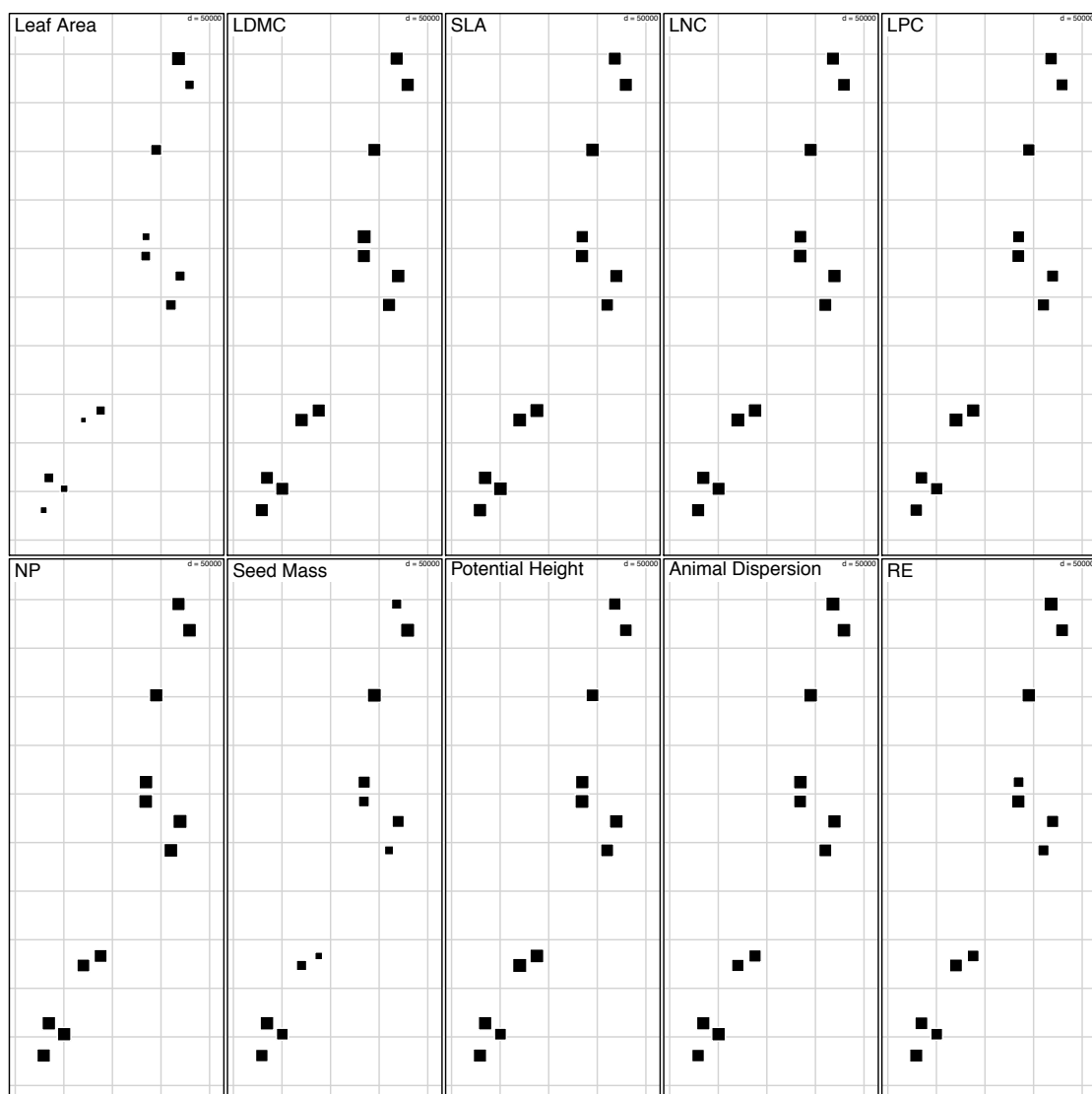


Figure 4 – Community-weighted mean trait values across the range of the latitudinal gradient. Square sizes represent CWM in each community (matrix **T** values). Square positions represent the spatial position of the site following UTM coordinates that range between 733712 and 579249.1 south and from 7205383.7 to 6730794.3 west.



## DISCUSSION

Our results indicated that among the factors used in the analysis space is the main driver of functional composition in the Southern Brazilian Atlantic rainforest, considering the metacommunity scale of this study. Nonetheless, the amount of explanation and models selected are different regarding functional and taxonomic approaches. The pure environmental fraction [a] explains only taxonomic composition variation, but the spatially structured environmental, fraction [b], explains an important portion of variation also for matrix **X** variation. Total amount of explanation increased in functional composition analyses and spatial variation is the main driver of functional composition variation in the metacommunity as well, in contrast with our hypothesis predictions.

The low explanation of species composition variation (i.e. fraction [a+b+c]= 18% of total variation) by space and environment found in the results can be caused by three main factors (Legendre & Legendre 1998): random variation of taxonomic composition, historical events not included in analysis or not spatially structured and the scale of the analysis not allowing the detection of some important processes. As the only spatial variable selected for this analysis was a latitudinally-structured PCNM axis (Figure 3), some important finer scale relations between space and species variation could have been omitted. Taxonomic composition most varies on a finer scale (e.g. plot scale) and variables may have been sampled at a too broad scale to reveal relationships between species and environmental or spatial variation (i.e. with more sampling units along the gradient, other patterns would be observed). Also considering the scale issue, biotic interactions (e.g. competition) could be structuring the metacommunity, but as it happens on a lower level of organization (individuals) and scale (plot) it could not be deeply discussed by this study. In any case, biotic

interactions are the main explanation for a high fraction [d] in this kind of analysis (Legendre, Borcard & Peres-Neto 2005), so some portion of our high [d] value should be due to biotic interactions that are working at the community site level.

The increase of total explanation [a+b+c] in functional composition approach, in comparison with the taxonomic composition approach, was also found by Meynard et al. (2011), so functional information may be important in detecting patterns in a metacommunity scale as we consider similarities between species and add information to the analysis. Spatial fraction [b+c] which contains environmental spatially structured explanation (the untestable fraction [b]) explains 44% of variation of functional beta composition for matrix **X**. As fraction [b] explains an important portion of functional and taxonomic approach (Table 3), it must also be considered a driver of metacommunity variation, despite its untestable condition. If we look at Figure 2 we can see that rainfall seasonality, the environmental variable selected for all data sets, is spatially structured. This explains the environmental influence for species and functional composition approaches revealed only by the fraction [b]. Rainfall is known to drive species composition variation between different Atlantic Forest formations (Oliveira-Filho & Fontes 2000; Bergamin, Müller & Mello in press). And, combining with soil drainage, it may be that it physiologically restricts the presence of some plant species in different Atlantic rainforest types (Marques, Swaine & Liebsch 2011). Temperature seasonality was selected as well as an environmental variable at the taxonomic approach. Although it did not show a clear spatial pattern variation, the fraction [a] was significant. Temperature is known as the main factor responsible for the north–south floristic differentiation of Atlantic forests (Oliveira-Filho & Fontes 2000). We found here that rainfall seasonality has an important role in structuring communities even in the same forest formation type (i.e.

the Atlantic rainforest *stricto sensu*) when considering species and also functional composition, and that combining with temperature seasonality it drives species composition in the southernmost portion of Atlantic rainforest.

Historical events may be the main origin of Southern Brazilian Atlantic rainforest functional and taxonomic variation. Latitude, here represented by PCNM 1 – a broad spatial scale that was latitudinally structured (Figure 3) -, seems to be the main driver of taxonomic composition as this PCNM was the unique selected as spatial variable to this analysis and was responsible for explaining 14% of total variation. Such a pattern can be linked with the idea of the forest's north-south migration after the last glacial maximum (LGM). This idea is supported by studies using pollen records, which found that southern the region of the Brazilian Atlantic rainforest was occupied by non-forest vegetation at the time of LGM (Behling *et al.* 2002; Jeske-Pieruschka, Pillar & Behling for reviewing). During that time the forest might have been restricted to some refugia along the coast, located north of our study area (Carnaval & Moritz 2008; Carnaval *et al.* 2009). So, species composition variation may be a consequence of north-south forest migration and assessing the phylogenetic structure of the metacommunity might give important insights into understanding this process.

On the other hand, four PCNMs were selected as cause of functional composition including not only the broader scale (PCNM 1 and 2), but even the finer scale (PCNM 6 and 7). PCNM 7 separate communities four and five that are located at the Vale do Itajaí region, which has been recognized as an important regional endemism centre (Klein 1979; Klein 1980). Also PCNM 3 separates communities 10 and 11, which are close to the Porta de Torres region described by Rambo (1951), who considered it an important migration route of tropical plant species towards the

south, as well as being the southern distribution limit for many species (Veloso & Klein 1968). If we are right in these assumptions, then species differing in relation to mean functional traits became important to those communities, leading them to differ from functional patterns of the others in the available metacommunity. However, the selection of PCNMs could also be representing unmeasured environmental fine scale variables (Peres-Neto *et al.* 2006), such as soil features or earlier local disturbances. In any case, the PCNMs selected for the present study represent biogeographical localities and endemism centres, so forest history could be playing an important role in metacommunity functional composition patterns as well. Another issue that should be taken into account is that the functional composition approach (i.e. patterns of traits that also include the degree of variation between species density) was related to different spatial explanation factors, leading us to identify finer patterns that would not be evident using only the taxonomic approach.

Ordinations of functional raw data matrices showed that spatially distant communities could be functionally closely-related. As the species composition scatter diagram revealed a latitudinal distribution of communities, we can assume that species composition and functional traits are following different patterns along Southern Brazilian Atlantic rainforest confirming the results of variation partitioning analysis. Scatter diagrams of both functional composition matrices (**T** and **X**) showed the same general pattern of community distribution as the proportion of fractions in the partitioning variation analyses (Table 3). As matrix **T** expresses convergence and matrix **X** convergence and divergence patterns (Pillar *et al.* 2009) the absence of novel patterns by matrix **X** can be related as a lack of divergence patterns in this metacommunity. We did not test convergence or divergence patterns *sensu* Pillar (2009), neither over and underdispersion within each site but these analyses could be

complementary to ours in helping to understand assembly rules in the metacommunity. In addition, testing functional beta composition, that we suppose to be lower than expected by chance regarding the similarity of spatially distant communities, could give important insights into metacommunity patterns.

In summary, we can conclude that different variables are driving taxonomic and functional composition variation in the Southern Brazilian Atlantic rainforest's tree metacommunity. Functional composition variation may be driven by historical factors, whereas taxonomic composition may be driven by environmental variables, latitude and biotic interactions. So, partitioning functional composition variation based on matrix **X** proved to be an important tool to understand metacommunity processes. Moreover, the same analysis applied to matrix **T** did not show significative results. Furthermore, the selection of finer scale spatial variables for functional composition variation also revealed complex historical forest dynamics, already described by earlier botanists using flora information (Rambo 1951; Veloso & Klein 1968; Klein 1984a). These results show that to conserve Southern Brazilian Atlantic Forest metacommunity functionality, conservation areas all over the gradient are required. The information that could not be assessed only by species composition variation analyses is essential regarding the continuous pressures of urbanization and agriculture on these areas.

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## CONSIDERAÇÕES FINAIS

Com o presente trabalho foi possível ter um panorama regional sobre a estrutura funcional da metacomunidade de árvores da Floresta Ombrófila Densa Submontana do Sul do Brasil. É interessante perceber que apenas 5 graus de variação latitudinal sejam os principais determinantes na estruturação das comunidades em termos de composição de espécies. A proximidade funcional de comunidades geograficamente distantes mostra a homogeneidade da formação (Floresta Ombrófila Densa Submontana) quando à morfologia, e por consequência função, de suas espécies ao longo do gradiente.

Nossos resultados mostraram que a diversidade funcional é causada basicamente por fatores históricos enquanto a diversidade taxonômica, além dos fatores históricos, sofre uma influência de variáveis ambientais (sazonalidade da temperatura e da pluviosidade) espacialmente estruturadas e provavelmente de interações biológicas. Como causas da diversidade funcional foram selecionadas variáveis espaciais de escala mais fina que podem ser relacionadas a processos históricos de expansão da floresta ligados a centros de endemismos regionais e a rotas de migração de espécies.

A Floresta Ombrófila Densa do Sul do Brasil é ainda pouco estudada quando aos aspectos ecológicos. Até a divulgação dos dados do Inventário Florístico Florestal de Santa Catarina (IFFSC) pouco se sabia sobre as espécies e suas proporções, em toda a extensão do litoral catarinense. O acréscimo de informação proporcionado por este levantamento permitirá um grande avanço no entendimento da floresta. Análises integrando informação funcional de outras

formações vegetais da região levantada por outros pesquisadores do grupo de trabalho trarão um grande avanço no entendimento das dinâmicas florestais da região.

Acessar as causas da diversidade-beta funcional pode auxiliar no entendimento dos ecossistemas sobretudo em escala regional. Neste sentido é complementar às técnicas propostas para encontrar padrões de regras de montagem na metacomunidade que seriam percebidos em escalas mais finas. As matrizes utilizadas para particionar a variação da diversidade funcional se mostraram boas alternativas para expressar padrões da composição funcional em nível de metacomunidades.

Essas abordagens carecem de interpretação teórica. Supomos que as hipóteses tradicionais sobre fatores neutros ou nicho devam ter outras implicações quando se passa do nível taxonômico para o funcional. Quando testamos se a variação do espaço tem relação com a diversidade beta funcional, por exemplo, devemos levar em conta que estamos abordando a variação da diversidade de atributos na comunidade. A atribuição desta relação à teoria neutra, elaborada pensando em padrões de distribuição de espécies, deve ser feita com cuidado levando em consideração o pano de fundo teórico. Discussões teóricas acerca desta abordagem bem como sua relação com questões evolutivas ainda estão sendo desenvolvidas.

Ainda há muito a ser respondido sobre este sistema de estudo. Questões relacionadas à filogenia, como se as espécies que conseguiram chegar mais ao sul são mais aparentadas entre si sendo essas barreiras biogeográficas e corredores migratórios funis filogenéticos. Questões referentes à influência antrópica sobre as comunidades também demandam respostas. Alguns estudos com essa

abordagem têm sido realizados ao longo do gradiente estudado relacionando a estrutura funcional e os estágios sucessionais. Contudo, uma abordagem regional integrando esses estudos ainda não foi realizada. É urgente a necessidade de unir o conhecimento que tem sido produzido sobre este ecossistema na região e estabelecer diretrizes para sua conservação. Sobretudo no estado de Santa Catarina fortes pressões tem sido exercidas sobre as unidades de conservação visando alterações em seus limites para favorecer a expansão urbana, turística e industrial. Espero que essas questões e atitudes sejam temas de outros capítulos e que possam proteger e aumentar nosso entendimento sobre estas florestas.

## APÊNDICE

Tabela 1 – Densidade das espécies nas Unidades Amostrais (Matriz **W<sub>B</sub>**). Termos em destaque representam as famílias botânicas. Colunas representam os 12 sítios de amostragem.

Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<b>Anacardiaceae</b>												
<i>Tapirira guianensis</i> Aubl.	20.00	0	0	57.50	25.00	5.00	0	0	0	0	0	0
<b>Annonaceae</b>												
<i>Annona cacans</i> Warm.	0	0	0	0	7.50	0	0	0	0	10.00	74.00	0
<i>Annona neosericea</i> H. Rainer	10.00	11.67	0	0	7.50	10.00	5.00	0	0	20.00	0	1.96
<i>Annona rugulosa</i> (Schltdl.) H. Rainer	0	0	0	0	0	0	0	0	0	0	37.00	7.84
<i>Guatteria australis</i> A.St.-Hil.	3	0	0	15.00	0	15.00	32.50	17.50	0	0	0	0
<i>Xylopia brasiliensis</i> Spreng.	0	0	0	15.00	0	12.50	12.50	0	0	0	0	0
<b>Apocinaceae</b>												
<i>Aspidosperma australe</i> Müll. Arg.	0	0	0	10.00	10.00	22.50	2.50	0	0	20.00	0	3.92
<b>Aquifoliaceae</b>												
<i>Ilex paraguariensis</i> A. St.-Hil.	0	0	0	0	0	2.50	5.00	0	0	0	52.00	1.96
<b>Aquifoliaceae</b>												
<i>Euterpe edulis</i> Mart.	56.67	0	2.50	32.50	30.00	0	37.50	2.50	0	30.00	262.00	96.08
<b>Bignoniaceae</b>												
<i>Jacaranda puberula</i> Cham.	0	0	0	0	7.50	0	0	15.00	0	0	1.00	0
<b>Boraginaceae</b>												
<i>Cordia trichotoma</i> (Vell.) Arráb. ex Steud.	0	0	0	0	0	0	0	17.50	7.50	0	2.00	3.92
<b>Burseraceae</b>												
<i>Protium kleinii</i> Cuatrec.	0	13.33	0	10.00	0	12.50	12.50	10.00	0	2.50	3.00	0

(continuação)												
Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<b>Cannabaceae</b>												
<i>Trema micrantha</i> (L.) Blume	0	0	0	0	0	0	0	2.50	0	2.50	6.00	23.53
<b>Chysobalanaceae</b>												
<i>Hirtella hebeclada</i> Moric. ex DC.	13.33	1.67	0	10.00	2.50	15.00	0	0	0	5.00	21.00	5.88
<b>Clethraceae</b>												
<i>Clethra scabra</i> Pers.	0	0	0	0	7.50	0	47.50	0	0	0	0	0
<b>Clusiaceae</b>												
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	3	11.67	10.00	5.00	0	2.50	0	0	0	2.50	48.00	7.84
<b>Cunoniaceae</b>												
<i>Lamanonia ternata</i> Vell.	0	0	0	0	0	5.00	0	12.50	5.00	2.50	16.00	11.76
<b>Elaeocarpaceae</b>												
<i>Sloanea guianensis</i> (Aubl.) Benth.	110.00	23.33	25.00	80.00	2.50	45.00	27.50	0	0	0	0	0
<b>Euphorbiaceae</b>												
<i>Alchornea glandulosa</i> Poepp.	13.33	0	0	0	7.50	0	0	0	0	0	0	1.96
<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg.	30.00	1.67	7.50	0	2.50	32.50	2.50	27.50	35.00	45.00	63.00	35.29
<i>Gymnanthes concolor</i> (Spreng.) Müll.Arg.	0	0	0	0	0	0	0	0	0	7.50	130.00	29.41
<i>Pausandra morisiana</i> (Casar.) Radlk.	0	16.67	0	0	7.50	0	0	0	0	0	0	0
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	13.33	1.67	0	27.50	7.50	2.50	7.50	2.50	0	0	0	0
<i>Sapium glandulosum</i> (L.) Morong	0	0	0	0	0	0	0	15.00	0	7.50	61.00	19.61
<i>Tetrorchidium rubrivenium</i> Poepp. & Endl.	0	0	0	0	2.50	0	0	12.50	2.50	5.00	69.00	41.18
<b>Fabaceae</b>												
<i>Inga marginata</i> Willd.	0	3.33	0	0	0	0	0	12.50	5.00	17.50	20.00	37.25
<i>Lonchocarpus cultratus</i> (Vell.) A.M.G. Azevedo & H.C. Lima	0	0	0	0	0	0	0	0	0	0	0	23.53
<i>Machaerium paraguariense</i> Hassl.	0	0	0	0	0	0	0	0	20.00	0	0	9.80

(continuação)												
Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<i>Platymiscium floribundum</i> Vogel	0	0	0	0	20.00	0	0	0	0	0	0	0
<i>Pterocarpus rohrii</i> Vahl	0	0	0	2.50	10.00	7.50	0	0	0	0	0	0
<i>Inga sessilis</i> (Vell.) Mart.	6.67	1.67	0	0	2.50	0	2.50	0	0	7.50	7.00	0
<i>Machaerium stipitatum</i> (DC.) Vogel	0	0	0	2.50	0	0	0	40.00	35.00	0	0	0
<b>Flacourtiaceae</b>												
<i>Casearia sylvestris</i> Sw.	3.3	5.00	2.50	0	22.50	7.50	12.50	95.00	50.00	17.50	149.00	41.18
<b>Lamiaceae</b>												
<i>Aegiphila sellowiana</i> Cham.	3	0	0	0	0	2.50	0	0	0	0	59.00	3.92
<b>Lauraceae</b>												
<i>Aniba firmula</i> (Nees & C. Mart.) Mez	0	3.33	0	5.00	0	17.50	2.50	0	0	0	0	0
<i>Cinnamomum glaziovii</i> (Mez) Kosterm.	0	0	0	0	0	0	0	0	0	0	27.00	5.88
<i>Cryptocarya mandioccana</i> Mez	0	6.67	0	50.00	15.00	0	2.50	0	0	0	0	0
<i>Nectandra megapotamica</i> (Spreng.) Mez	0	0	2.50	0	0	0	0	100.00	62.50	47.50	2.00	23.53
<i>Nectandra membranacea</i> (Sw.) Griseb.	0	11.67	0	0	15.00	0	0	0	5.00	0	1.00	0
<i>Nectandra oppositifolia</i> Nees	0	1.67	0	0	12.50	5.00	50.00	7.50	0	0	26.00	52.94
<i>Ocotea aciphylla</i> (Nees) Mez	0	0	0	37.50	0	15.00	0	0	0	0	0	0
<i>Ocotea catharinensis</i> Mez	0	0	0	2.50	7.50	42.50	0	0	0	0	0	0
<i>Ocotea indecora</i> Schott ex Meisn.	0	0	0	0	0	0	0	0	0	0	26.00	7.84
<i>Ocotea puberula</i> (Rich.) Nees	0	0	5.00	0	0	0	0	25.00	60.00	0.00	0	23.53
<i>Ocotea urbaniana</i> Mez	0	0	0	0	0	10.00	0	0	0	0	27.00	0
<b>Magnoliaceae</b>												
<i>Magnolia ovata</i> (A. St.-Hil.) Spreng.	3.3	5.00	0	2.50	5.00	0	0	15.00	0	15.00	1.00	0
<b>Malpighiaceae</b>												
<i>Byrsonima ligustrifolia</i> A. Juss	0	0	0	7.50	0	2.50	15.00	0	0	0	5.00	0



(continuação)												
Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<b>Malvaceae</b>												
<i>Luehea divaricata</i> Mart.	0	0	0	0	0	0	0	35.00	0	0	0	7.84
<i>Pseudobombax grandiflorum</i> (Cav.) A. Robyns	0	0	0	0	2.50	0	7.50	2.50	0	15.00	3.00	5.88
<b>Melastomataceae</b>												
<i>Miconia cabucu</i> Hoehne	13.33	0	0	5.00	0	5.00	77.50	15.00	0	0	0	0
<b>Melastomataceae</b>												
<i>Miconia cinnamomifolia</i> (DC.) Naudin	0	8.33	0	0	12.50	2.50	97.50	0	0	0	0	0
<i>Tibouchina mutabilis</i> Meyen	0	0	0	0	0	0	142.50	0	0	0	0	0
<i>Tibouchina sellowiana</i> (Cham.) Cogn.	0	0	0	0	0	0	0	0	0	0	0	60.78
<b>Meliaceae</b>												
<i>Cabralea canjerana</i> (Vell.) Mart.	0	6.67	7.50	0	30.00	12.50	27.50	7.50	77.50	75.00	50.00	147.06
<i>Cedrela fissilis</i> Vell.	0	1.67	5.00	0	7.50	5.00	0	57.50	25.00	5.00	6.00	17.65
<i>Trichilia claussenii</i> C. DC.	0	0	0	0	0	0	0	0	2.50	2.50	0	25.49
<i>Trichilia lepidota</i> Mart.	0	1.67	2.50	0	2.50	2.50	5.00	0	0	5.00	20.00	0
<b>Miristicaceae</b>												
<i>Virola bicuhyba</i> (Schott) Warb.	7	13.33	7.50	2.50	7.50	17.50	2.50	0	0	15.00	0	5.88
<b>Monimiaceae</b>												
<i>Mollinedia schottiana</i> (Spreng.) Perkins	13.3	5.00	0	0	0	0	0	0	0	0	31.00	3.92
<b>Moraceae</b>												
<i>Ficus adhatodifolia</i> Schott	0	0	0	0	20.00	2.50	0	0	0	22.50	0	11.76
<i>Ficus luschnathiana</i> (Miq.) Miq.	0	0	0	0	0	0	0	30.00	12.50	0	1.00	0
<i>Sorocea bonplandii</i> (Baill.) W.C.Burger, Lanj. & Boer	0	0	2.50	0	0	0	0	0	0	7.50	57.00	15.69
<b>Myrtaceae</b>												
<i>Calyptranthes grandifolia</i> O.Berg	0	18.33	2.50	0	0	5.00	2.50	0	0	2.50	26.00	5.88
<i>Calyptranthes lucida</i> Mart. ex DC.	0	18.33	5.00	2.50	2.50	7.50	0	0	0	0	0	1.96

(continuação)												
Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<i>Calyptranthes strigipes</i> O. Berg.	0	6.67	0	0	2.50	15.00	2.50	0	0	0	0	0
<i>Campomanesia xanthocarpa</i> O. Berg.	0	0	2.50	0	0	0	0	10.00	0	7.50	2.00	3.92
<i>Eugenia brevistyla</i> D. Legrand	0	0	17.50	0	2.50	0	0	0	0	0	0	0
<i>Eugenia handroi</i> (Mattos) Mattos	0	0	0	0	0	0	0	15.00	0	5.00	12.00	0
<i>Eugenia multicostata</i> D. Legrand	0	3.33	2.50	0	0	0	0	0	0	20.00	1.00	15.69
<i>Eugenia schuechiana</i> (Vell.) Angely	0	0	0	0	0	0	0	0	0	0	51.00	1.96
<i>Eugenia subterminalis</i> DC.	0	0	0	0	0	0	0	0	0	0	29.00	0
<i>Marlierea obscura</i> O. Berg.	20.00	0	0	0	0	0	0	0	0	0	0	0
<i>Marlierea silvatica</i> (Gardner) Kiaersk.	40.00	0	0	0	0	0	0	0	0	0	0	0
<i>Marlierea tomentosa</i> Cambess.	0	0	2.50	7.50	5.00	2.50	2.50	2.50	27.50	2.50	0	0
<i>Myrcia pubipetala</i> Miq	0	1.67	0	5.00	0	7.50	2.50	0	0	2.50	17.00	5.88
<i>Myrcia tijuensis</i> Kiaersk.	0	10.00	0	2.50	12.50	0	2.50	0	0	7.50	35.00	0
<i>Myrciaria plinioides</i> D. Legrand	0	0	0	0	0	0	0	0	0	0	29.00	0
<b>Nyctaginaceae</b>												
<i>Guapira opposita</i> (Vell.) Reitz	36.67	8.33	17.50	5.00	32.50	35.00	22.50	0	2.50	32.50	13.00	5.88
<i>Pisonia zapallo</i> Griseb.	0	0	12.50	0	2.50	0	0	0	5.00	25.00	18.00	0
<b>Olaceaceae</b>												
<i>Heisteria silvianii</i> Schwacke	0	5.00	12.50	17.50	0	17.50	2.50	0	0	2.50	0	0
<b>Phyllanthaceae</b>												
<i>Hieronyma alchorneoides</i> Allemão	100.00	3.33	7.50	0	25.00	20.00	67.50	42.50	0	30.00	27.00	5.88
<b>Primulaceae</b>												
<i>Myrsine coriacea</i> (Sw.) R.Br.	0	0	0	0	0	0	2.50	40.00	0	0	0	50.98
<i>Myrsine umbellata</i> Mart.	0	3.33	0	7.50	0	0	0	0	0	2.50	16.00	0
<b>Proteaceae</b>												
<i>Roupala montana</i> Aubl.	0	0	7.50	0	0	0	0	17.50	0	0	0	0

(continuação)												
Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<b>Rhamnaceae</b>												
<i>Hovenia dulcis</i> Thunb.	0	0	0	0	0	0	0	30.00	0	0	0	0
<b>Rosaceae</b>												
<i>Prunus myrtifolia</i> (L.) Urb.	0	0	0	0	0	2.50	2.50	0	12.50	10.00	9.00	1.96
<b>Rubiaceae</b>												
<i>Amaioua guianensis</i> Aubl.	6.7	5.00	0	15.00	0	5.00	0	0	0	0	0	0
<i>Bathysa australis</i> (A. St.-Hil.) Hook. f. ex K. Schum.	80.00	0	10.00	0	10.00	22.50	7.50	7.50	0	25.00	5.00	0
<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult.	0	0	7.50	2.50	0	0	0	10.00	0	0	2.00	0
<i>Psychotria nuda</i> (Cham. & Schltdl.) Wawra	30.00	10.00	2.50	0	0	0	0	0	0	0	0	0
<i>Psychotria suterella</i> Müll. Arg.	26.67	1.67	2.50	0	0	0	0	5.00	0	0	289.00	0
<i>Psychotria vellosiana</i> Benth.	0	0	0	0	2.50	10.00	62.50	0	0	0	0	0
<i>Rudgea jasminoides</i> (Cham.) Müll. Arg.	23.33	1.67	5.00	0	0	0	0	0	0	2.50	350.00	0
<b>Rutaceae</b>												
<i>Zanthoxylum rhoifolium</i> Lam.	0	0	0	0	0	0	2.50	2.50	2.50	0	34.00	0
<b>Sabiaceae</b>												
<i>Meliosma sellowii</i> Urb.	0	5.00	7.50	0	0	2.50	0	0	0	20.00	26.00	27.45
<b>Salicaceae</b>												
<i>Casearia obliqua</i> Spreng.	13.3	5.00	0	0	5.00	0	0	0	0	7.50	7.00	0
<b>Sapindaceae</b>												
<i>Allophylus edulis</i> (A. St.-Hil., Cambess. & A. Juss.) Radlk.	0	0	2.50	0	0	0	0	30.00	10.00	7.50	6.00	1.96
<i>Cupania vernalis</i> Cambess.	0	0	5.00	0	15.00	2.50	0	52.50	140.00	5.00	3.00	23.53
<b>Sapotaceae</b>												
<i>Chrysophyllum inornatum</i> Mart.	3.3	5.00	0	0	25.00	0	0	0	0	55.00	6.00	11.76
<i>Chrysophyllum viride</i> Mart. & Eichler	0	10.00	22.50	0	2.50	7.50	0	0	0	30.00	32.00	1.96

(continuação)												
Família e Espécie	1	2	3	4	5	6	7	8	9	10	11	12
<b>Solanaceae</b>												
<i>Solanum sanctaecatharinae</i> Dunal	0	0	0	0	0	0	0	2.50	15.00	15.00	8.00	5.88
<b>Urticaceae</b>												
<i>Cecropia glaziovii</i> Snehl.	0	0	37.50	0	7.50	5.00	5.00	20.00	0	15.00	0	1.96
<i>Cecropia pachystachya</i> Trécul	16.67	10.00	0	0	0	0	0	0	0	0	0	0
<i>Coussapoa microcarpa</i> (Shott) Rizzini	0	1.67	0	0	12.50	0	0	0	0	2.50	5.00	7.84

Tabela 2 – Valor médio de atributos funcionais por espécie (Matriz B). Termos em destaque representam as famílias botânicas. LDMC = Conteúdo de matéria seca foliar; SLA= Área Foliar Específica; LNC = Conteúdo de Nitrogênio Foliar; LPC= Conteúdo de Fósforo Foliar. Variáveis binárias: Zoocoria 1= espécie zoocórica e 0= espécie não zoocórica; Sistema Reprodutivo, 1= espécie dióica e 0= espécie monóica.

Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<b>Anacardiaceae</b>										
<i>Tapirira guianensis</i> Aubl.	27.35	442.98	8.89	1.7	0.13	13.08	0.025189	40	1	1
<b>Annonaceae</b>										
<i>Annona cacans</i> Warm.	54.97	375.00	14.21	2.62	0.17	15.41	0.222965	20	1	0
<i>Annona neosericea</i> H. Rainer	24.94	375.65	12.84	2.05	0.14	14.64	0.058310	25	1	1
<i>Annona rugulosa</i> (Schltdl.) H. Rainer	23.85	283.37	23.37	2.45	0.12	20.42	0.247000	14	1	0
<i>Guatteria australis</i> A.St.-Hil.	32.61	402.44	14.82	2.17	0.11	19.73	0.100000	15	1	0
<i>Xylopia brasiliensis</i> Spreng.	5.08	427.97	14.31	2.09	0.11	19	0.072993	30	1	0
<b>Apocinaceae</b>										
<i>Aspidosperma australe</i> Müll. Arg.	18.02	322.12	16.80	1.9	0.08	23.75	0.125	20	0	0
<b>Aquifoliaceae</b>										
<i>Ilex paraguariensis</i> A. St.-Hil.	29.29	452.18	5.38	1.3	0.12	10.83	0.00789182	15	1	1
<b>Aquifoliaceae</b>										
<i>Euterpe edulis</i> Mart.	40.89	407.24	6.56	1.42	0.11	12.91	1.3	20	1	0
<b>Bignoniaceae</b>										
<i>Jacaranda puberula</i> Cham.	5.90	444.08	17.13	1.92	0.17	11.29	0.00606061	8	0	0
<b>Boraginaceae</b>										
<i>Cordia trichotoma</i> (Vell.) Arráb. ex Steud.	48.55	309.65	10.04	2.3	0.19	12.11	0.03487541	30	0	0
<b>Burseraceae</b>										
<i>Protium kleinii</i> Cuatrec.	53.90	442.15	12.25	1.51	0.13	11.62	0.38086102	25	1	0
<b>Cannabaceae</b>										
<i>Trema micrantha</i> (L.) Blume	11.92	364.50	13.83	2.25	0.23	9.78	0.0045977	20	1	1

(continuação)										
Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<b>Chysobalanaceae</b>										
<i>Hirtella hebeclada</i> Moric. ex DC.	50.57	419.06	9.05	1.62	0.19	8.53	0.51282051	15	1	0
<b>Clethraceae</b>										
<i>Clethra scabra</i> Pers.	29.22	412.57	5.81	1.73	0.09	19.22	0.00025	30	0	0
<b>Clusiaceae</b>										
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	37.23	424.56	11.20	1.01	0.07	14.43	2.6	15	1	0
<b>Cunoniaceae</b>										
<i>Lamanonia ternata</i> Vell.	25.60	314.90	17.51	1.03	0.1	10.3	0.00066667	30	0	0
<b>Elaeocarpaceae</b>										
<i>Sloanea guianensis</i> (Aubl.) Benth.	48.83	525.13	10.25	1.28	0.09	14.22	0.2	25	1	0
<b>Euphorbiaceae</b>										
<i>Alchornea glandulosa</i> Poepp.	85.16	397.18	21.88	2	0.14	14.29	0.05128205	25	1	1
<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg.	25.33	455.49	9.92	1.65	0.13	12.69	0.1	35	1	1
<i>Gymnanthes concolor</i> (Spreng.) Müll.Arg.	30.65	360.91	8.14	1.31	0.07	18.71	0.38086102	10	0	0
<i>Pausandra morisiana</i> (Casar.) Radlk.	207.92	343.93	13.77	1.68	0.09	18.67	0.38086102	10	0	1
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	32.12	383.86	10.63	1.87	0.1	18.7	0.01960784	10	1	1
<i>Sapium glandulosum</i> (L.) Morong	23.82	228.35	16.30	1.75	0.15	11.67	0.05494506	22	1	0
<i>Tetrorchidium rubrivenium</i> Poepp. & Endl.	47.59	206.20	14.72	2.89	0.23	12.57	0.02518892	25	1	1
<b>Fabaceae</b>										
<i>Inga marginata</i> Willd.	12.57	492.77	10.64	2.62	0.15	17.47	0.52910053	20	1	0
<i>Inga sessilis</i> (Vell.) Mart.	62.43	529.99	11.42	1.88	0.14	13.86	0.33704078	25	1	0
<i>Lonchocarpus cultratus</i> (Vell.) A.M.G. Azevedo & H.C. Lima	12.84	320.50	27.65	2.09	0.11	19	0.16393443	25	0	0
<i>Machaerium paraguariense</i> Hassl.	19.62	493.75	14.90	1.88	0.14	13.86	0.38086102	8	0	0

(continuação)										
Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<i>Platymiscium floribundum</i> Vogel	23.29	345.42	15.18	3.28	0.2	16.4	0.71428571	20	0	0
<i>Pterocarpus rohrii</i> Vahl	24.94	441.05	14.81	1.88	0.14	13.86	0.50890585	32	0	0
<i>Machaerium stipitatum</i> (DC.) Vogel	5.38	497.53	25.54	2.44	0.14	17.43	0.38086102	25	0	0
<b>Lamiaceae</b>										
<i>Aegiphila sellowiana</i> Cham.	168.26	258.84	15.49	1.88	0.14	13.86	0.03125	15	1	1
<b>Lauraceae</b>										
<i>Aniba firmula</i> (Nees & C. Mart.) Mez	56.28	412.87	12.84	1.88	0.14	13.86	2.17391304	20	1	0
<i>Cinnamomum glaziovii</i> (Mez) Kosterm.	27.25	412.90	11.32	1.88	0.14	13.86	0.16129032	30	1	0
<i>Cryptocarya mandioccana</i> Mez	40.25	428.29	10.72	1.88	0.14	13.86	0.38086102	35	1	0
<i>Nectandra megapotamica</i> (Spreng.) Mez	10.41	430.98	5.67	1.7	0.07	24.29	0.40816327	30	1	0
<i>Nectandra membranacea</i> (Sw.) Griseb.	69.54	403.11	8.68	1.88	0.14	13.86	0.76923077	30	1	0
<i>Nectandra oppositifolia</i> Nees	58.80	509.73	4.34	1.46	0.08	18.25	0.38086102	24	1	0
<i>Ocotea aciphylla</i> (Nees) Mez	18.57	402.20	12.72	1.88	0.14	13.86	0.38086102	21	1	0
<i>Ocotea catharinensis</i> Mez	15.14	487.71	12.47	3.57	0.11	32.45	0.83333333	45	1	0
<i>Ocotea indecora</i> Schott ex Meisn.	17.66	446.88	12.35	2.32	0.09	25.78	0.19	30	1	0
<i>Ocotea puberula</i> (Rich.) Nees	23.69	411.77	11.30	3.04	0.2	15.2	0.14428973	25	1	1
<i>Ocotea urbaniana</i> Mez	7.61	510.00	14.92	1.88	0.14	13.86	0.38086102	8	1	0
<b>Magnoliaceae</b>										
<i>Magnolia ovata</i> (A. St.-Hil.) Spreng.	254.67	339.17	10.68	1.33	0.14	9.5	0.22222222	30	1	0
<b>Malpighiaceae</b>										
<i>Byrsonima ligustrifolia</i> A. Juss	48.07	293.10	16.96	1.88	0.14	13.86	0.38086102	12	1	0
<b>Malvaceae</b>										
<i>Luehea divaricata</i> Mart.	32.95	352.81	22.34	1.68	0.23	7.3	0.00396864	30	0	0

(continuação)										
Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<i>Pseudobombax grandiflorum</i> (Cav.) A. Robyns	109.52	364.31	13.22	1.97	0.21	9.38	0.08	25	0	0
<b>Melastomataceae</b>										
<i>Miconia cabucu</i> Hoehne	456.92	426.56	6.64	1.41	0.14	10.07	0.00282201	15	1	0
<i>Miconia cinnamomifolia</i> (DC.) Naudin	21.59	315.65	10.68	1.38	0.06	23	0.00064206	15	1	0
<i>Tibouchina mutabilis</i> Meyen	14.01	313.74	13.40	1.85	0.25	7.4	0.00030303	12	0	0
<i>Tibouchina sellowiana</i> (Cham.) Cogn.	9.66	270.67	11.15	1.62	0.09	18	0.0000278	5	0	0
<b>Meliaceae</b>										
<i>Cabralea canjerana</i> (Vell.) Mart.	42.11	335.00	16.34	2.11	0.15	14.07	0.44025157	35	1	1
<i>Cedrela fissilis</i> Vell.	32.36	235.74	32.24	3.02	0.3	10.07	0.0271449	40	0	1
<i>Trichilia clausenii</i> C. DC.	34.49	401.39	14.00	1.82	0.11	16.55	0.16129032	12	1	0
<i>Trichilia lepidota</i> Mart.	94.73	362.17	16.69	2.68	0.18	14.89	0.38086102	30	1	1
<b>Miristicaceae</b>										
<i>Virola bicuhyba</i> (Schott) Warb.	82.20	292.13	16.33	1.63	0.1	16.3	2.95420975	35	1	1
<b>Monimiaceae</b>										
<i>Mollinedia schottiana</i> (Spreng.) Perkins	31.02	287.17	20.76	1.87	0.18	10.39	0.38086102	6	1	1
<b>Moraceae</b>										
<i>Ficus adhatodifolia</i> Schott	137.88	286.22	11.87	2.52	0.13	19.38	0.38086102	40	1	0
<i>Ficus luschnathiana</i> (Miq.) Miq.	31.68	387.96	10.13	2.25	0.17	13.24	0.00020833	26	1	0
<i>Sorocea bonplandii</i> (Baill.) W.C.Burger, Lanj. & Boer	26.89	422.67	10.65	1.23	0.1	12.3	0.3125	15	1	1
<b>Myrtaceae</b>										
<i>Calyptanthes grandifolia</i> O.Berg	84.61	348.48	12.80	1.06	0.08	13.25	0.0952381	14	1	0
<i>Calyptanthes lucida</i> Mart. ex DC.	29.79	438.12	11.66	1.72	0.09	19.11	0.38086102	15	1	0



(continuação)										
Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<i>Calyptanthes strigipes</i> O. Berg.	40.99	396.69	10.94	1.46	0.06	24.33	0.38086102	20	1	0
<i>Campomanesia xanthocarpa</i> O. Berg.	33.53	349.95	26.05	1.375	0.13	11.92307 692	0.04842615	25	1	0
<i>Eugenia brevistyla</i> D. Legrand	67.07	385.73	11.53	1.88	0.14	13.86	0.38086102	15	1	0
<i>Eugenia handroi</i> (Mattos) Mattos	9.07	361.21	18.17	1.88	0.14	13.86	0.38086102	15	1	0
<i>Eugenia multicostata</i> D. Legrand	25.71	416.47	9.57	1.42	0.08	17.75	4	20	1	0
<i>Eugenia schuechiana</i> (Vell.) Angely	30.33	338.54	25.36	1.29	0.11	11.73	0.38086102	8	1	0
<i>Eugenia subterminalis</i> DC.	7.41	414.49	10.43	1.88	0.14	13.86	0.2753	4	1	0
<i>Marlierea obscura</i> O. Berg.	59.58	404.52	10.07	1.14	0.14	8.14	0.2	18	1	0
<i>Marlierea silvatica</i> (Gardner) Kiaersk.	325.95	437.98	7.35	1.88	0.14	13.86	0.30	12.00	1.00	0.00
<i>Marlierea tomentosa</i> Cambess.	325.95	437.98	7.35	1.88	0.14	13.86	0.3	12	1	0
<i>Myrcia pubipetala</i> Miq	79.97	417.35	13.02	1.21	0.05	24.2	0.2	20	1	0
<i>Myrcia tijuensis</i> Kiaersk.	19.52	303.63	17.95	1.53	0.06	25.5	0.38086102	15	1	0
<i>Myrciaria plinioides</i> D. Legrand	7.15	523.38	12.62	1.88	0.14	13.86	0.65700001	5	1	0
<b>Nyctaginaceae</b>										
<i>Guapira opposita</i> (Vell.) Reitz	27.38	250.03	16.35	2.78	0.14	19.86	0.14285714	20	1	1
<i>Pisonia zapallo</i> Griseb.	129.84	168.20	25.05	1.88	0.14	13.86	0.38086102	20	1	1
<b>Olacaceae</b>										
<i>Heisteria silvianii</i> Schwacke	44.56	377.89	9.11	2.09	0.1	20.9	0.46511628	15	1	0
<b>Phyllanthaceae</b>										
<i>Hieronyma alchorneoides</i> Allemão	215.68	283.48	10.97	1.72	0.11	15.64	0.02083333	40	1	1
<b>Primulaceae</b>										
<i>Myrsine coriacea</i> (Sw.) R.Br.	14.20	278.47	16.67	1.82	0.11	16.55	0.021	20	1	1
<i>Myrsine umbellata</i> Mart.	60.81	355.44	7.19	1.09	0.06	18.17	0.06535948	20	1	1
<b>Proteaceae</b>										

(continuação)										
Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<i>Roupala montana</i> Aubl.	10.58	474.53	6.07	1.88	0.14	13.86	0.02	12	0	0
<b>Rhamnaceae</b>										
<i>Hovenia dulcis</i> Thunb.	39.68	339.83	18.81	2.12	0.16	13.25	0.01811266	15	1	0
<b>Rosaceae</b>										
<i>Prunus myrtifolia</i> (L.) Urb.	5.76	403.89	5.41	1.88	0.14	13.86	0.13274924	15	1	0
<b>Rubiaceae</b>										
<i>Amaioua guianensis</i> Aubl.	67.94	421.94	12.01	1.88	0.14	13.86	0.008	12	1	1
<i>Bathysa australis</i> (A. St.-Hil.) Hook. f. ex K. Schum.	798.88	292.03	10.78	2.15	0.1	21.5	0.00016667	8	1	0
<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult.	43.82	358.60	7.28	1.48	0.12	12.33	0.8	15	1	0
<i>Psychotria nuda</i> (Cham. & Schltl.) Wawra	36.07	201.08	22.82	2.46	0.12	20.5	0.38086102	4	1	0
<i>Psychotria suterella</i> Müll. Arg.	21.26	227.32	24.53	1.75	0.09	19.44	0.38086102	3	1	0
<i>Psychotria vellosiana</i> Benth.	24.14	227.44	19.53	2.36	0.12	19.67	0.38086102	7	1	0
<i>Rudgea jasminoides</i> (Cham.) Müll. Arg.	49.35	310.93	15.93	2.12	0.11	19.27	0.2	5	1	0
<b>Rutaceae</b>										
<i>Zanthoxylum rhoifolium</i> Lam.	7.13	361.89	13.65	2.04	0.12	17	0.01374552	23	1	1
<b>Sabiaceae</b>										
<i>Meliosma sellowii</i> Urb.	24.22	322.93	8.36	1.23	0.1	12.3	2	11	1	0
<b>Salicaceae</b>										
<i>Casearia sylvestris</i> Sw.	19.30	384.07	11.51	1.99	0.12	16.58	0.00636943	20	1	0
<i>Casearia obliqua</i> Spreng.	11.12	400.73	22.47	2.76	0.5	5.52	0.38086102	11.5	1	0
<b>Sapindaceae</b>										
<i>Allophylus edulis</i> (A. St.-Hil., Cambess. & A. Juss.) Radlk.	14.60	313.28	18.72	1.39	0.13	10.69	0.01820665	20	1	0
<i>Cupania vernalis</i> Cambess.	27.61	380.46	12.96	1.72	0.19	9.05	0.26357406	25	1	0

(continuação)

Família e Espécie	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
<b>Sapotaceae</b>										
<i>Chrysophyllum inornatum</i> Mart.	21.36	345.66	14.73	1.7	0.08	21.25	0.33149171	12	1	0
<i>Chrysophyllum viride</i> Mart. & Eichler	18.31	432.38	13.21	1.88	0.14	13.86	0.93023256	25	1	0
<b>Solanaceae</b>										
<i>Solanum sanctaecatharinae</i> Dunal	32.00	266.37	24.64	3.14	0.21	14.95	2.4899	12	0	0
<b>Urticaceae</b>										
<i>Cecropia glaziovii</i> Snethl.	337.80	294.08	20.17	1.88	0.14	13.86	0.0005	16	1	1
<i>Cecropia pachystachya</i> Trécul	609.83	346.93	4.72	1.62	0.15	10.8	0.00133333	25	1	1
<i>Coussapoa microcarpa</i> (Shott) Rizzini	32.36	235.74	32.24	3.02	0.3	10.07	0.0271449	40	0	1

Tabela 3 –Valores médios de atributos nas comunidades ponderados pela abundância das espécies (CWM – Matriz **T**) em cada um dos 12 sítios amostrados. LDMC = Conteúdo de matéria seca foliar; SLA= Área Foliar Específica; LNC = Conteúdo de Nitrogênio Foliar; LPC= Conteúdo de Fósforo Foliar.

Áreas de Estudo	Área Foliar(m <sup>2</sup> )	LDMC (mg g <sup>-1</sup> )	SLA (m <sup>2</sup> kg <sup>-1</sup> )	LNC (mg g <sup>-1</sup> )	LPC (mg g <sup>-1</sup> )	Razão N/P	Massa da Semente(g)	Altura da Planta (m)	Zoocoria	Sistema Reprodutivo
1	0.559	0.287	0.275	0.281	0.285	0.282	0.216	0.257	0.327	0.358
2	0.263	0.292	0.281	0.269	0.262	0.300	0.402	0.267	0.310	0.298
3	0.341	0.278	0.302	0.283	0.278	0.284	0.390	0.270	0.309	0.331
4	0.182	0.321	0.250	0.268	0.261	0.293	0.303	0.298	0.306	0.211
5	0.276	0.284	0.288	0.305	0.299	0.300	0.238	0.318	0.272	0.323
6	0.295	0.300	0.279	0.294	0.263	0.315	0.295	0.307	0.299	0.273
7	0.326	0.287	0.256	0.276	0.271	0.298	0.167	0.273	0.274	0.225
8	0.252	0.284	0.318	0.301	0.323	0.265	0.120	0.312	0.250	0.250
9	0.099	0.295	0.310	0.322	0.356	0.262	0.214	0.328	0.250	0.300
10	0.281	0.275	0.297	0.291	0.291	0.290	0.372	0.297	0.292	0.298
11	0.169	0.278	0.305	0.281	0.276	0.287	0.279	0.232	0.301	0.248
12	0.139	0.281	0.294	0.288	0.285	0.284	0.315	0.290	0.260	0.311

