

**DECIFRANDO A FUNÇÃO DE PROCESSOS  
ECOLÓGICOS E EVOLUTIVOS NA  
DISTRIBUIÇÃO LOCAL E REGIONAL DE  
ARTRÓPODES EM PLANTAS**

**Thiago Gonçalves Souza**

DOUTORADO



PÓS GRADUAÇÃO  
EM BIOLOGIA ANIMAL

Biologia  
Estrutural

**UNIVERSIDADE ESTADUAL PAULISTA**  
**INSTITUTO DE BIOCIÊNCIAS, LETRAS E CIÊNCIAS EXATAS**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL**

**THIAGO GONÇALVES-SOUZA**

**DECIFRANDO A FUNÇÃO DE PROCESSOS ECOLÓGICOS E EVOLUTIVOS  
NA DISTRIBUIÇÃO LOCAL E REGIONAL DE ARTRÓPODES EM PLANTAS**

Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Campus de São José do Rio Preto.

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# INTRODUÇÃO GERAL

## 1. Estrutura do hábitat e distribuição local das espécies

A variação na estrutura do hábitat e seus efeitos na determinação da abundância e composição em espécies de comunidades animais e vegetais é um dos principais focos em estudos de ecologia de comunidades desde a década de 1960 (MacArthur & MacArthur 1961, Gorman & Karr 1978, Rotenberry & Wiens 1980, Bell et al. 1991, Knick et al. 2008). A estrutura do hábitat pode afetar as comunidades animais através da organização de comunidades específicas a uma determinada arquitetura ou tipo de hábitat e, além disso, hábitats estruturalmente mais complexos podem prover maior quantidade de nichos, contribuindo para o aumento da diversidade biológica (Bell et al. 1991, Langellotto & Denno 2004). Para artrópodes, alguns trabalhos mostraram que a arquitetura da vegetação ou a composição em espécies de plantas são fundamentais para a organização das comunidades (Robinson 1981, Beals 2006, Schaffers et al. 2008; Artigo 1, Pág. 25) e que a abundância e a riqueza em espécies estão positivamente correlacionadas com a diversidade estrutural ou a biomassa da planta hospedeira (Greenstone 1984, Halaj et al. 2000).

## 2. Aranhas sobre plantas

Embora não se alimentem de plantas, aranhas dependem da variação arquitetural (complexidade) da vegetação para construir teias (Greenstone 1984, McNett & Rypstra 2000), para forragear (Romero & Vasconcellos-Neto 2005), para encontrar parceiros sexuais e para criar a prole (Rossa-Feres et al. 2000) e para se abrigarem contra condições climáticas severas ou contra inimigos naturais (Uetz 1991, Romero & Vasconcellos-Neto 2005). O exemplo mais comum de plantas com uma arquitetura complexa e que provêm tais benefícios para aranhas e outros

organismos são plantas da família Bromeliaceae. As bromélias possuem arquitetura tridimensional e folhas organizadas em roseta que, geralmente, formam um tanque que acumula água e detritos ricos em nutrientes (Benzing 2000). Tais características fornecem uma grande variedade de micro-habitats para animais terrestres (Romero 2006, Romero & Vasconcellos-Neto 2005) e aquáticos (Greeney 2001). Associações entre aranhas e bromélias foram apenas recentemente exploradas e parecem ser bem comuns na natureza (Romero 2006). A aranha bromelícola *Psecas chapoda* (Salticidae), por exemplo, é capaz de diferenciar sua planta hospedeira, *Bromelia balansae* (Bromeliaceae), de outras plantas de acordo com as características arquiteturais das folhas (Omena & Romero 2008). Em outro estudo, Gonçalves-Souza et al. (2010, 2011) mostraram que a comunidade de aranhas é compartimentada em relação ao tipo do habitat e que bromélias representam um substrato fundamental para a estruturação das comunidades de aranhas em uma área de Mata Atlântica no sudeste do Brasil. Se bromélias de fato representam um substrato vantajoso para os animais associados e se a arquitetura de tais plantas é um fator ativamente escolhido por aranhas, espera-se que a presença destas plantas represente uma característica estrutural fundamental para a dinâmica e estrutura de comunidades em restingas do litoral brasileiro (Artigos 1, 2, 4, 5: Págs. 25, 50, 122, 159).

A associação entre aranhas e plantas, especialmente bromélias, é um sistema bastante oportuno para se testar as teorias do nicho e neutra, pois as aranhas dependem da estrutura da vegetação para construção de teias e para forragear. Por um lado, é possível testar se a variação arquitetural da vegetação e as diferenças climáticas entre as regiões explicam a variação na composição em espécies de aranhas associadas a plantas (Artigo 2, Pag. 50). Por outro lado, a distância geográfica pode afetar a composição em espécies de aranhas resultando em padrões de

diversidade determinados por processos espaciais e não pela estrutura do hábitat (Artigo 2, Pág. 50).

### **3. Dicotomia entre processos ambientais e espaciais**

A influência de processos ambientais e espaciais nos padrões de diversidade de espécies animais e vegetais é um dos grandes debates atuais em ecologia (Bell 2001, Hubbell 2001, Gilbert & Lechowicz 2004, Cottenie 2005, Thompson & Townsend 2006), atualmente presente no confronto entre teorias neutras e baseadas em nicho.

A teoria do nicho propõe que a composição das comunidades é determinada pela auto-ecologia das espécies, pela competição interespecífica e pela diversidade de recursos e hábitats (Graves & Rahbek 2005). Nesta teoria assume-se que os requerimentos espécie-específicos em resposta a um gradiente ambiental geram modificações na composição em espécies, seja em escala local ou regional (Chase & Leibold 2002). Por outro lado, a teoria neutra assume uma equivalência ecológica entre as espécies (Hubbell 2001) para demonstrar que apenas colonizações, migrações e extinções aleatórias podem modificar os padrões de similaridade na composição em espécies (Gotelli 2006). Além disso, a similaridade entre duas comunidades diminui em relação à distância geográfica (Nekola & White 1999) dependendo da capacidade de dispersão das espécies e da presença de barreiras geográficas (Hubbell 2001) (Artigo 2, Pág. 50).

A hipótese do decréscimo da similaridade é difícil de distinguir em ecossistemas naturais, pois as condições ambientais são geralmente correlacionadas com a distância geográfica (Gilbert & Lechowicz 2004). Porém, Legendre et al. (2005) sugeriu um método em que a variação na composição em espécies é dividida em frações explicadas por fatores ambientais, espaciais e pela interação entre ambas, resolvendo de maneira elegante o problema de autocorrelação espacial.

Apesar da aparente dicotomia entre as duas teorias, alguns estudos têm sugerido que processos ambientais e espaciais operam conjuntamente na organização das comunidades (Chase & Myers 2011; Artigo 2, Pág. 50). Além disso, é possível que esses processos atuem em escalas diferentes comunidades (Chase & Myers 2011). Por exemplo, processos ambientais podem influenciar a composição de espécies em escala local, enquanto processos espaciais influenciam as comunidades em escala regional ou latitudinal (Artigo 2, Pág. 50).

#### **4. Relação entre riqueza regional e local**

No início do desenvolvimento da ecologia como disciplina, os pesquisadores estavam interessados em entender os processos que explicam a abundância e riqueza local de espécies (Ricklefs and Miller 1999, Begon et al. 2006, Krebs 2008, Ricklefs 2008a). Um dos focos principais desses trabalhos era como as interações entre espécies que coexistiam e a interação com o meio em que viviam explicavam os seus padrões de distribuição. Esse ponto de vista foi mudando ao longo do tempo para uma abordagem mais regional que considerava outros processos além de interações, como processos biogeográficos, evolutivos e históricos (Ricklefs 1987, Huston 1999, Srivastava 1999, Harrison and Cornell 2008, Vellend 2010). Os proponentes da abordagem regional sugerem que as peculiaridades de comunidades locais limitam a compreensão de processos em larga escala, enquanto processos regionais, por sua vez, são mais poderosos por considerarem a distribuição ecogeográfica das espécies em uma região (Ricklefs 1987, 2004, 2008b). Essas duas abordagens tem gerado debates importantes para o avanço da teoria ecológica, uma vez que entender a importância relativa de processos locais e regionais determinando a estrutura de comunidades locais ainda é uma questão em aberto (Ricklefs 1987,

Cornell and Lawton 1992, Shurin and Srivastava 2005, Harrison and Cornell 2008, Vellend 2010; mas veja Cottenie 2005).

Para testar a importância relativa de processos locais e regionais um método comumente utilizado consiste em testar a relação entre riqueza local com a riqueza regional com regressão linear (Cornell and Lawton 1992, Srivastava 1999, Hillebrand and Blenckner 2002). Se a riqueza local estiver positiva e linearmente associadas com a riqueza regional, conclui-se que as comunidades estão insaturadas e que processos regionais são mais importantes em determinar a riqueza local (Srivastava 1999). Por outro lado, se interações locais limitam a riqueza local independente do valor da riqueza regional, conclui-se que as comunidades estão saturadas (Fig. 1, Pág. 25: Ricklefs 1987, Cornell and Lawton 1992, Srivastava 1999). Este método é bastante utilizado em ecologia, apesar de ter recebido várias críticas nos últimos anos (Artigo 3, Pág. 99).

Ao invés de testar se a riqueza regional tem um efeito unidirecional nas comunidades locais, alguns estudos indicam processos regionais e locais provavelmente interagem para determinar tanto a riqueza regional e local (Lewinsohn 1991, Lortie et al. 2004, Brooker et al. 2009). Além disso, entender os aspectos evolutivos que contribuem para a formação do pool regional de espécies indica um grande avanço para ecologia (Lessard et al. 2012 a-b, Peres-Neto et al. 2012). Desse modo, além de entender como processos regionais e locais determinam a estrutura de comunidades, o componente evolutivo pode auxiliar a revelar padrões que podem não ser compreendidos por abordagens convencionais (Artigo 5, Pág. 159).

## OBJETIVOS GERAIS

Nesta tese amostramos artrópodes associados a plantas em restingas ao longo de 2040 km do litoral brasileiro (Pranchas 1, 2 e 3, Págs. 13, 14, 15). Em especial, focamos em plantas com arquiteturas distintas para testar qual o papel das plantas na distribuição de artrópodes que vivem na vegetação. Além disso, investigamos qual a importância relativa de processos espaciais (distância entre plantas dentro de uma mesma localidade, e distância entre localidades) e evolutivos (relação de parentesco entre as espécies) na variação fenotípica de aranhas. Ainda, comparamos e discutimos como plantas com arquiteturas diferentes poderiam gerar padrões evolutivos distintos em aranhas de teia e errantes. Um assunto bastante abordado durante a tese foi a relação entre comunidades locais e regionais. Pelo fato do método tradicional utilizado para testar a relação entre a riqueza regional e local ser bastante criticado, fizemos uma reavaliação dos dados publicados em 113 comunidades com um método potencialmente não enviesado.

Esta tese está composta por 5 artigos, com os seguintes objetivos:

**Artigo 1:** Testar a importância relativa da filogenia e do nicho ecológico (diferenças morfológicas entre plantas) para a variação de tamanho e forma de aranhas;

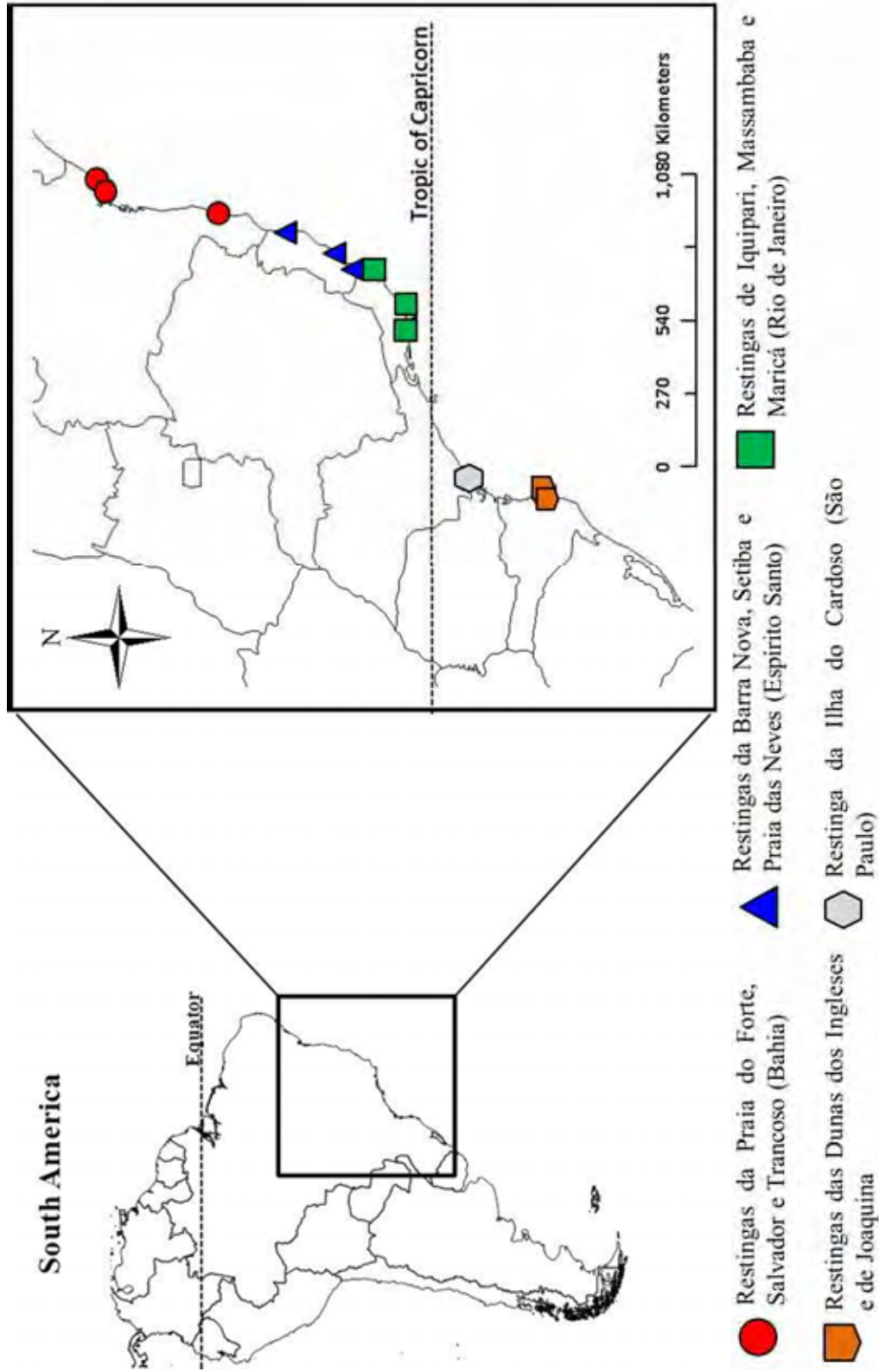
**Artigo 2:** Testar se existem sinais filogenéticos na diversidade de atributos de aranhas e se a arquitetura e localização das plantas predizem a diversidade filogenética e de atributos das aranhas. Além disso, testamos se atributos de aranhas errantes são mais lábeis do que atributos de aranhas de teias.

**Artigo 3:** Investigar se os padrões de diversidade beta de múltiplos grupos de artrópodes varia entre arquiteturas de plantas e entre localidades diferentes (Prancha 1, Pág. 13);

**Artigo 4:** Testar se aranhas e larvas de Lepidoptera (que possuem modos de dispersão distintos) respondem diferentemente a processos espaciais (distância entre plantas) e ambientais (diferenças morfológicas entre plantas);

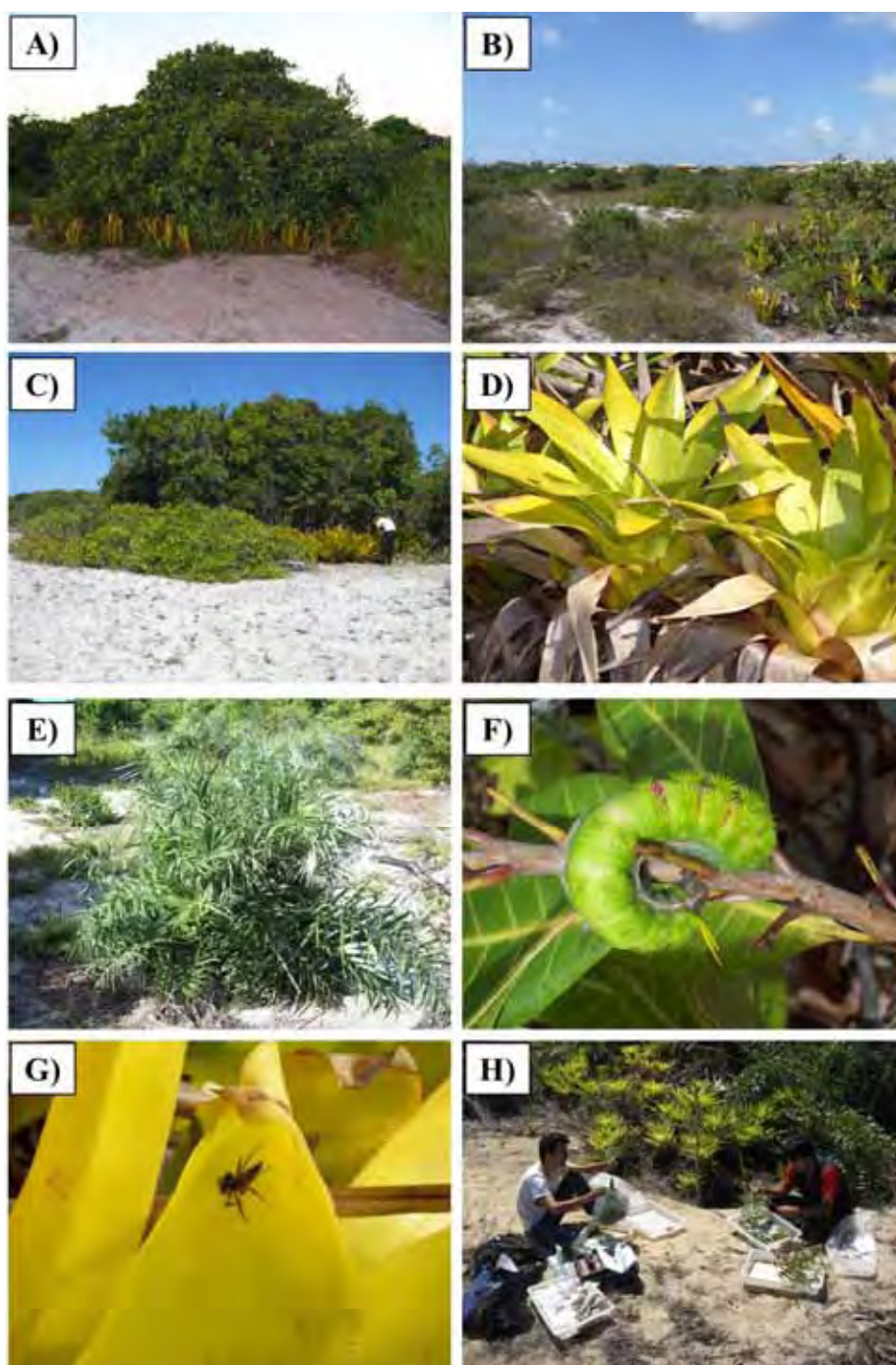
**Artigo 5:** Reavaliar o resultado de estudos que utilizaram o método tradicional de testar a relação entre riqueza regional e local e investigar os mesmos resultados com um método não enviesado;

**PRANCHA 1.** Distribuição das 12 restingas amostradas ao longo do litoral brasileiro, entre latitudes -12S (Praia do Forte) e -28S (Dunas de Joaquina).

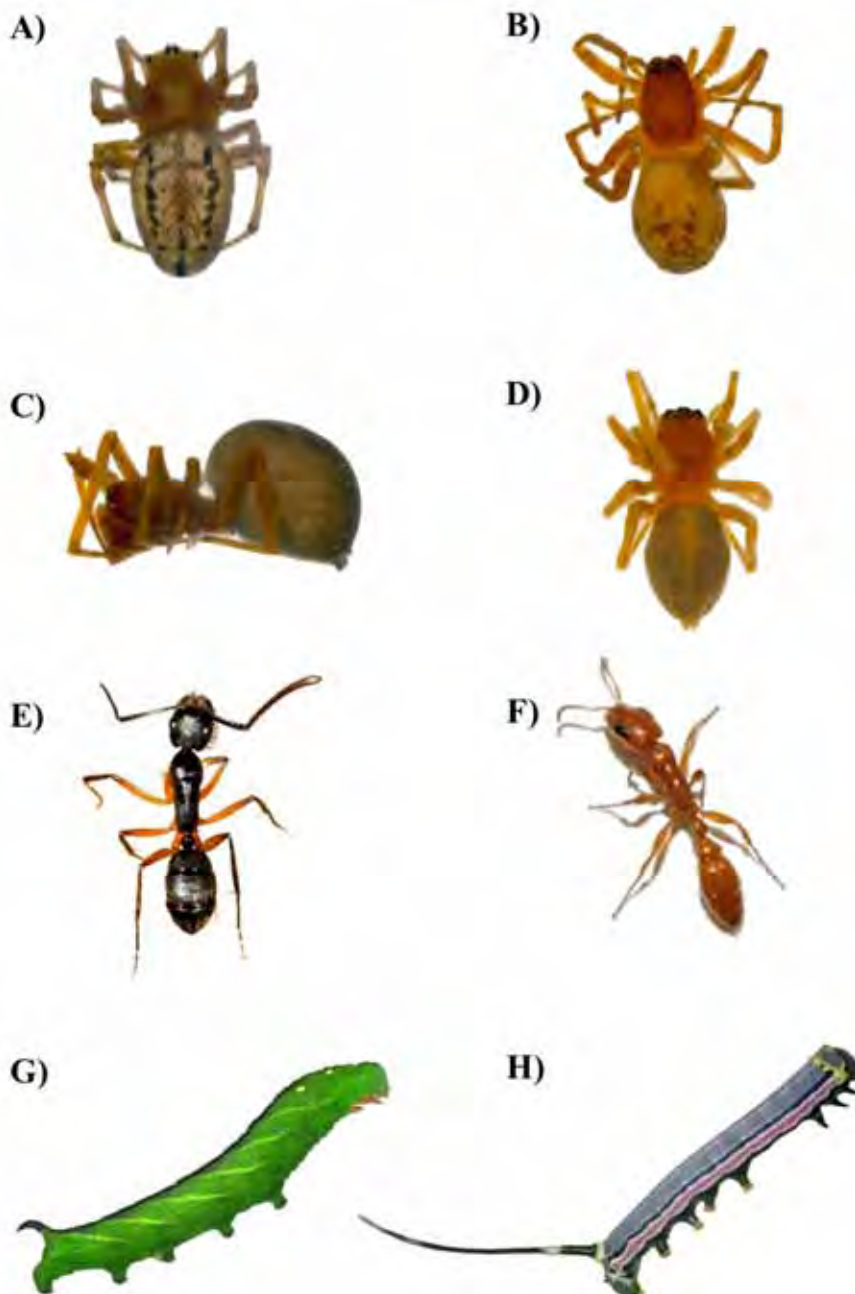




**PRANCHA 2.** Fotos da (A) restinga de Setiba – ES, (B) restinga da Praia do Forte – BA, (C) restinga de Trancoso – BA, (D) bromélia *Vriesea* sp. amostrada em Setiba, (E) palmeira *Allagoptera* sp., (F) lagarta da família Saturniidae, (G) aranhas Salticidae forrageando em bromélia e (H) detalhe do procedimento de coleta: pesagem de folhas a esquerda e amostragem de artrópodes nos ramos coletados. Créditos: Gustavo Q. Romero (A, D) e Adriano Mendonça e Hilário Azol (B, C, E-H)



**PRANCHA 3.** Fotos de artrópodes associados à vegetação. Aranhas: (A) espécie não identificada da família Araneidae, (B) *Sanogasta* sp. (Anyphaenidae), (C) *Metaltella* sp. (Amaurobiidae) e (D) espécie não identificada de Anyphaenidae; Formigas: (E) *Camponotus* sp., e (F) *Pseudomyrmex* sp.; Larvas de Lepidoptera da Família Sphingidae (G, H). Créditos: Thiago G. Souza (A-D), Sebastian Sendoya (E-F), e Eduardo Barbosa (G-H).





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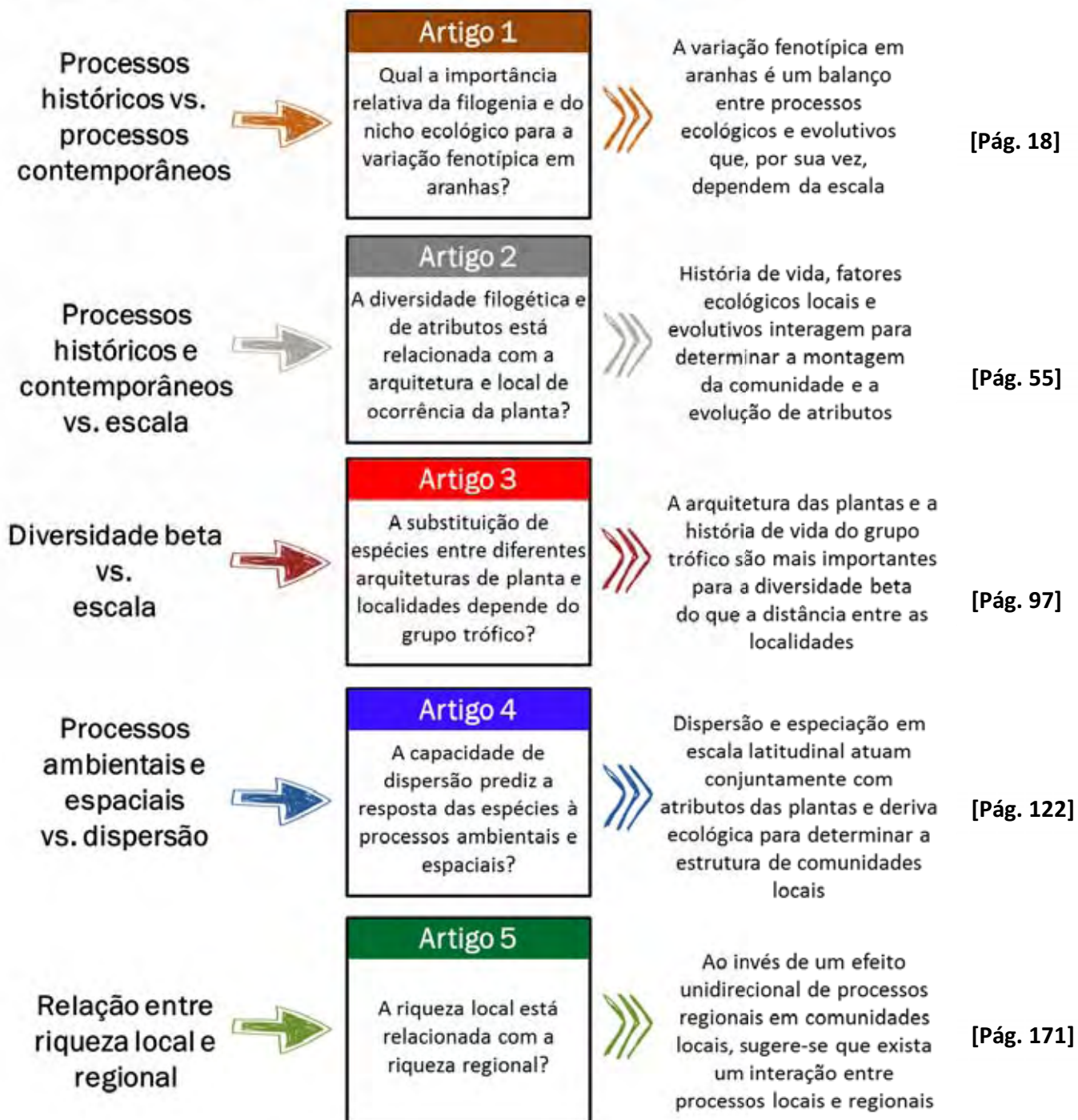


Figura 1. Principais questões e conclusões dos cinco artigos da tese.

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## **ARTIGO 1**

# **[DISENTANGLING THE PHYLOGENETIC AND ECOLOGICAL COMPONENTS OF SPIDER PHENOTYPIC VARIATION]**

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## **ABSTRACT**

An understanding of how the degree of phylogenetic relatedness influences the ecological similarity among species is crucial for inferring the mechanisms governing the assembly of species. As closely related species often share similar morphological traits, both phylogeny and ecology can explain the convergence or divergence of species morphology. We evaluated the relative importance of spiders' phylogeny and ecological niche to the variation in spider body size and shape by comparing spiders (i) between bromeliads and dicot plants and (ii) among bromeliads with distinct architectural features. We tested whether bromeliad-living spiders have similar morphological traits to spiders from surrounding dicots and whether the differences in spider body size and shape are related to bromeliad architecture or to the spiders' phylogeny. Spiders from bromeliads were larger and flatter than spiders associated with the surrounding dicots; this pattern was explained only by the spiders' phylogeny. However, spider flatness was related to both phylogeny and ecological niche, suggesting that both historical processes and recent adaptations drive the evolution of spider body shape. Bromeliads appear to favour larger and flatter spiders because they provide a larger resource supply and their leaves are tightly interlocked compared to surrounding dicot plants, providing shelters from predators. By partitioning the phylogenetic and ecological components of phenotypic variation, we were able to disentangle the evolutionary history of distinct spider traits and show that plant architecture plays a role in the evolution of spider body size and shape.

**Keywords:** Body size and shape, Bromeliads, Phylogenetic relatedness, Phylogenetic eigenvector regression, Plant-animal interactions

## INTRODUCTION

The interplay between environmental and behavioral traits results in a distribution of different body sizes that are associated with distinct patterns of resource use. Optimality models predict that life history traits that maximize fitness in a particular selective environment are likely to be conserved in the evolutionary history of an organism (i.e., life-history theory; Atkinson and Hirst 2007). In general, habitat structure (e.g., plant architecture) selects for certain species and drives the evolution of their body size and shape by means of natural selection (Polo and Carrascal 1999). Most studies considering the relationship between morphology and ecology fail to take phylogeny into account. If closely related species share similar morphology and ecological niches, then not taking phylogeny into account implicitly treats them as independent observations (Felsenstein 1985) when they are in fact not independent of one another.

The integration of phylogeny into community ecology provides a historical framework within which to understand the contributions of ecological and evolutionary processes in dictating the contemporary distributions of species (Cavender-Bares et al. 2009). Competition and environmental filtering processes are considered essential for explaining community assembly and body size distribution (Cavender-Bares et al. 2004). In communities that are structured by competitive interactions, it is expected that closely related species will compete more intensely in comparison to distantly related species, which may limit their capacity to coexist (Mayfield and Levine 2010). Thus, in similar habitats, competition favors the occurrence of ecologically similar species but drives the repulsion of closely related species (i.e., phylogenetic overdispersion; Cavender-Bares et al. 2004). In contrast, under environmental filtering, it is expected that closely related species will occupy similar habitats (i.e., phylogenetic clustering) because they are similar in other regards (e.g., behavior, physiology) (Cavender-

Bares et al. 2009). Although these hypotheses predict opposite results, they share the primary assumption that a species' phenotype interacts with its ecological niche.

Plant-living spiders represent a good system for studying the relationship between ecological niche and morphology because of the prolonged, intimate relationship between spiders and individual plants (e.g., Romero et al. 2008). For instance, plant traits could determine which taxa of spiders choose to live on a given plant, based on the prior match between spider morphology and plant architecture. Thus, we could expect that spiders that occur in plants with similar traits share similar body sizes because plant morphology has favored the selection of particular sizes over the community's evolutionary history. Bromeliads could be a good example of such plants, because they have a rosette-like architecture and a tight arrangement of leaves that are highly distinctive from dicot plants in the Neotropics (Benzing 2000). Animals that are associated with bromeliads benefit from an increase in feeding opportunities compared to dicot-living relatives, as they can access both aquatic and terrestrial food sources (Romero and Srivastava 2010). Bromeliad could thus select for lineages of large spiders with higher energy requirements. Thus, natural selection could prevent a species from changing its niche which, by its turn, decrease individual fitness (Wiens and Graham 2005). In addition, the arrangement of bromeliad leaves could favor the selection of species that are able to forage in this tight space, such as those spiders with flatter bodies. In fact, the reduction of some morphological traits generally improve species' performance (e.g., sexual display, foraging), as predicted by the maneuverability hypothesis (Norberg 1994). This reduction was previously reported in other restrictive habitats, such as caves, rock crevices and dense habitats (e.g., Bro-Jorgensen 2008, Goodman et al. 2008).

This study evaluated how plant species with distinct architectural features select for spider traits (body size and flatness) and how much of the variation in those traits is explained by the spiders' phylogeny vs. differences in plant architectural features. We evaluated whether spider body size is related to habitat constraints by comparing two adjacent habitat types, bromeliads and both herbaceous and shrubby vegetation (hereafter 'dicot'). We also evaluated the effect of microhabitat characteristics by comparing spiders among 14 bromeliad species with distinctive architectural features. We addressed the following questions. Are bromeliad-living spiders larger and flatter than dicot-living spiders? Is spider body size related to bromeliad architecture? Do phylogenetic history and ecological niches explain the phenotypic variation in spider body size and flatness among habitats and microhabitats? We used a phylogenetic comparative method to decompose the variation in spider body size and flatness into phylogenetic, niche conservatism and ecological components based on the habitat and microhabitat constraints on phenotypic variation. We used bromeliads and dicots as two different habitat types and the specific architectural features of bromeliad species as microhabitats.

## **Materials and methods**

### **STUDY SITE AND ORGANISMS**

This work was carried out at the Estação Biológica Santa Lúcia (EBSL) (19°57'S, 40°31'W; 600-900 m a.s.l.), an area of 440 ha in Santa Teresa, state of Espírito Santo, south-eastern Brazil. The vegetation of the EBSL is characterized as Atlantic Rainforest. At the EBSL, the Bromeliaceae family dominates many strata of the understory. In general, bromeliads make up large agglomerates of multispecific patches that naturally occur between forests and rocky outcrops, on shallow and structurally poor ground (hereafter named "bromeliad patches"; Wendt

et al. 2008). Small patches vary from 0.005 to 0.14 ha and large ones from 0.43 to 0.93 ha. The forest vegetation is dominated by members of the family Myrtaceae, Lauraceae, Sapotaceae, and Melastomataceae (Thomaz and Monteiro 1997). We classified the spider species in two guilds: active hunting spiders and web-building spiders (Table S1, Appendix). The basic difference between these guilds is the ability to weave webs. Although web building probably influences on feeding characteristics, we referred to these two groups as guilds, instead of feeding guilds.

## DATA SURVEY

We sampled spiders from bromeliads and from both herbaceous and shrubby vegetation in nine bromeliad patches ranging from 125 m to 1031 m in distance from each other. The survey comprised 24 permanent plots surveyed over ten sampling periods at monthly intervals between February 2006 and September 2007. The number of plots per patch and plot size were proportional to the area of each patch. Plot size for bromeliad and ground samples was 7 x 3 m ( $n = 6$ ) for small patches and 20 x 3 m ( $n = 18$ ) for large patches. In bromeliad patches with at least two plots ( $n = 5$  patches), each plot was 21 m from its nearest neighbor. We sampled terrestrial and epiphytic bromeliads (up to 1.5 m in height) in all plot areas and manually collected spiders from the surfaces of all plant foliage (dead and living leaves), the interiors of the rosettes and between the leaf axils of 1110 bromeliads comprising 32 species. Bromeliads sampling was performed using non-destructive methods. We fixed the spiders in 75% ethanol for later identification. To minimize bias in the analyses, we only used the spiders from the 14 bromeliad species that matched the minimum abundance criteria of eight plants and six spiders per bromeliad species (see Gonçalves-Souza et al. 2011).

Spider density on vegetation is typically lower than on bromeliads, thus requiring us to increase the sampling effort (plot size); we used plots of 20 x 20 m (n = 18) in large patches and 20 x 7 m (n = 6) in small patches. The plots were 1 m apart; although this distance might not distinguish between two vegetation communities, plots at a distance of more than 1 m could include fauna from outside the bromeliad patch. The number of plots per bromeliad patch varied from one to five depending on the size of the patch. For example, for the smallest bromeliad patch (0.005 ha), we made a single 7 x 3 m plot, whereas for the largest one (0.93 ha), we made five plots of 20 x 3 m. To avoid temporal discrepancies in comparative analysis, the three habitat types were sampled concomitantly in each sampling period. We used beating trays to sample 20 herbaceous-shrubby plants from each large plot (n = 18) and 10 plants from each small plot (n = 6), which totaled 420 sampled plants. The selected plants were less than or equal to 3 m in height and the distance between them varied from 1 to 3 m. The beating trays were made up of a 1 x 1 m square wooden beam frame holding a 1m<sup>2</sup> cotton cloth; these trays were placed under the shrub to be sampled and, with the help of a stick, we beat the shrub 20 times so that the spiders would fall onto the cloth. After this procedure, the spiders were fixed and preserved in 75% ethanol. Voucher specimens are deposited in the Instituto Butantan (Brazil). We used different sampling methods for each habitat type to maximize spider collection. Each method used here is the most appropriate for the purpose of this study (Gonçalves-Souza et al. 2010).

#### SPIDER BODY SIZE MEASUREMENTS

We took photographs and measured spider prosoma length and height as well as body length in a stereoscopic microscope (Leica® MZ 16). We use prosoma length as a measure of body size and the ratio between prosoma height and body length as spider flatness (i.e., body



shape). Because we were interested in understanding the associations of spider species with habitat types and bromeliad species, the body sizes of males and females were averaged for each spider species. A minority of the spider genera collected were from dimorphic lineages, with the exception of a few genera from the families Araneidae, Tetragnathidae and Thomisidae. The difference between the sexes is smaller when comparing prosoma size because the most drastic modification is to opisthosoma size. In addition, our samples included both males and females for only a few spider species. Hormiga et al. (2000) considered dimorphic species to be those with a ratio of prosoma sizes between females and males of less than 0.5 or higher than 2. We calculated the female/male prosoma size ratio from our data and did not find dimorphic species (range = 0.698 – 1.77, Table S2, Appendix). Thus, male-female body size pooling is unlikely to affect our conclusions. To construct the phylogeny used for the analyses, we combined all of the available information about the relationships among species. Detailed information about the literature sources that were utilized and details on phylogeny construction are available in the Appendix. Due to the lack of detailed information on branch lengths and difficulties in assigning dates to past lineage separations, which would be required for calibrating the phylogeny, we manually produced a consensus topology describing the phylogenetic relationships among species. Because of this lack of resolution and definition regarding branch lengths, more refined inferences on evolutionary models are not adequate and we used a more statistical overall approach to analyze the relationships (see below) and interpret the results. We then used the software programs PDTREE and PDDIST to draw the consensus phylogeny and to calculate a pairwise patristic distance from which eigenvectors were extracted respectively (see below) (Garland and Ives 2000).

## STATISTICAL ANALYSES

We performed variance partitioning of the dependent variables (spider body size and flatness) using two groups of ecological predictors, guild (active hunting or web-building spiders), considered an intrinsic ecological feature, and species habitat occupancy (bromeliad or dicot), an extrinsic ecological feature.

To account for the phylogenetic non-independence among species and test for phylogenetic effects, we used the approach proposed by Desdevises et al. (2003), which is based on Phylogenetic Eigenvector Regression (PVR) analyses (Diniz-Filho et al. 1998). The original PVR method uses a Principal Coordinates Analysis (PCoA) to extract the eigenvectors of the phylogenetic distance matrix (D) after a double-centered transformation (Diniz-Filho et al. 1998; Fig. 1A). Some of these eigenvectors are then used as a predictor variable in further multiple and partial regressions (Figs 1B and 1C). Because PVR does not assume an explicit evolutionary model that would require a better knowledge of branch lengths (but see Diniz-Filho et al. 2012), it is an appropriate method for utilizing the unconfirmed and topology-based phylogenetic information available for our species.

In the original PVR procedure, the estimated value of the multiple regression expresses the shared phylogenetic variance among the species, thus representing an estimate of the P-component, whereas the residuals of the multiple regression express the proportion of the variation in Y (spider body size and flatness) that is independent of phylogeny (as expressed by the eigenvectors). The residuals of the model thus express the S-component of the variation in Y in species, independent of ancestral values, or at least the effects of phylogenetic variation at shorter scales, close to the tips of the phylogeny and resulting from recent adaptations (Diniz-Filho et al. 2009). Desdevises et al. (2003) improved the original PVR approach and, rather than

using the S-components for inferences, used a more general partial regression to explain the proportions of the variation in Y due directly to ecological and to phylogenetic components and their overlap (see below).

In our hierarchical approach, we first evaluated the pattern of spider body size variation between habitats (the presence of spider species in bromeliads or dicot), i.e., at the habitat scale. Then, we compared the distribution of spider body sizes to different microhabitat features (architectural variation among 14 bromeliad species), i.e., at the microhabitat scale. We then performed the following analyses in these two scales.

In the habitat analysis, we partitioned the variation in the response matrix Y (spider body size and flatness) between the ecological matrix (component a: habitat type or guild as dummy variables), the phylogenetic matrix obtained with the PVR analysis (component c), and the overlap of these effects (component b) following three steps: *step 1*, we regressed the response variable Y against the ecological variable (habitat type or guild). The coefficient  $R^2_{eco}$  of this regression is equal to components a + b of the decomposition (Desdevises et al. 2003). In this step, we retained the estimated ( $eco_{est}$ ) and residual ( $eco_{res}$ ) values for the microhabitat analysis (see below; Figs 1B and 1C). *Step 2*, we regressed the response variable Y against the phylogenetic eigenvectors (X), retained in a stepwise selection model following Desdevises et al. 2003. The coefficient  $R^2_{phy}$  of this regression is equal to components b + c of the decomposition. In this step, we retained the estimated ( $phy_{est}$ ) and residual ( $phy_{res}$ ) values for the microhabitat analysis (Figs 1B and 1C). *Step 3*, we implemented a multiple regression on both ecological and phylogenetic variables. The coefficient  $R^2_{tot}$  represents components a + b + c of the decomposition. At this step, we retained the estimated ( $total_{est}$ ) and residual ( $total_{res}$ ) values for the microhabitat analysis (Figs 1B and 1C). After these three steps, we calculated the individual

value of each component following the subtraction proposed by Desdevises et al. (2003):

component a =  $R^2_{tot} - R^2_{phy}$ ; component b =  $R^2_{env} + R^2_{phy} - R^2_{tot}$ ; component c =  $R^2_{tot} - R^2_{env}$ .

Component a is the ecological component, component b is the phylogenetically structured environmental variation, i.e., the “phylogenetic niche conservatism”, and component c is the phylogenetic component (Desdevises et al. 2003, Staggemeier et al. 2010). If the variation in a morphological trait is related to the ecological component, the community is structured by phylogenetic overdispersion. In contrast, if the phenotypic variation is related to the phylogenetic component, the community is structured by phylogenetic clustering. We performed the partitioning method twice, once for habitat type (i.e., bromeliad or dicot) and once for guild.

In the microhabitat analysis (Fig. 1C), we utilized only the exclusively bromeliad-living spider fauna. Thus, our ecological component is only attributed to guild once we do not have habitat comparisons. We used the retained estimated and residual values from the three regression analyses (steps 1-3, above) to extract the ecological, niche conservatism and phylogenetic components of the total variation. To obtain the ecological component (habitat or guild component), we subtracted the values of “ $total_{res}$ ” from the values of “ $phy_{est}$ ” (Fig. 1C); to obtain the niche conservatism component, we subtracted the values of “ $eco_{est}$ ” from the values of “ $total_{res} - phy_{est}$ ” (Fig. 1C). This component, the correlation of the ecological and phylogenetic components, represents the phylogenetically structured ecological variation (Desdevises et al. 2003). By definition, the correlation between habitat occupancy (ecological component) and the phenotypic similarity of closely related species (phylogenetic component) represents niche conservatism (Ackerly 2003). To obtain the phylogenetic component (P), we subtracted the values of “ $phy_{est}$ ” from the values of “ $eco_{est} + (total_{res} - phy_{est})$ ” (Fig. 1C). These new vectors, the phylogenetic (P), ecological (S) and niche conservatism (PS) components of phenotypic

variation, were used in the following analysis. We calculated the mean values of Y (body size or flatness), P, S and PS for each bromeliad species and regressed these variables against the predictors of plant architecture (i.e., the number of leaves, leaf width and length) (Fig. 1C). We selected the best bromeliad predictors as those having the smallest Akaike Information Criterion values to conduct the regression analysis. Before all analyses, the data on prosoma length and spider flatness were log transformed to meet test assumptions.

## Results

We found 145 spider species associated with bromeliad and dicot habitats. Of these, 117 species were exclusively related to one habitat; 47 were associated with bromeliads and 70 with dicots. Bromeliad-living spiders were on average 50% larger than dicot-living spiders (separate variances  $t$  test = 2.46; df= 58.81;  $P$  = 0.016). In addition, bromeliad spiders were 9% flatter than dicot spiders (separate variances  $t$  test = -4.03; df= 288,4;  $P$  < 0.001; Fig. 1). This effect is larger for hunting spiders (Salticidae) than for web-building ones. The bromeliad-living salticids were 47% larger than those salticids inhabiting dicots (separate variances  $t$  test = -5.24; df= 56.46;  $P$  < 0.0001) (Fig. 1). In contrast, the body size of web-building spiders, such as Linyphiidae (body size: separate variances  $t$  test = -1.267; df= 56.69;  $P$  = 0.21) and Theridiidae (separate variances  $t$  test = -0.489; df= 24.80;  $P$  = 0.628), was not affected by habitat type (Fig. 2A). The body flatness of these three families did not differ between bromeliads and dicots (Fig. 2B).

Partitioning out the total phenotypic variation of spiders in relation to guilds (hunting vs. web spiders) and habitat occupancy (bromeliad vs. dicots), we found a strong phylogenetic signal (component c of partitioning) in body size (guild,  $R^2$  = 0.26; habitat,  $R^2$  = 0.641) and flatness (guild,  $R^2$  = 0.203; habitat,  $R^2$  = 0.29), indicating that phenotypic similarity is related to

phylogenetic relatedness (Table 1). Comparing phenotypic variation and habitat occupancy using partial regressions, we found a weak explanation of the niche conservatism component (component b, which represents the shared influence of ecology and phylogeny) in the variation of spider body size ( $R^2 = 0.038$ ) and flatness ( $R^2=0.02$ ). However, we found that the niche conservatism component explains the patterns in spider body size ( $R^2 = 0.419$ ) and flatness ( $R^2=0.106$ ) when guild alone is taken into account (Table 1). Thus, this phylogenetically structured phenotypic variation suggests that body size and flatness are conserved in relation to species guild, an intrinsic ecological trait. However, the ecological component (component a) does not explain the variation in spider body size (guild,  $R^2=0.012$ ; habitat,  $R^2=0.003$ ) and flatness (guild,  $R^2=0.002$ ; habitat,  $R^2=0.001$ ) (Table 1), reinforcing the importance of niche conservatism in the patterns of body size variation among guilds and habitats.

When we compared the variations in spider body size and flatness at the microhabitat scale without controlling for phylogeny, we found that the mean value of bromeliad-living spiders' body size was negatively correlated to leaf length ( $\beta=-0.617$ ,  $R^2_{\text{adj}}=0.486$ ,  $P=0.015$ ) and the number of leaves ( $\beta=-0.481$ ,  $R^2_{\text{adj}}=0.486$ ,  $P=0.045$ ). Partitioning out the variation in body size among bromeliad-living spiders, we found that the phylogenetic component is negatively related to leaf length ( $\beta=-0.756$ ,  $R^2_{\text{adj}}=0.785$ ,  $P<0.001$ ) and the number of leaves ( $\beta=-0.602$ ,  $R^2_{\text{adj}}=0.785$ ,  $P<0.001$ ), whereas the values of the ecological and niche conservatism components of spider body size were not related to microhabitat traits (Table 2). The absence of ecological and niche conservatism effects and the strong phylogenetic signal in spider body size suggest that phylogenetic relatedness is related to bromeliad morphological resemblance. Thus, it appears that bromeliads with elongated leaves selected for small-bodied spider clades. Conversely, the flatness of bromeliad spiders was not affected by bromeliad leaf length without

controlling for phylogeny ( $\beta=0.502$ ,  $R^2_{\text{adj}}=0.252$ ,  $P=0.069$ ). However, the phylogenetic and ecological components of spider flatness were both related to bromeliad leaf length. The mean ecological component (component *a*) of spider flatness is negatively correlated with bromeliad leaf length ( $\beta=-0.566$ ,  $R^2_{\text{adj}}=0.321$ ,  $P=0.037$ ), suggesting that spiders that occur in elongated bromeliads were more flattened. Combined with the habitat scale analysis, these results suggest that spider flatness is phylogenetically clustered at the habitat scale, whereas it is phylogenetically overdispersed at the microhabitat scale. The scale dependence of the relationship between phylogenetic relatedness and phenotypic resemblance shows that niche occupancy affects spider morphology in different ways ranging from clustered to overdispersed. In turn, the mean phylogenetic component was positively associated with leaf length ( $\beta=0.566$ ,  $R^2_{\text{adj}}=0.427$ ,  $P=0.029$ ), indicating that large-bodied closely related species occur in bromeliads with elongated leaves. The mean niche conservation component was not related to any of the bromeliad traits (leaf width:  $\beta=0.289$ ,  $R^2_{\text{adj}}=0.083$ ,  $P=0.318$ ) (Table 2), suggesting that phenotypic variation is not conserved in relation to microhabitat characteristics.

## **Discussion**

We have demonstrated that both habitat and microhabitat scales affect the phylogenetic and phenotypic patterns in plant-living spiders. Bromeliad-living spiders are larger and flatter than spiders that forage in the surrounding dicots. The novel contribution of our results is that even on a scale of few centimeters, plant traits are selecting for spiders' body size and shape. In addition, the diversification of body size and shape had distinct pattern of evolution considering both phylogenetic relatedness and recent ecological adaptations.

*Habitat scale: phylogenetic signal and the conservatism of body size among guilds*

At the habitat scale, we found that only phylogeny explained the variation in spider body size and flatness, suggesting that spiders occupying architecturally similar plant species are phylogenetically clustered. The phylogenetic signals in the body size of the spiders in response to habitat type indicate that environmental filtering processes are important in structuring phenotypic resemblance among the studied species.

Bromeliads can select for large-bodied closely related spiders because, in general, large organisms have higher resource requirements, which constrain them from occupying neighbouring habitats with lower resource inputs. It has been demonstrated that the retention of rainwater in bromeliad phytotelmata favors the accumulation of aquatic and terrestrial invertebrates in comparison to surrounding plants that do not accumulate rainwater (Romero and Srivastava 2010). Thus, it is reasonable to infer that bromeliads can provide greater resources for spiders, as these animals can eat both aquatic and terrestrial prey (Piccoli 2011). The positive relationship between habitat quality (e.g., habitat size/complexity, prey density) and individual size was previously demonstrated for vertebrates (Kelt and Brown 2001) and invertebrates such as spiders (Lighton and Fielden 1995). For instance, Smith et al. (2010) reported that the evolution of giant terrestrial mammals was apparently influenced by ecological niches and land area in response to energy acquisition.

In addition, it is possible that the ability to dive into the water accumulated in bromeliads' phytotelmata influence spider body size. Previous works have demonstrated that large animals dive deeper, which in its turn, can improve foraging efficiency by providing access to large prey and aid in avoiding predators (Hare and Miller 2009, Weise et al. 2010); this mechanism could favor large bromeliad-living spiders, which frequently dive to capture aquatic prey and flee from



predators. In fact, only large bromeliad spiders (e.g., *Corinna* sp., *Nothroctenus fuxico*, *Pachistopelma* sp., *Psecas* sp.) dive into bromeliad water, whereas young, small spiders do not (T. Gonçalves-Souza, pers. obs.).

Bromeliad can also select for flatter spiders, because this morphology can favour organisms to reach the tight spaces between bromeliad leaf axils (even when diving) to foraging and predation avoidance. It has been widely recognized that shared ancestry favors the co-occurrence of closely related species with similar body size and shape, as well as similar ecological niches (Ackerly 2009). In the evolutionary history of the spider-bromeliad association, flatter closely related spiders could forage better among plant axils than less flat spiders. Predation may also be an important mechanism dictating body flatness. For instance, Sillett et al. (1997) reported that *Pseudocolaptes lawrencii* (Furnariidae), a bird specialized in foraging in bromeliads, avoids eating isopods because they are dorsoventrally flattened, which make them difficult to catch. A flattened body has also been found in other vertebrates and invertebrates that forage in habitats with narrow spaces, such as bromeliads, caves, rocks (e.g., Hedges 1989, Benzing 2000, Dias and Brescovit 2004, Goodman and Isaac 2008). If the success of foraging in bromeliads is related to the ability to use all available leaf surfaces, spiders that are able to forage in small spaces between leaves (i.e., flatter spiders) could have advantages in terms of foraging and predator avoidance. These results are in accordance with the maneuverability hypothesis (Norberg 1994), which predicts the reduction of morphological traits when such a reduction improves performance (e.g., sexual display, foraging) for species in restrictive habitats, such as rock crevices and dense habitats. These results indicate that bromeliad architecture could drive the evolution of larger and flatter spiders by means of energy supply, foraging efficiency and the ability to avoid natural enemies.

The phenotypic variation among spider guilds was explained by both phylogeny and niche conservatism. This result suggests that closely related spiders have similar body sizes and belong to the same guild. Within each guild, spiders share the ability to weave webs or lack thereof, which has a drastic influence on their locomotion, foraging behavior and habitat selection. In addition, spiders' foraging behavior (i.e., upside-down walking and standing) is reflected in body position, which could generate different patterns of body size and shape between web-building and hunting spiders (Moya-Laraño et al. 2008). As a result, the phenotypic similarity in spider body sizes should be higher within than among guilds, and this resemblance most likely accounts for the strong phylogenetic signals.

*Microhabitat scale: phylogenetic signals in body size, and the shared influence of phylogeny and ecology on spider flatness*

At the microhabitat scale, spiders' morphological traits were affected by both phylogeny and ecological niche. Bromeliad leaf length and the number of leaves had a negative correlation with the phylogenetic component of spider body size and explained 78% of its variation. This result indicates that large bromeliads select for small-bodied closely related spiders. We found a shared influence of phylogenetic and ecological (guild) components on spider flatness in relation to bromeliad architecture. Specifically, bromeliad leaf length was positively correlated with the phylogenetic component and negatively with the ecological component of body flatness. These results suggest that the variation in spider flatness depends partly on ancestral body shape, but recent adaptations are apparently enforcing the negative deviation of those ancestral values, meaning that flatness of larger spiders is intensified after subsequent specialization to bromeliads.

The morphological variation had strong phylogenetic signals also within bromeliad-living spiders. For example, closely related round (i.e., less flattened) spiders were selected for in bromeliads with greater leaf length and so this variation was inherited throughout the lineages. In contrast, the ecological component of variation exhibited an inverse correlation with leaf length (Table 2), suggesting that contemporary factors are also influencing the variation in body size independently of historical factors, by independent selective pressures driving phenotypic variation in each species.

The occurrence of small-bodied spider species on large bromeliads appears to be an intriguing pattern of body size distribution among plant-living spiders. For many animals, it is well established that body size is positively correlated with fecundity and resource-rich habitats (e.g., Rimmel and Tammaru 2009). However, the developmental time necessary to achieve a large size generally increases the probability of predation, which in turn acts against the selection for larger size (Blanckenhorn 2000). As a result of this trade-off, small-bodied species could benefit from occupying large bromeliads because they can more effectively avoid predation by finding more retreats. In fact, it has been suggested that small animals are more agile and maneuverable (Norberg 1994, Blanckenhorn 2000). Otherwise, where spiders occur in larger habitats/microhabitats, it is reasonable that large bromeliads should support a greater number of small spiders than large ones. Thus, we suggest that predation and the ability to support more small spiders are not mutually exclusive factors; it is possible that they work together against the increase in body size of spiders within bromeliads.

The negative correlation between the ecological component (guild) and bromeliad leaf length suggests that bromeliad spiders' flatness is most likely an adaptive response to the tight arrangement of bromeliad leaves. Patterns of spider body size/shape evolution (or conservatism)

could arise from both selection on habitat use and competitive processes, depending on either the ecological relevance of species' traits or the scale considered (e.g., regional or local, habitat or microhabitat). Habitat and microhabitat type differences favour the occurrence of closely related spiders of similar size (i.e., phylogenetic clustering), most likely because these spiders share similar ecological requirements, such as energetic requirements. In contrast, to better explore resources in tightly arranged microhabitats while escaping from predators, it appears that microhabitat constraints favor the evolution of flatter spiders on bromeliads. We argue that the method used in this study is straightforward and allowed us to disentangle the phylogenetic and ecological components of variation in spider morphology. In fact, this type of study can shed light on the roles of phylogenetic and ecological components in shaping species' evolutionary history.

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**Table 1.** Coefficients of determination of partial regression models of spider traits against phylogenetic (PVR eigenvectors) and ecological (habitat and guild) components.

Spider trait	Strictly phylogeny	Niche conservatism	Strictly ecology	Unexplained
<b>Habitat</b>				
Body size	0.641	0.038	0.003	0.317
Flattening	0.29	0.02	0.001	0.69
<b>Guild</b>				
Body size	0.26	0.419	0.012	0.309
Flattening	0.203	0.106	0.002	0.689

**Table 2** -Linear regressions of body size (A) and flatness (B) and their partitioned components from phylogenetic eigenvector

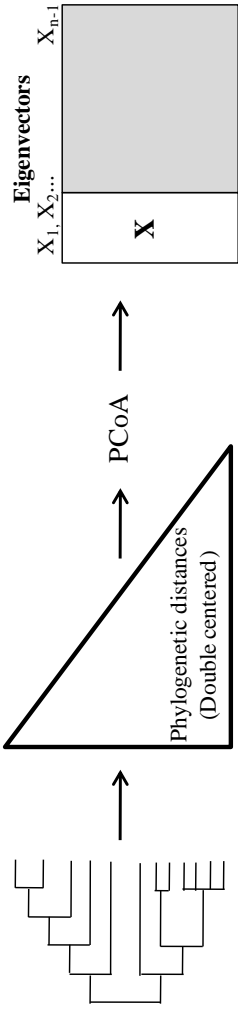
regression analysis (PVR) against leaf length (LL), leaf width (LW), number of leaves (NL) and total leaf area (TLA). The regression analysis was made only with the bromeliad traits retained as the best model based on the Akaike Information Criterion. The first regression analysis does not consider phylogenetic information, whereas in the second one we used the partitioning method (PVR). The variations in the values of spider body size and flatness were partitioned into ecological, niche conservatism and phylogenetic components (see text for details). Bromeliad traits related (i.e.,  $P < 0.05$ ) to the ecological or the phylogenetic components indicate phylogenetic overdispersion and clustering, respectively.

Bromeliad trait	Regression analysis			PVR + Regression analysis									
	B	R <sup>2</sup> <sub>adj</sub>	P	Ecological component		Niche conservatism component		Phylogenetic component					
				B	R <sup>2</sup> <sub>adj</sub>	P	B	R <sup>2</sup> <sub>adj</sub>	P	B	R <sup>2</sup> <sub>adj</sub>	P	
		Body size											
LL	-0.617	0.486	0.015	-	-	-	-	-	-	-0.756	0.785	<0.001	
LW	-	-	-	0.449	0.201	0.11	-0.257	-0.066	0.377	-	-	-	
NL	-0.481	0.486	0.045	-	-	-	-	-	-	-0.602	0.785	<0.001	
		Flattening											
		Ecological component											
LL	0.502	0.252	0.067	-0.566	0.321	0.037	-	-	-	0.566	0.427	0.029	
LW	-	-	-	-	-	-	0.289	0.083	0.318	-	-	-	
NL	-	-	-	-	-	-	-	-	-	0.479	0.427	0.056	
		Niche conservatism component											
		Phylogenetic component											

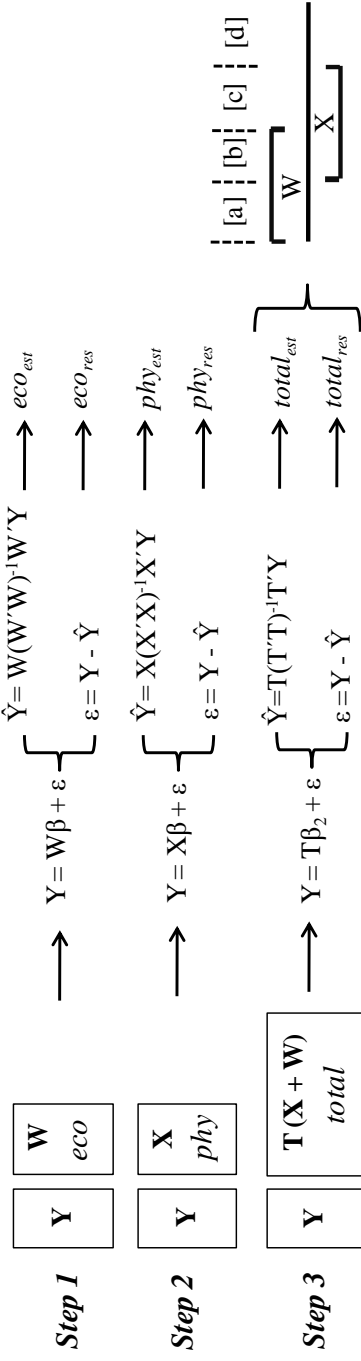
**Figure 1.** Schematic representation of the habitat and microhabitat analyses used to decompose the total variation in spider body size and flatness into phylogenetic (P), ecological (S) and niche conservatism (PS) components. Phylogenetic eigenvector regression (PVR) is represented by a back-transformation of the phylogeny with a double-centralization of the resulting matrix and is followed by a principal coordinates analysis (PCoA); the matrix X represents the eigenvectors that are significantly correlated with species' body size (Fig. 1A). Figure 1B shows the partial regressions used to calculate components a, b, c and d; first, we calculated the estimated and residual values ( $eco_{est}$  and  $eco_{res}$ ) for a regression between body size and the ecological data; then, we regressed body size and the phylogenetic data and saved the estimated and residual values ( $phy_{est}$  and  $phy_{res}$ ); finally, we computed the regression between body size and both the ecological and the phylogenetic data to obtain the percentages of the variance explained ( $R^2$  of the regression method) by each component, a (ecology), b (niche conservatism), c (phylogeny) and d (unexplained variation), following the procedure proposed by Desdevises et al. (2003). Figure 1C illustrates the procedure used to obtain the mean value of spider body size (or flatness) and the components calculated in Figure 1B in each bromeliad species. We then constructed a linear regression between each value (Y, P, S and PS) and the mean value of bromeliad species traits (leaf length, leaf width and number of leaves) after the selection of best models with the Akaike Information Criterion (AIC).

**Figure 2.** Average spider body size (A) and flatness (B) between bromeliads and surrounding dicots for all spiders, Linyphiidae, Theridiidae (both families of web-spiders) and Salticidae (hunting spiders). Error bars denote  $\pm 1SE$  and asterisks indicate significant difference ( $P < 0.05$ ).

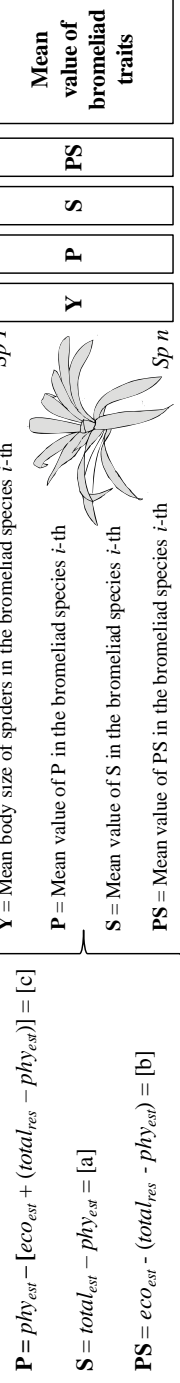
### A) PVR method



### B) Habitat analysis (partial regression)



### C) Microhabitat analysis



**Figure 1**

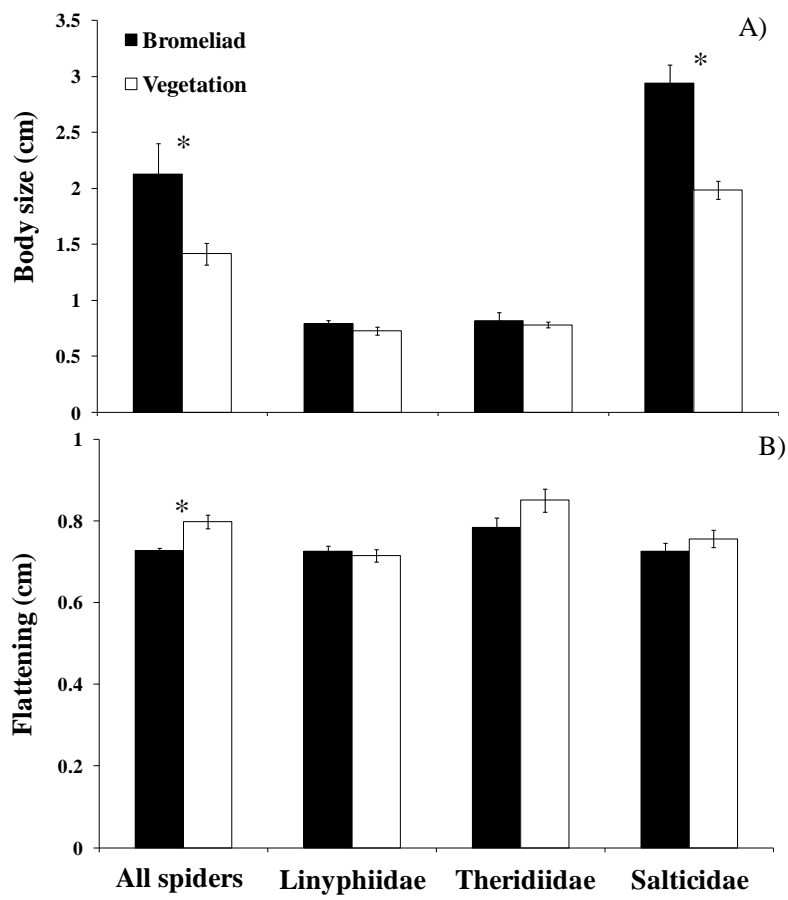


Figure 2

## **APPENDIX: Phylogeny construction and spider guilds**

We compiled data from morphological and molecular phylogenies of spiders to create one unique tree, which was used to estimate the phylogenetic (patristic) distance among species. We used data from a general phylogeny (Coddington and Levi 1991) and other phylogenies made at the family or superfamily levels: Agnarsson (2004; family Theridiidae), Álvarez-Padilla et al. (2009; Tetragnathidae), Griswold et al. (1998; Orbicularie: Deinopoidea, Araneoidea), Hedin and Maddison (2001; Salticidae), Hormiga (1994; Linyphiidae), and Maddison and Hedin (2003; Salticidae). The composite tree was based on the 145 spider species observed in this study occurring in either bromeliad or dicot (herbaceous and shrubby plants) habitats. We based our tree on the general phylogeny of Coddington and Levi (1991) and attributed the longest node at the family level to ensure that genera and species were more similar within families than between families. Within each family with a defined phylogeny (references above), we organised the genera and species based on their proposed kinship. For example, Maddison and Hedin (2003) proposed the genera *Sarinda*, *Zuniga* and *Agelista* as sister groups. Thus, as we collected one species of *Sarinda* and one of *Zuniga* but no *Agelista* species, we defined *Sarinda* sp. and *Zuniga* sp. as a monophyletic group in our composite tree. We considered as monophyletic and polytomous (Vamosi and Vamosi 2007) those families (e.g., Corinnidae, Hahniidae) or genera (e.g., *Corinna*, *Theridion*) without phylogenetic information. As the species we collected were not dimorphic (Table A1), the body sizes of males and females were averaged for each species. We used the program PDTREE to draw the phylogenetic tree and PDDIST to calculate phylogenetic distances (Garland and Ives 2000).

**Table S1.** Spider species as assigned to families and guilds

<b>Species</b>	<b>Family</b>	<b>Guild</b>
<i>Oonops</i> sp.1	Oonopidae	hunting spiders
<i>Orchestina</i> sp.1	Oonopidae	hunting spiders
<i>Carapoia ubatuba</i> Huber, 2005	Pholcidae	web-building spiders
<i>Mesabolivar</i> sp.1	Pholcidae	web-building spiders
<i>Metagonia</i> sp.1	Pholcidae	web-building spiders
<i>Metagonia</i> sp.2	Pholcidae	web-building spiders
<i>Psilochorus</i> sp.1	Pholcidae	web-building spiders
<i>Tupigea</i> sp.1	Pholcidae	web-building spiders
<i>Tupigea nadleri</i> Huber, 2000	Pholcidae	web-building spiders
<i>Ochyrocera</i> sp.1	Ochyroceratidae	web-building spiders
<i>Scytodes</i> sp.1	Scytodidae	hunting spiders
<i>Radulphius laticeps</i>	Miturgidae	hunting spiders
<i>Ero</i> sp.1	Miturgidae	hunting spiders
<i>Dictyna</i> sp.1	Dictynidae	web-building spiders
Hahniidae sp.1	Hahniidae	hunting spiders
Hahniidae sp.2	Hahniidae	hunting spiders
Hahniidae sp.3	Hahniidae	hunting spiders
<i>Castianeira</i> sp.1	Corinnidae	hunting spiders
<i>Corinna rubripes</i>	Corinnidae	hunting spiders
<i>Corinna</i> sp.2	Corinnidae	hunting spiders
<i>Corinna</i> sp.3	Corinnidae	hunting spiders
<i>Corinna</i> sp.4	Corinnidae	hunting spiders
<i>Corinna</i> sp.5	Corinnidae	hunting spiders
<i>Aysha</i> gr. <i>helvola</i>	Anyphaenidae	hunting spiders
<i>Bromelina oliola</i> Brescovit, 1993	Anyphaenidae	hunting spiders
<i>Iguarima censoria</i> Keyserling, 1891	Anyphaenidae	hunting spiders
<i>Katissa</i> sp.1	Anyphaenidae	hunting spiders
<i>Osoriella rubella</i> Keyserling, 1891	Anyphaenidae	hunting spiders
<i>Osoriella</i> sp.1	Anyphaenidae	hunting spiders
<i>Macrophyes jundiai</i> Brescovit, 1993	Anyphaenidae	hunting spiders
<i>Teudis</i> sp.1	Anyphaenidae	hunting spiders
<i>Wulfilopsis leopoldina</i> Brescovit, 1997	Anyphaenidae	hunting spiders
<i>Alcmena</i> sp.1	Salticidae	hunting spiders
<i>Arnoliseus</i> sp.1	Salticidae	hunting spiders
<i>Chirothecia</i> cf. sp.1	Salticidae	hunting spiders
<i>Consingis</i> sp.1	Salticidae	hunting spiders
<i>Coryphasia</i> sp.1	Salticidae	hunting spiders
Salticidae sp.1	Salticidae	hunting spiders
Salticidae sp.2	Salticidae	hunting spiders



Euophryinae sp.1	Salticidae	hunting spiders
Euophryinae sp.2	Salticidae	hunting spiders
Euophryinae sp.3	Salticidae	hunting spiders
Euophryinae sp.5	Salticidae	hunting spiders
Euophryinae sp.6	Salticidae	hunting spiders
Euophryinae sp.7	Salticidae	hunting spiders
Euophryinae sp.8	Salticidae	hunting spiders
Euophryinae sp.9	Salticidae	hunting spiders
<i>Chira micans</i> Simon, 1902	Salticidae	hunting spiders
<i>Myrmarachne</i> sp.3	Salticidae	hunting spiders
<i>Beata</i> sp.1	Salticidae	hunting spiders
<i>Psecas</i> sp.1	Salticidae	hunting spiders
<i>Noegus</i> sp.1	Salticidae	hunting spiders
<i>Cylistella</i> sp.1	Salticidae	hunting spiders
<i>Sarinda</i> sp.1	Salticidae	hunting spiders
<i>Zuniga</i> sp.1	Salticidae	hunting spiders
<i>Cotinusa</i> sp.1	Salticidae	hunting spiders
<i>Cotinusa</i> sp.2	Salticidae	hunting spiders
<i>Erica</i> sp.1	Salticidae	hunting spiders
<i>Fluda</i> sp.1	Salticidae	hunting spiders
<i>Martella</i> sp.1	Salticidae	hunting spiders
<i>Vinnius</i> sp.1	Salticidae	hunting spiders
<i>Lyssomanes</i> sp.1	Salticidae	hunting spiders
<i>Lyssomanes</i> sp.3	Salticidae	hunting spiders
<i>Acentroscelus</i> sp.1	Thomisidae	hunting spiders
<i>Epicadus</i> sp.1	Thomisidae	hunting spiders
<i>Strophius</i> sp.1	Thomisidae	hunting spiders
<i>Tmarus</i> sp.1	Thomisidae	hunting spiders
<i>Tobias</i> sp.1	Thomisidae	hunting spiders
<i>Olios</i> sp.1	Sparassidae	hunting spiders
<i>Enoploctenus cyclothorax</i> Bertkau, 1880	Ctenidae	hunting spiders
<i>Isoctenus</i> sp.1	Ctenidae	hunting spiders
<i>Architis</i> sp.1	Pisauridae	hunting spiders
<i>Barrisca</i> sp.1	Trechaleidae	web-building spiders
<i>Miagrammopes</i> sp.1	Uloboridae	web-building spiders
<i>Ocrepeira gnomo</i> Mello-Leitão, 1943	Araneidae	web-building spiders
<i>Testudinaria</i> sp.1	Araneidae	web-building spiders
<i>Hypognatha</i> sp.1	Araneidae	web-building spiders
<i>Micrathena</i> sp.1	Araneidae	web-building spiders
<i>Micrathena acuta</i> Walckenaer, 1842	Araneidae	web-building spiders
<i>Cyclosa fililineata</i> Hingston, 1932	Araneidae	web-building spiders

<i>Araneus</i> sp.1	Araneidae	web-building spiders
<i>Araneus stabilis</i> Keyserling, 1892	Araneidae	web-building spiders
<i>Mangora</i> sp.1	Araneidae	web-building spiders
<i>Mangora aripeba</i>	Araneidae	web-building spiders
<i>Metazygia</i> sp.1	Araneidae	web-building spiders
<i>Alpaida</i> sp.1	Araneidae	web-building spiders
<i>Alpaida atomaria</i> Simon, 1895	Araneidae	web-building spiders
<i>Eustala</i> sp.1	Araneidae	web-building spiders
<i>Homalometa</i> sp.1	Araneidae	web-building spiders
<i>Chrysometa</i> sp.1	Tetragnathidae	web-building spiders
<i>Chrysometa</i> sp.2	Tetragnathidae	web-building spiders
<i>Leucauge</i> sp.1	Tetragnathidae	web-building spiders
<i>Leucauge</i> sp.2	Tetragnathidae	web-building spiders
<i>Tetragnatha</i> sp.1	Tetragnathidae	web-building spiders
<i>Symphytognatha</i> sp.1	Symphytognathidae	web-building spiders
<i>Chthonos</i> sp.1	Theridiosomatidae	web-building spiders
<i>Naatlo</i> sp.1	Theridiosomatidae	web-building spiders
<i>Ogulnius</i> sp.1	Theridiosomatidae	web-building spiders
<i>Meioneta</i> sp.1	Linyphiidae	web-building spiders
Linyphiidae sp.1	Linyphiidae	web-building spiders
Linyphiidae sp.2	Linyphiidae	web-building spiders
Linyphiidae sp.3	Linyphiidae	web-building spiders
Linyphiidae sp.5	Linyphiidae	web-building spiders
<i>Dubiaranea</i> sp.1	Linyphiidae	web-building spiders
<i>Dubiaranea</i> sp.2	Linyphiidae	web-building spiders
<i>Eurymorion insigne</i> Millidge, 1991	Linyphiidae	web-building spiders
<i>Anodoration claviferum</i> Millidge, 1991	Linyphiidae	web-building spiders
<i>Fissiscapus pusillus</i> Millidge, 1991	Linyphiidae	web-building spiders
<i>Sphecozone</i> sp.1	Linyphiidae	web-building spiders
<i>Sphezocone</i> sp.3	Linyphiidae	web-building spiders
<i>Phycosoma altum</i> Keyserling, 1886	Theridiidae	web-building spiders
<i>Audifia</i> sp.1	Theridiidae	web-building spiders
<i>Dipoena</i> sp.1	Theridiidae	web-building spiders
<i>Dipoena</i> sp.2	Theridiidae	web-building spiders
<i>Dipoena</i> sp.3	Theridiidae	web-building spiders
<i>Dipoena</i> sp.4	Theridiidae	web-building spiders
<i>Dipoena woytkowskii</i> Levi, 1963	Theridiidae	web-building spiders
<i>Euryopsis</i> sp.1	Theridiidae	web-building spiders
<i>Tekellina</i> sp.1	Theridiidae	web-building spiders
<i>Spintharus gracilis</i> Keyserling, 1886	Theridiidae	web-building spiders
<i>Thwaithesia</i> sp.1	Theridiidae	web-building spiders

<i>Thwaitesia affinis</i> O.P. Cambridge, 1882	Theridiidae	web-building spiders
<i>Episinus</i> sp.1	Theridiidae	web-building spiders
<i>Episinus</i> sp.2	Theridiidae	web-building spiders
<i>Faiditus</i> sp.1	Theridiidae	web-building spiders
<i>Argyrodes</i> sp.1	Theridiidae	web-building spiders
<i>Rhomphae</i> sp.1	Theridiidae	web-building spiders
<i>Chryso</i> sp.1	Theridiidae	web-building spiders
<i>Chryso</i> sp.2	Theridiidae	web-building spiders
<i>Achaearana</i> sp.1	Theridiidae	web-building spiders
<i>Echinotheridion</i> sp.1	Theridiidae	web-building spiders
<i>Keijia mneon</i> Bösenberg & Strand, 1906	Theridiidae	web-building spiders
<i>Thymoites</i> sp.1	Theridiidae	web-building spiders
<i>Thymoites</i> sp.2	Theridiidae	web-building spiders
<i>Thymoites</i> sp.3	Theridiidae	web-building spiders
<i>Theridion</i> sp.1	Theridiidae	web-building spiders
<i>Theridion</i> sp.2	Theridiidae	web-building spiders
<i>Theridion</i> sp.3	Theridiidae	web-building spiders
<i>Theridion</i> sp.4	Theridiidae	web-building spiders
<i>Theridion</i> sp.5	Theridiidae	web-building spiders
<i>Theridion</i> sp.6	Theridiidae	web-building spiders
<i>Synotaxus</i> sp.1	Synotaxidae	web-building spiders

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**Table S2.** Ratio between female and male prosoma size of each species with at least one individual of both sexes. Species with values of female/male ratio less than 0.5 and higher than 2 were considered dimorphic <sup>\*1</sup>.

<b>Spider species</b>	<b>Prosoma size ratio</b>
<i>Anodoration claviferum</i> Millidge, 1991	0.899
<i>Arnoliseus</i> sp.1	1.770
<i>Barrisca</i> sp.1	1.016
<i>Beata</i> sp.1	0.757
<i>Castianeira</i> sp.1 <sup>*2</sup>	1.117
<i>Castianeira</i> sp.1	1.180
<i>Chrysometa</i> sp.2	0.879
<i>Chryso</i> sp.1	0.908
<i>Chryso</i> sp.2	0.783
<i>Chthonus</i> sp.1	0.946
<i>Coryphasia</i> sp.1	0.895
<i>Cotinusa</i> sp.1	0.950
<i>Cotinusa</i> sp.2	1.359
<i>Cyclosa fililineata</i> Hingston, 1932	0.945
<i>Cylistella</i> sp.1	0.983
<i>Dipoena</i> sp.1	1.048
<i>Dipoena</i> sp.3	1.052
<i>Epicadus</i> sp.1	1.500
<i>Euophryinae</i> sp.3	0.726
<i>Fissiscapus pusillus</i> Millidge, 1991	1.141
<i>Hahniidae</i> sp.1	0.868
<i>Hahniidae</i> sp.2	0.910
<i>Hahniidae</i> sp.3	1.093
<i>Linyphiidae</i> sp.1	0.831
<i>Linyphiidae</i> sp.1	1.049
<i>Linyphiidae</i> sp.3	0.793
<i>Mesabolivar</i> sp.1	0.917
<i>Miagrammopes</i> sp.1	1.231
<i>Noegus</i> sp.1	0.928
<i>Oonops</i> sp.1	0.820
<i>Phycosoma altum</i> Keyserling, 1886	0.698
<i>Psilochorus</i> sp.1	0.970
<i>Rhomphaea</i> sp.1	1.309
<i>Scytodes</i> sp.1	0.843
<i>Sphecozone</i> sp.1	0.905
<i>Spintharus gracilis</i> Keyserling, 1886	0.945
<i>Testudinaria</i> sp.1	1.386
<i>Tetragnatha</i> sp.1	0.943
<i>Theridion</i> sp.1	1.284
<i>Theridion</i> sp.2	1.001

<i>Theridion</i> sp.4	1.109
<i>Thymoites</i> sp.1	0.868
<i>Tmarus</i> sp.1	1.120
<i>Vinnius</i> sp.1	1.091

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\* 1 – These cutoff values to decide which species are considered dimorphic was based on Hormiga et al. 2000.

\* 2 – Some species have two values of dimorphism because their occurred at bromeliad and dicot.

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## **ARTIGO 2**

# **[UNRAVELING THE ROLE OF HABITAT STRUCTURE, GEOGRAPHIC DISTANCE AND PHYLOGENY TO SPIDER TRAIT DIVERSITY]**

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## ABSTRACT

The interplay between ecological and evolutionary processes brings several advances to ecology in the last decade. However, two main issues are still part of ecophylogenetics: the bias to plant studies and the absence of studies (with other groups except plants) considering how environmental and geographic factors contribute to phylogenetic and trait diversity. We evaluated vegetation-living spiders occurring at different plant species in 12 sites along ~2000 km of the Brazilian coast. We first tested if there are phylogenetic signals in spider trait diversity. Then, we asked whether plant architecture and location (geographic distance) predict spider phylogenetic and trait diversity. In addition, we compared the pattern of trait variation between hunting and web-building spiders. We found that trait diversity was not homogeneously distributed in the phylogenetic tree, which suggests that we cannot consider phylogeny as the only predictor of spider trait diversity. We showed that plant architecture and location act as filters of spider trait diversity, which means that within each locality or within each plant architecture spiders are morphologically similar. Furthermore, besides the diversification of traits in early evolution of spiders, the ability to use webs for hunting preys has drastic influence on body size conservatism. Conversely, the abandonment of web for hunting influenced more lability on spider traits, which suggest that foraging mode has influencing trait diversity. Overall, our study adds voice to recent claims that life history, local (ecological) factors and large-scale (biogeographic, evolutionary) processes are interacting to determine species assembly and body trait evolution.

Keywords: phylogenetic clustering, phylogenetic signals, habitat filtering, spiders, body size



## INTRODUCTION

The way interaction among species and their habitats modulate species phenotype, and the consequences to ecological differentiation experienced outstanding attention throughout the development of the ecological theory [1]. It has been assumed that habitat features are pivotal in determining species co-occurrence and persistence along evolutionary history. Perhaps more important, species relatedness could dictate the strength in which habitat features affect community assembly [2]. Two main processes are considered when predicting the phylogenetic structure of species assemblages. First, under environmental filtering expectations, closely related species sharing similar physiological limitations will co-occur in the same habitat (phylogenetic clustering) [3]. On the other hand, under limiting similarity process it is expected that closely related species compete more intensely for a limited resource; thus, distantly related species are expected to occur in the same habitat (phylogenetic overdispersion) [3]. Likewise, habitat filtering and limiting similarity processes will cause phenotypic clustering and overdispersion, respectively [4]; but see [5]. Despite the increasing number of studies addressing questions on phenotypic and phylogenetic patterns of communities [6], it is critical the bias toward certain taxa (i.e., plants) and scales [6–9].

By incorporating different scales to understand phylogenetic community structure, it has been shown that the relative importance of habitat filtering and limiting similarity can change from small to large scales [8–11]. However, there is no consistent pattern in the literature concerning scale and phylogenetic/phenotypic structure. For instance, whereas Swenson et al. [10] showed that the phylogenetic structure of plant communities changed from overdispersed to clustered as spatial scale increases, Gómez et al. [12] found for antbirds a shift from clustering to overdispersion as spatial scale increase. Due to this lack of generality, a recent review paper

asked for further exploration of the relationship between scale and phylogenetic and functional diversity [9]. In our study, we used vegetation-living spiders occurring in plants with distinct architectures and at different spatial scales to test whether architectural and scale variation can predict phylogenetic and phenotypic diversity.

Spiders are terrestrial predators that use physical structure of habitats to forage and attach their webs [13]. Previous studies showed that fine-scale physical variations in habitats (e.g., plant architecture) have strong effect on spiders [14–15], resulting in compartmentalized communities [16–17], i.e., each subset of the spider assemblage living in a specific plant architecture. However, there is little information about how habitat structure affects spiders of varying life history (e.g., hunting mode: web-builders or active hunters). For instance, Souza and Martins [18] compared the distribution of different spider guilds on inflorescences and vegetative branches. The authors showed that whereas foliage runner and stalker guilds were larger on inflorescence than on vegetative branches, the size of ambushers and web-building guilds did not differ between branches [18]. These results suggest that life history is a reliable predictor of guild distribution, although no study has tested if those compartmentalized communities are an outcome of ecological or evolutionary processes. However, if guild and size of spiders are phylogenetically and functionally structured, we can expect two evolutionary outcomes: first, closely related spiders sharing similar morphological traits occur in plant species with similar architecture, which means that plant architecture drives phylogenetic and phenotypic clustering [19]. Second, that phylogenetic and phenotypic clustering will increase (i.e., overdispersion will decrease) as spatial scale decrease, because similar species will be filtered into similar habitats [19].

In addition, it has been suggested that environmental and spatial variation can affect certain lineages (or a combination of lineages) more than others [11]. This pattern was illustrated by Entling et al. [20] that showed that climate constraints spider body size distributions by affecting species at family level. The authors argued that this family-sorting pattern depends on attributes of life history and latitude. The ability of some species to build webs is an attribute that differentiates spiders in two very distinctive guilds [21]: the web-building guild includes spiders that use web for foraging, while the hunting (also known as wondering) guild did not use web for foraging; instead, hunting spiders forage as ambushers, stalkers or active runners [21]. The ability to construct web will probably affect intra and interspecific interactions and habitat preferences of spiders (e.g. [22]). In particular, the differential exploitation of both prey and habitat suggest that these two guilds are evolving in different ways. To date, studies comparing spider phenotypic variation among different habitats rarely take into account variations between these two guilds. In addition, the phylogenetic information is barely used to explain the importance of evolutionary processes to contemporary patterns of spider phenotypic divergence (e.g. [19]). Some questions remain unknown, for instance, how much of the variation in individual phenotype is either reflecting phylogenetic relatedness (e.g., within- family conservatism), environmental filtering or limiting similarity?

To investigate how environmental filtering (plant architecture) and limiting similarity, as well as the distance among communities (i.e., latitude), affect phylogenetic and phenotypic diversity, we collected vegetation-living spiders in 12 localities along 2200 km of the Brazilian coast, between latitudes -12 and -28. We chose sites sharing the same vegetation type (i.e., *restinga*), which removed as much as possible differences in environmental heterogeneity among sites [23]. We asked the following questions: (i) Are there phylogenetic signals in spider trait

diversity? (ii) Is plant architecture driving spider trait diversity? (iii) Is hunting spider traits more labile than web spider traits? (iv) Are spider traits and phylogeny related to plant architecture and location (geographical distance)?

We predicted that (i) phylogenetic signals are present in spider traits, which means that some nodes in the root of the phylogeny concentrate trait diversity; (ii) Plant architecture drives phylogenetic and phenotypic clustering, i.e., within each architecture the traits will be more similar than among architectures. Yet, the rosette-like architecture, the interlocked leaves, the capacity to accumulate water of bromeliads, and better food opportunities (e.g., aquatic and terrestrial food sources) provided by these plants will be filtering larger and/or flattened organisms when compared for instance with the fauna occurring in the surrounding vegetation (e.g., [19]). (iii) We predicted that variations in habitat structure affect mainly hunting spiders' phenotype, but did not affect the web. This prediction can be explained by the fact that hunting spiders, by not using web to capture their prey and having direct contact with habitat surface, probably could suffer faster phenotypic evolution (e.g. [19]). On the other hand, web spiders attach their webs in habitat surface to capture their preys, which indicates that web architecture should be more affected by environmental variation than body size *per se*. (iv) As suggested above, we expected phylogenetic and phenotypic clustering (i.e., environmental filtering) within architecture at the local scale. Since we chose the same plant architectures at different sites, we predicted the same clustered pattern at the regional scale (i.e., among-plant comparisons at different sites) being influenced by plant architecture.

## METHODS

### *Study area*

We selected 12 areas of *restinga* vegetation ranging from Northeast to South of the continent (Appendix S1, Pag. 81; Prancha 1, Pag. 13). Scarano [24] defined *restingas* as plant communities that grow in sandy plains (formed in the late Quaternary) occupying stretches between the sea and the Atlantic Rainforest. We choose a type of *restinga* named “open *restingas*”, which is characterized by patchy vegetation surrounded by open areas covered either with sand or herbaceous vegetation [25]. The main plant families that are found in open *restingas* belong to the families Arecaceae, Bromeliaceae, Malpighiaceae, Myrtaceae, Rubiaceae and Sapindaceae [25].

We chose each plant species based on their architecture in order to increase differences in leaf and plant size. Specifically we chose at each site a bromeliad (family Bromeliaceae), a palm (family Arecaceae), and three different dicot plants species with small, medium and large leaves (Table S2 and S3, Pags. 84, 85; Appendix S1, Pag. 81). In sites without palms (four sites), we substituted the plant architecture for another common dicot plant architecture distinctive from bromeliads and the three other dicots. We considered plant architecture as a proxy of habitat structure.

### *Sampling design*

We collected arthropods occurring on five different plant species in each of 12 sites between September and November of 2009, and June and August of 2010. We selected 20 plots (30 x 30 m) at least 50 m apart within each site and randomized the order of plot sampling. The criterion for choosing these points was the presence of at least three of the five architectures, and from each architecture, we sampled 20 individual plants. Within each plot, we sampled up to 5 individual plants of each architecture. For example, if we found five bromeliad individuals in

each of the four first sampled plots, we did not sample bromeliads in the next plots. Thus, plants occurring at the same plot were considered at the same latitude and longitude (no spatial variation), while plants occurring in different plots had different spatial location (allowing us to make spatial analyses at the local scale; see below). This protocol was repeated in each site and both years. The plots that we chose in the first year were the same in the second year, but new randomizations were performed to decide the order of sampling. We consider each individual plant as the sampling unit to construct the matrices E, S and L (Fig. 1A).

### *Arthropod sampling*

We collected spiders in branches of each plant using the following protocol: (i) we used 100 L transparent plastic bags to pack four to ten branches (depending on branch size), and cut the branches off. (ii) We carefully shook the bag 20 times to release the arthropods from the branches. (iii) Then, we removed each branch to check for arthropods in a white tray. (iv) We collected every arthropod visible to the naked eye and conserved them in 75% alcohol. After carefully collecting the arthropods from each removed branch, (v) we weighed (PesolaMedio® precision scale 10g) all leaves from these branches to determine total leaf biomass. Thus, even from plants with different sizes, we may test if total leaf biomass affects arthropod abundance. This method was repeated for each individual plant. For bromeliads, however, we did not follow the steps i, ii, iii and v. Instead of, we collected the arthropods (visible to the naked eye) throughout plant surface. In addition, we counted the number of leaves of the plant and weighed three leaves (the smallest, one intermediate-sized, and the largest). Then, we multiplied the number of leaves times the average value of the three weighed leaves to estimate total leaf biomass.

### *Spider traits*

We measured the following traits of spiders related to size and shape: prosoma height, length and width (Fig. 1A, letters a, b, and c respectively), opistosoma length (Fig. 1A, letter d) and we used as spider flattening (a measure of spider shape) the ratio between prosoma height and the sum of prosoma and opistosoma length. These measures were collected on individual adult spiders by using a stereomicroscopic. Previous works have showed that habitat structure (e.g., plant fractal dimension or plant size) affected spider body size (e.g., [19, 26]). As we measured spider size, when we mention spider functional traits, we are considering spider size characteristics.

### *Environmental variables*

We chose five distinctive architectures of plants (see above) based on two levels of measurement, plant and leaf level. We measured tree canopy height (CH), the longest (LLTC) and the shortest length of tree canopy (SLTC) variables at the plant level, and leaf length (LL), leaf width (LW), the distance between the second and third leaf (DBL), and total leaf biomass (TLB) at the leaf level. Thus, the matrix E (Fig. 1) presents individual plants as rows and each plant architecture variables as columns.

### *Phylogeny*

To construct the phylogeny of collected spider species we compiled data from morphological and molecular phylogenies of spiders to create one unique tree, which was used to estimate the phylogenetic distance among species. We started with the phylogeny hypothesized by Coddington and Levi [27] to organize the unique tree by family level. Then, we used phylogenies within family or superfamily (see references in Appendix, Pag. 151) to organize the

relationship among subfamilies, genera and species. We used the exact cladistic structure hypothesized by Coddington and Levi [27] to construct the cladogram among families, as well as the exact cladistic structure of within family and superfamily phylogenies (see details in Appendix, Pag. 151). We constructed the phylogeny with the software MESQUITE 2.75 [28] following the methods outlined by Hortal et al. [29]. Since branch length based on dated nodes is not available for spiders, we attributed a value of 1 for each branch to compute the distance among species [30]. However, in polytomous nodes we created minimum distances of 0.1 and 0.2 respectively for species within the same polytomous genera and family, and 0.3 for species from different families within a polytomous node. For example, the branch length of the two species from the polytomous genera *Theridion* was 0.99 and 0.98, respectively. Thus, we could estimate the distance among species even in polytomous nodes. We calculated the Euclidean distance among species with package *ade4* in R 2.14 [31]. The phylogenetic matrix P (Fig. 1A) presents spider species as columns and species pairwise Euclidean distance as rows [11].

#### *Geographic distance and spatial variables*

We used the latitude and longitude coordinates of each individual plant location to obtain the spatial matrix S. If two individual plants are considered *neighbours* (spatially “connected”) they received a value of 1, and plants not considered *neighbours* received a value of 0 [11]. These neighbours are defined by a truncation distance, i.e., the minimum value that connects all sampling units [32]. All plants closer to each other based on the truncation distance are thus defined as neighbours. The columns of the spatial matrix S (Fig. 1) are the *eigenvectors* obtained from this *neighbour* matrix [11].

#### *Statistical analyses*



We tested whether phylogenetic signals in traits are skewed to phylogeny roots (i.e., more different trait values in distantly related species) or whether few nodes or a single node expressed the whole or part of trait diversity, by using the skewness test proposed by Pavoine et al. [33] that decomposes trait diversity among the nodes of the phylogeny. These authors provide three tests to decompose trait diversity considering different evolutionary models. First, in the “tips/root skewness test” we can investigate if the node contributions are concentrated at the tips or the root of the phylogeny. Second, the “few-nodes skewness test” is a complement to the first test, which compares if few nodes contribute more to trait diversity than the remainder of the phylogeny [33]. Third, in the “single-node skewness test” we can investigate if trait diversity is determined by a single node [33]. If traits are skewed to the tips, it means that distantly related species have similar traits (e.g., convergent evolution). On the other hand, if traits are skewed to the root, it means that trait values are more different in distantly related species (e.g., phylogenetic signals) [33]. The permutation method used in these skewness tests was described in Pavoine et al. [33].

To test if spider phylogeny and plant architecture explain spider trait diversity we used the quadratic entropy applied for phylogenetic (*PQE*) and trait distance (*TQE*) (Fig. 1A; [33]). These measures of quadratic entropy are based on Rao’s measure of diversity [34]. Thus, *PQE* and *TQE* analyses measure respectively phylogenetic and trait diversity based on distance matrices. We used Euclidean metric to calculate the distance between species in the phylogeny and between spider traits. To test if phylogeny and trait diversity is not randomly distributed, we performed the permutation (n = 999 simulations) procedure developed by Pavoine et al. [33]. If the observed value obtained in the *PQE* analysis was greater or less than the random expectation, phylogeny is respectively clustered and overdispersed; similarly for *TQE* and trait distribution

(Fig. 1B). We implemented the PQE and TQE analyses both at the regional (i.e., among sites) and local scales (within site analyses). At each analysis we combine the phenotypic and phylogenetic patterns to infer their possible explanatory mechanisms (Fig. 1B; [33]). For example, it has been suggested that environmental filtering and phylogenetic signals are the possible explanatory mechanisms to communities characterized by phylogenetic and phenotypic clustering (Fig. 1B; [33]).

To test if spider traits and phylogeny are related to plant architecture and location (based on spatial variables and the neighbour analysis), we used the extension of the RLQ approach [35] proposed by Pavoine et al. [11]. This method compares the following matrices: matrix P (phylogenetic variables as rows and spider species as columns), matrix T (spider traits as rows and spider species as columns), matrix E (individual plants as rows and their architectural variables as columns), matrix S (individual plants as rows and spatial variables as columns), and matrix L (individual plants as rows and spider species abundance as columns) (Fig. 1A). (1) We first analyzed the abundance data (matrix L) with a Correspondence analysis; (2) we analysed the matrices E and S by Principal Component Analysis (PCA), and matrices P and T by Principal Coordinate Analysis (PCOA) (Fig. 1A), to calculate the square root of the first eigenvalue of each analysis. The utilization of PCA or PCOA standardizes the four matrices allowing direct comparison between them. (3) We combine the standardized environmental and spatial matrices  $X_E^*$  and  $X_S^*$  ( $X_E^* | X_S^*$ : namely matrix R), and the standardized phylogenetic and trait matrices  $X_P^*$  and  $X_T^*$  ( $X_P^* | X_T^*$ : namely matrix Q) with factorial analyses. (4) Then, we analyzed the connections between matrices Q, R and L (based on weighted abundance) with the multivariate fourth-corner approach with centred PCA (Fig. 1A). The axes of this analysis present the relationship between trait and phylogeny with plant architecture and location. By using this

approach coupled with graphical exploratory analysis we can test (i) if trait lability (or conservatism) varies among clades, (ii) the combination of those traits that are filtered by environmental variables, (iii) if the environmental filters act at different spatial scales [9]. As proposed by Pavoine et al. [11], we did not perform significance tests for that approach to avoid false significance tests. Thus, we tested the significance of the fourth corner approach between traits and plant architecture, phylogeny and plant architecture, traits and plant location (space), and phylogeny and plant location with the null model 4 proposed by Dray and Legendre [36]. In addition, we used the Moran's  $I$  test [37] to test if plant architecture variables are spatially structured.

## RESULTS

We found 172 species of spiders distributed in 28 families (17 from the hunting spiders' guild and 11 from the web-spiders' guild) in the 12 sites (Appendix S1, Pag. 81). The  $PQE$  and  $TQE$  tests showed different patterns in relation to the scale. At the regional scale (comparison of different plants among sites) we found trait clustering (observed value = 0.165,  $P = 0.014$ ) and phylogenetic randomness (observed value = 0.789,  $P = 0.142$ ). The results of  $PQE$  (random) and  $TQE$  (clutested) tests were the same by using presence / absence data. At the local scale we found both trait ( $P > 0.05$  for 9 of the 11 sites) and phylogenetic randomness ( $P > 0.05$  for all sites). Phylogenetic signals are present in trait diversity, but they vary among nodes. Node contribution to trait diversity was significant in the root (observed value = 0.208,  $P = 0.001$ ) and few-nodes skewness tests (observed value = 0.721,  $P = 0.001$ ), but was not significant in the single node test (observed value = 0.165,  $P = 0.621$ ). The contribution of the phylogeny's root to the total trait diversity was 16.5%. In addition, the few nodes skewness test showed that besides

the contribution of the phylogeny's root to trait diversity, two other nodes were important to trait diversity: one node that separates the two major groups of hunting spiders (Salticidae, Anyphaenidae, Corinnidae, Sparassidae, Thomisidae, Selenopidae and Gnaphosidae from Ctenidae, Lycosidae, Oxyopidae and Philodromidae) and another one separating hunting spiders from web building spiders (Fig. 4); these two nodes concentrate 25% of the trait diversity of the phylogeny. Taken together, these three nodes explain 41.5% of total trait diversity.

The two first axis of the RLQ analysis – which considers phylogeny, plant architecture, spider traits and space – explained 42.6% and 16.4% of the total variation, respectively. We found that all spider traits were significantly related to plant architecture ( $P = 0.03$ ). When analyzed individually, prosoma length ( $P = 0.045$ ), width ( $P = 0.036$ ) and height ( $P = 0.034$ ) were also related to plant architecture. Spider traits such as prosoma length, width and height were positively related to the first RLQ axis. Plants with large leaves and total leaf biomass were related with the positive side of the RLQ axis (Fig. 3). Thus, by analysing response of spider traits and plant architectural variables we can infer that large spider species occur in plants with large leaves. However, plant architectural variables related to crown size (i.e., crown height, and the longest and shortest crown length) and leaf shape (respectively distance between the second and third leaves) was negatively related to the first RLQ axis. Thus, although large spiders occur in large-leaved plants, these large spiders occur in plants with smaller crown size and with interlocked leaves, i.e., large spiders occur in bromeliads (Fig. 3). Conversely, large-sized web-building spiders occur in plants with larger crowns.

The values of hunting spiders along the phylogeny are related to the positive side of the first RLQ axis, while web-spiders are negatively related to this axis (Fig. 2B). The traits of hunting spiders (Fig. 2A, C) did not follow the tendency of the phylogenetic-based pattern (Fig.

2B), with both positive and negative values along the first RLQ axis. However, the majority of web-spider trait values were negatively related to the first RLQ axis, the same negative pattern as in the phylogenetic-based coordinates (Fig. 2B). These patterns show that hunting and web building spider traits are labile and conserved, respectively.

## DISCUSSION

### *Phylogenetic signal and the effects of plant architecture and scale on phylogenetic and trait diversity*

The decomposition of spider trait diversity was skewed to the root and in few nodes of its phylogeny (Fig. 4), thus closely related spiders are morphologically similar (i.e., phylogenetic signal present). Especially, trait diversity was concentrated in three nodes of the phylogeny that present the three main spider groups (i.e., Mygalomorphae and two Araneomorphae: web-builders and hunting spiders; Fig. 4), which share many similar aspects such as behavioral, ecological and physiological ones [38]. However, since traits diversity was not homogeneously distributed throughout the phylogenetic tree, we cannot consider phylogeny as the only predictor of trait diversity [11]. Thus, it suggests that other factors contribute to trait diversity. We showed that plant architecture and location act as filters of spider trait diversity, which means that within each locality or within each plant architecture spiders are morphologically similar. In addition, plant architecture and location (i.e., spatial scale) did not affect phylogenetic diversity more or less than expected by chance. Although it is reasonable to expect that phylogenetic signals will favor the occurrence of species within each group in similar habitats (environmental filtering acting in phylogenetically conserved traits), in our study phenotypic variation seems to be more affected by plant architecture and location.

The variation on spider traits among localities illustrates how spatial regulation contributes to metacommunity structure [39]. It has been considered that if distance among patches is long enough to limit dispersal, local communities should be compositionally different [40], and thus one can expect that body size structure will also respond to distance [9]. We found that trait diversity increases with geographic distance. That is, spiders were morphologically similar within each locality, which suggests that environmental filtering affects spider trait diversity. Few studies have considered spatial variation of spider communities [20, 41–42]. In addition, as far as we know no empirical studies have tested how spatial variation affects body size distribution, which make difficult any comparison with our data. However, some biological characteristics of spiders suggest a generalization of these results. The dispersal of spiders is passive, and depends on weather conditions [43]. As a passive movement, some stochasticity is expected in relation to spider dispersal and habitat occurrence, and thus some species will occur in their preferred habitat while other species will not [23]. As a result, spiders occurring in unfavorable habitats could not reproduce [43]. Therefore, as body size generally correlates with dispersal [43] and habitat characteristics [19], similar sized species will have optimal development on similar localities and habitats (e.g., plant species with similar architecture). Furthermore, as geographic distance increases, there will be an increasing availability of plant architectures which, by its turn, favor spider lability.

We found spider trait clustering and phylogenetic randomness in relation to plant architecture, suggesting that environmental filtering is the main process driving spider trait lability. It has long been suggested that plant architecture contribute to assembling compartmentalized arthropod communities from herbivores to predators [17, 22, 44]. However, as far as we know studies did not test or even mentioned the evolutionary implications of habitat

structure to that compartmentalized communities (but see [19]). For spiders, plant architecture determined the occurrence of compositionally and phenotypically similar communities. Thus, habitat compartmentalization could represent not only an ecological outcome of species sharing specific preferences to habitat/microhabitat characteristics [17], but also contribute to trait lability by filtering out similar-sized species. Despite the focus of the current literature on food-web compartments (which consider groups of species sharing similar characteristics such as diet, e.g., [45]) and mutualistic or antagonistic networks [46], we suggest that groups of species that are not directly linked (non-trophic interactions such as predators and plants) could also evolve to compartmentalized communities (e.g., [17]). For example, Marino et al. [47] found that groups of aquatic invertebrate communities were specific of certain tank-bromeliad species and suggested environmental filtering acting on invertebrates' functional traits as the main processes driving this compartmentalization.

Since the variation in plant architecture possibly generates compartmentalized communities [17, 47], groups of plant species sharing similar architecture could also affect habitat compartmentalization. We showed that large spiders occurred on plants with larger leaves (i.e., bromeliads and palms: monocot plants), while small spiders occurred on plants with voluminous crowns (dicot plants). In addition, we showed that body size was structured throughout spiders' phylogeny, which suggest that compartmentalized communities have a phylogenetic signature (e.g. [48]). Furthermore, these results illustrate the interplay between habitat structure and evolutionary history in determining trait evolution. Certain architecture characteristics could also favor compartmentalization. For example, the distinctive architecture of bromeliads (i.e., large leaves and compact crown with interlocked leaves) is filtering large spiders from different hunting spider families. Gonçalves-Souza et al. [19] suggested that large

spiders occupy bromeliads because on this plant they could find more resource in comparison to surrounding plants. The explanation for small spiders living upon dicot plants could be that their voluminous crowns filtered smaller spiders from different web-building families (see, e.g., [49]). According to Craig [50], small web-building spiders probably evolve to construct webs on habitats that provide protection from wind. Thus, crown size and complexity could be a reliable cue for smaller web-builders in choosing places to attach and protect their webs.

#### *Contrasting trait diversity between hunting and web-building spiders*

We showed that phylogenetic signals are present in the phylogeny's root, as well as in other two phylogeny's nodes, one separating the two major hunting spider groups (e.g., Mygalomorphae vs. others) and another node separating hunting and web building spiders. In addition, by comparing the first axis of the RLQ analysis, we showed that traits of hunting spider are labile (positive and negative eigenvalues; Fig. 2 A, B) while traits of web building spiders are more conservative (mainly negative eigenvalues; Fig. 2 A, B). This result indicates that besides the diversification of traits in early evolution of spiders, the ability to use webs for hunting preys has drastic influence on body size conservatism. Conversely, the abandonment of web for hunting influenced more lability on spider traits, which suggest that foraging mode has influencing trait diversity.

It has been suggested that the increasing in body size of web-builders constraint their ability to bridging [51–52], which suggest that web building behavior should constraint the size of these spiders. We argue that web architecture/design could be more evolutionary labile than their bodies. This argument is supported by results of Craig [50, 53], which showed that there is a phyletic trend in evolutionary history of orb web builders and close relatives to small size. In



addition, she proposed that web diversification was a consequence of selection of spider size [50, 53]. These results illustrate how body size and web diversification may evolve in distinct ways (although possibly correlated, [53]) in response to habitat structure. An extreme example of web architecture plasticity is from the spider genus *Caerostris* (Araneidae) in which females construct webs upon Madagascar rivers and their webs measure up to 2.8m<sup>2</sup>; in this species web width was 10 times the size of spider prosoma [54]. Furthermore, Blackledge et al. [55] argued that the plasticity in web construction's behaviors among web builders have a key function in the evolution and diversification of spiders. It is important to note, however, that the body size conservatism of web building spiders did not mean that their body will not change [52, 56]. Instead, we suggest that the use of web as a tool to catch prey influences evolutionary changes on web architecture and diminishes selective pressures on spider body size.

Conversely, there is a clear lability of hunting spider traits (see Fig. 2 a,b). Unlike web-builders, hunting spiders pursue their preys and do not use web to catch them. As a result, the body of hunting spiders is the first "tool" used for catch preys, which means that selective pressures will act mainly on body traits. It has long been suggested that body size and habitat structure are correlated (e.g. [57]). According to this assertion, habitat structure may represent a selective pressure that selects for certain body traits, a pattern already found for vertebrates and other invertebrates (e.g. [19, 57]). For hunting spiders, the intimate contact with plant surface and the well-known response of these spiders to fine scale variation in plant architecture [14, 17, 19] reinforce our result. If some spider species are in fact specialized to certain physical structure of their host plants (e.g. [14]), it is reasonable to infer that throughout the evolution, optimal traits (e.g., morphological) that maximize fitness will succeed [58]. Considering spiders foraging

at different plant species, physical differences in plant architecture will probably filter “optimal” body sizes and will thus favor trait diversity.

Our findings reinforce previous studies that argued that forage mode has important implications to species’ life styles and, therefore, can affect from the evolution of morphological, physiological and behavioral characteristics of species [59] to intra and interspecific interactions and ecosystem functioning [60]. To our knowledge, this is the first empirical evidence demonstrating that the correlation of body size and habitat structure depend on evolutionary history and foraging strategies of species. Especially, the foraging mode seems to be a key element to spider evolution and also to the response of spiders to ecological factors.

## CONCLUSION

Our study shows that habitat structure, geographic distance and phylogeny successfully predict spider trait diversity. The association between spiders and plants seems to be an outcome of the interaction between ecological and evolutionary processes. Specifically, we demonstrated that plant architecture is filtering similar-sized spiders, which illustrates that habitat structure originates compartmentalized communities even for non-trophic interactions (i.e., predators and plants). We showed that the ability of spiders to build webs (which is strongly phylogenetic structured) dictates the strength in which habitat structure affects trait diversification. In particular, habitat structure is causing strong lability of hunting spider traits, while web-building spider traits are conserved. In addition, as geographic distance increases, there will be much more lability of those hunting spider traits. Overall, our study adds voice to recent claims that life history, local (ecological) factors and large-scale (biogeographic, evolutionary) processes are interacting to determine species assembly and body trait evolution. By combining phylogenetic

analyses with geographic distance and habitat structure, we provided new insights about the relative importance of those variables to trait diversification.

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**Figure captions:**

**Figure 1.** Schematic summary of data (top part A) and questions (B; italicized numbers), and the appropriate analysis (bottom part of A) to answer each question. A) The data used were: species phylogeny (details of phylogeny constructions in Appendix 1); spider traits, namely prosoma height (a), prosoma length (b), prosoma width (c), opistosoma length (d) and additionally we used as traits the spider flattening ( $a / b+d$ ); two sets of plant architecture variables, one at the plant level, namely crown height (e), the higher (e) and the lower (f) crown length, one at the leaf level, namely the distance between the second and the third leaves (h; note that this value is 0 for bromeliads, because bromeliad's leaves are inserted at the same point), leaf length (j) and leaf width (i); geographic distance, that presents the distance between each individual plant. Based on these data we obtained the matrices  $P^t$  (transposed phylogenetic matrix),  $T^t$  (transposed trait matrix), E (plant architecture variables), S (plant spatial variables obtained by using the eigenvectors of a neighbour matrix; Pavoine et al. 2011), and L (species abundance at each individual plant). At the bottom of 1A are the analyses (italicized words) performed between or among matrices (details in Methods section) to test each question (italicized numbers). B) Questions, analyses, patterns and possible explanatory mechanisms for quadratic entropy applied for trait distance (*TQE*) and phylogenetic distance (*PQE*) (Pavoine et al. 2010). The observed values of the TQE and PQE analyses were compared with 999 simulated values in a histogram. These values can be overdispersed (in the left side of the histogram: black bars), clustered (in the right side of the histogram: white bars), or random (in the middle of the histogram: grey bars). The possible explanatory mechanisms were based on Pavoine et al. 2010. The graphic in the question 3 presents illustrative results to the RLQ analysis and the way to interpret its results. Each circle presents observed values obtained from the factorial analyses of the matrices E, T, P,

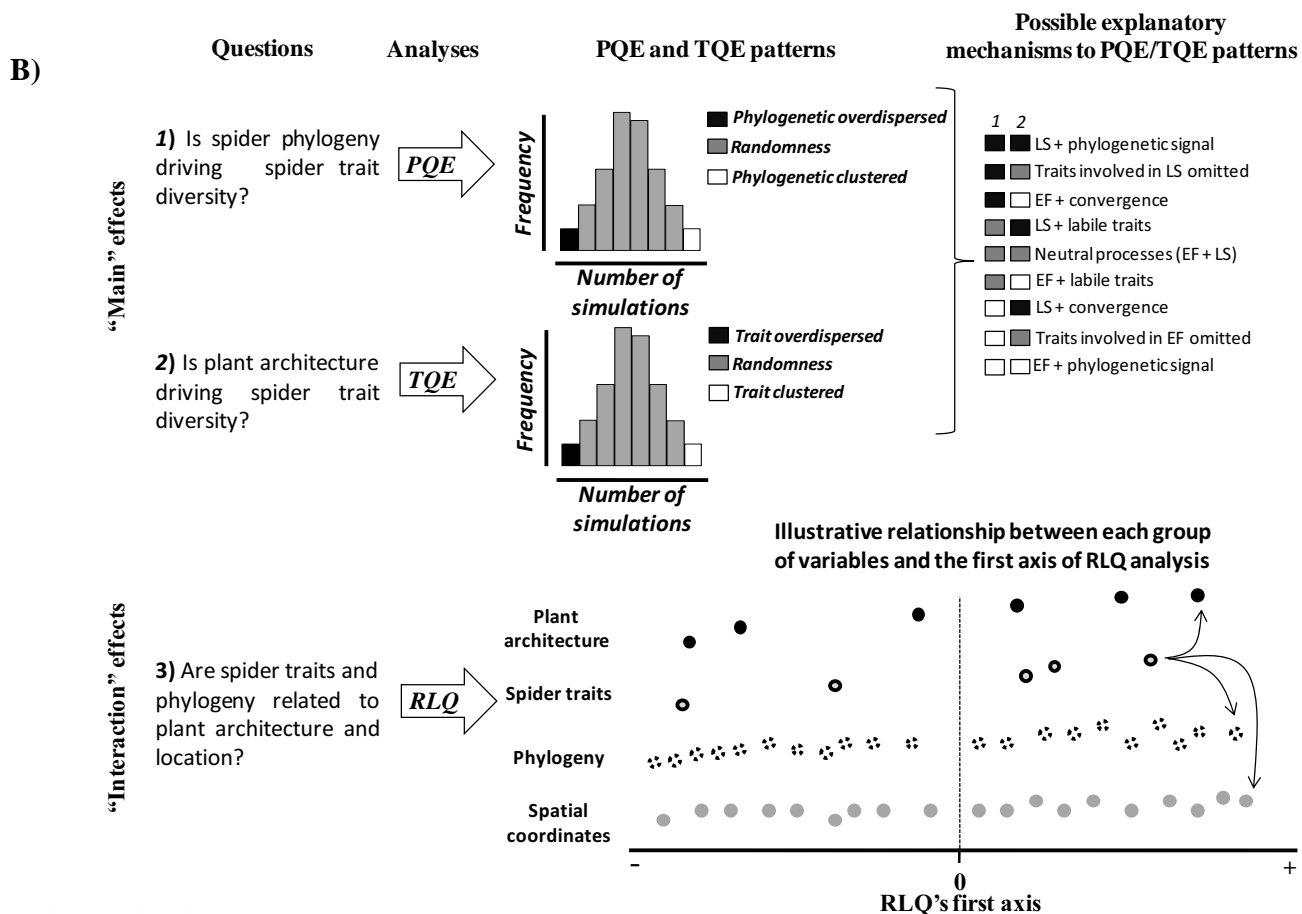
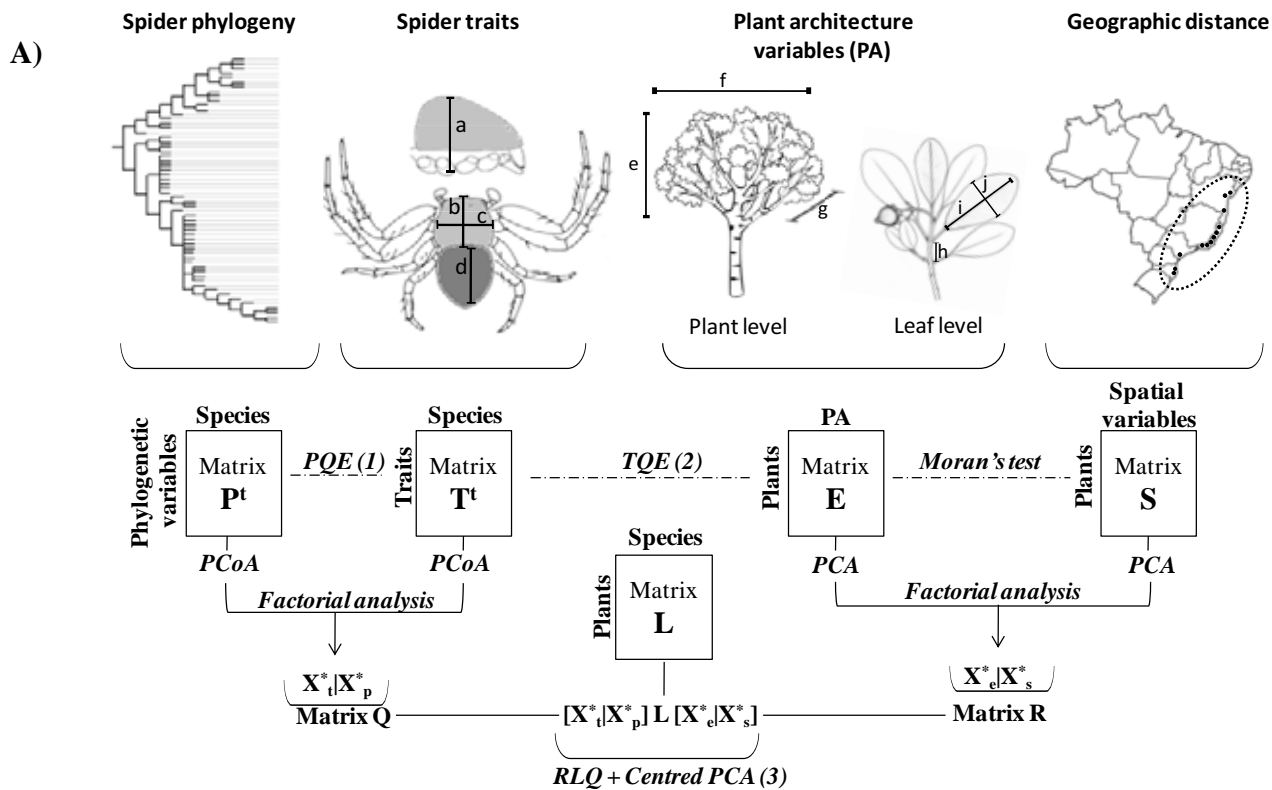
and S (Fig. 1A). For example, the last full circle of plant architecture variables at the right of RLQ figure presents leaf length, and the last empty circle of spider traits at the right of this figure presents prosoma size. The arrows in this figure present the correlative relationship among the individual values. Thus, we can interpret, for example, that prosoma size is positively related to leaf size. EF and LF at the top right of Fig. 1B are environmental filtering and limiting similarity, respectively. These explanatory mechanisms are based on Table 2 of Pavoine et al. (2010; pag. 495). We used Moran's test to evaluate if plant architecture variables are spatially autocorrelated (Pavoine et al. 2011).

**Figure 2.** Results of the relationship between trait- and phylogenetic based, and global coordinates (combination of the first axis of the RLQ analysis).

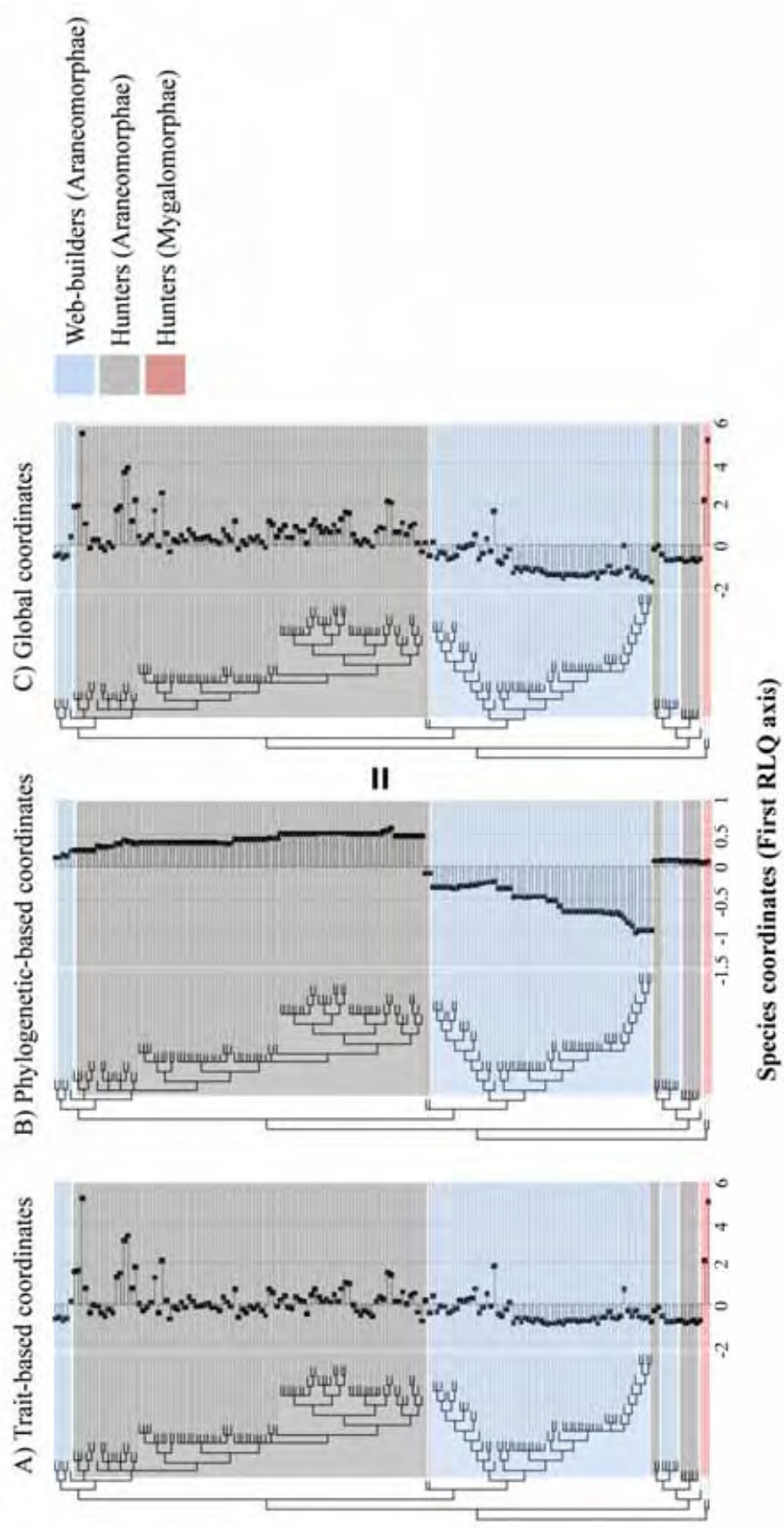
**Figure 3.** Correlation of plant architectural variables (A) and spider traits (B) with the first RLQ axis. Plant architectural variables were at the leaf level: leaf length (LL) and width (LW), the ratio between LW and LL, and the distance between the second and the third leaves (DSTL), and at the plant level: total leaf biomass, crown height, and the higher and lower crown length. The closer to zero (or zero in case of bromeliads) is the DSTL value, more interlocked are the plant leaves. Spider traits were prosoma length (PL), width (PW) and height (PH), opistosoma length (OL), and spider flattening ( $PH / PL + OL$ ). The closer to zero is the ratio  $PH / PL + OL$ , the higher is the spider flattening.

**Figure 4.** Decomposition of trait diversity among nodes of the phylogenetic tree of spiders. The values below the tree present the scale of node contribution (total trait diversity = 11.25) and thus

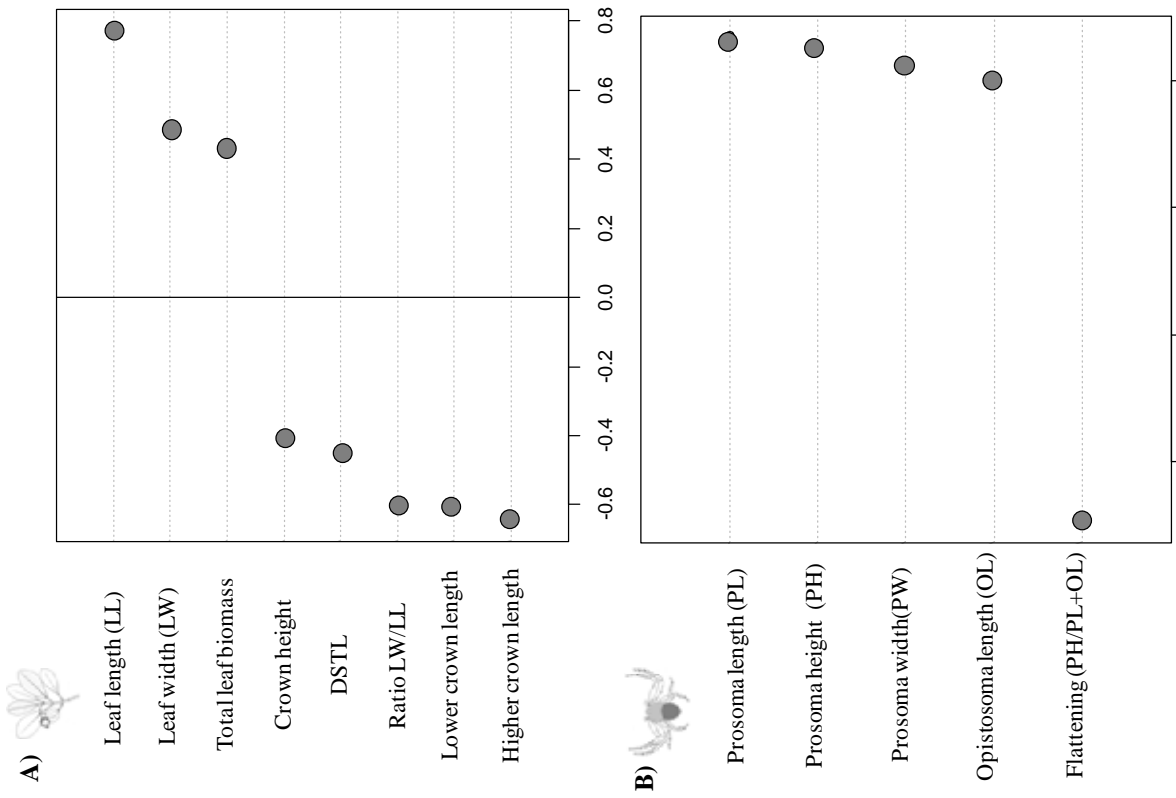
we can calculate the percentage explained by each node. The values inside the coloured circles are the percentage of individual contribution to total trait diversity. At the right side of the figure we illustrated the main families of the lineages that concentrate trait diversity. Additional details about the phylogenetic tree could be found on Appendix (Pag. 151). Spider picture credits to: Joe Lapp and Chris A. Hamilton (Theraphosidae spider).



**Figure 1**



**Figure 2**



**Figure 3**

Correlation with the first RLQ axis

**F**

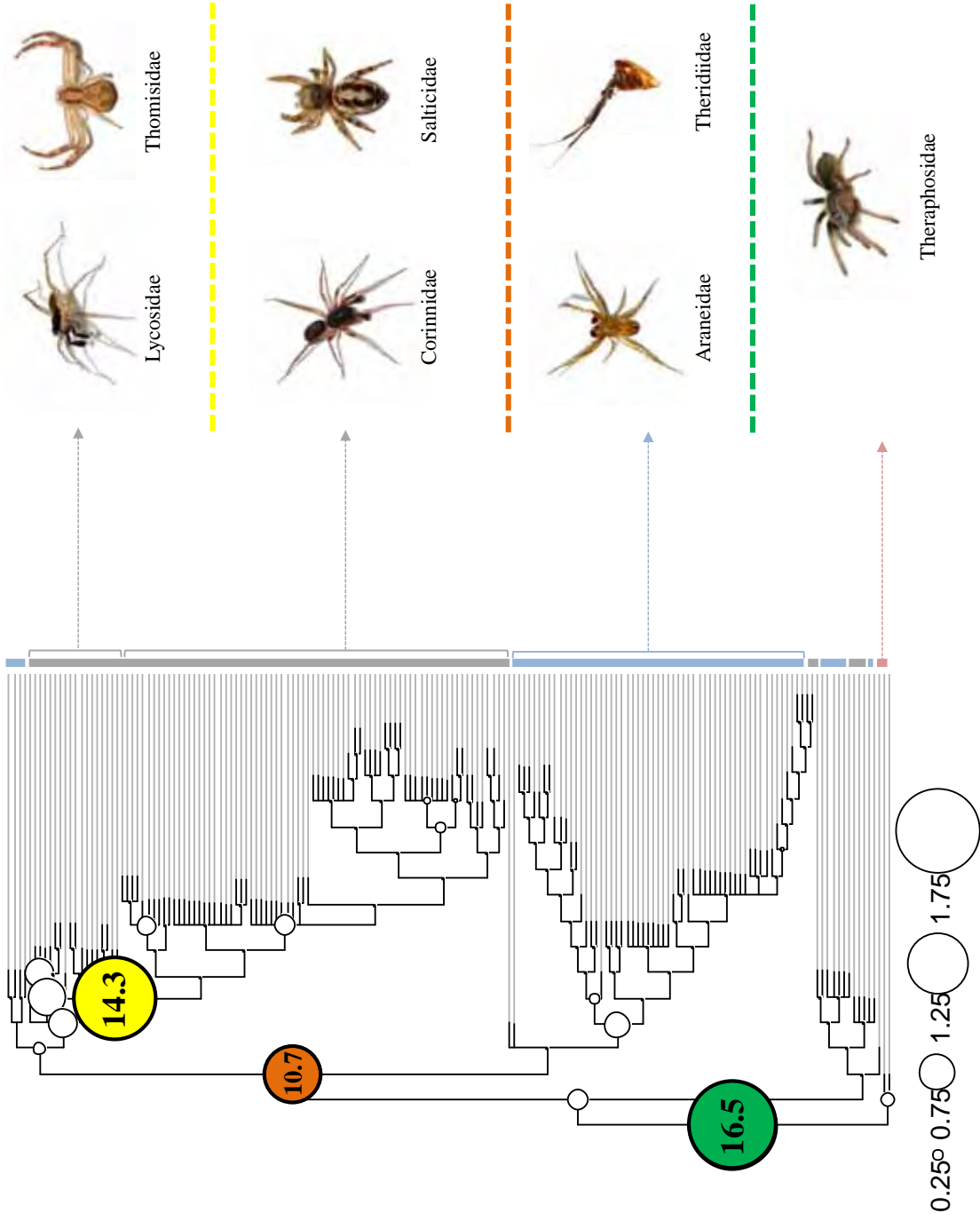








Figure 4



## Legend

-  Node separating Mygalomorphae from Araneomorphae spiders
-  Node separating hunting from web building spiders
-  Node separating two major groups of hunting spiders
-  Hunters (Mygalomorphae)
-  Web-builders (Araneomorphae)
-  Hunters (Araneomorphae)

## **ARTIGO 3**

# **[FINE-SCALE BETA-DIVERSITY PATTERNS ACROSS MULTIPLE ARTHROPOD TAXA OVER A NEOTROPICAL LATITUDINAL GRADIENT]**

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## ABSTRACT

Understand how diversity patterns vary at fine- and broad-scales may answer many questions in theoretical and applied ecology. However, the majority of the studies compare diversity patterns at the same scale and within the same taxonomic group, which limits the applicability and generalization of the results. Here, we investigated whether multiple vegetation-dwelling arthropods with distinct life histories (i.e., ants, caterpillars, cockroaches, and spiders) have different beta-diversity patterns at multiple scales. Specifically, we compared their beta diversity among architecturally distinct plants (fine-scale process) and sites over the latitudinal gradient (broad-scale process). We found that when rare species are not taken into account, fine-scale processes explain more than 60% of  $\alpha$ - and  $\beta$ -diversity patterns of ants, caterpillars, and spiders, but only a lesser extent (36%) to cockroaches. Conversely, broad-scale spatial processes affect more beta-diversity patterns of cockroaches than ants, caterpillars, and spiders. It seems that arthropods' life history are stronger predictors of large-scale diversity patterns than dispersal mode, for example. Although dispersal is primordial to organisms find suitable sites, local variations in habitat characteristics may be even more important because suitable habitats could benefit organism fitness. Thus, the information about different feeding guild and life history of arthropods will probably determine if an organism will succeed in that habitat. Our results suggest that species life history could be a better predictor of the relative importance of fine- and broad-scale processes to species distribution than other traits, such as dispersal mode. Consequently, future theoretical and applied ecological studies should integrate information about differences in species' life history.

**Keywords:** plant architecture,  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity, dispersal, life history, diversity deconstruction.

## INTRODUCTION

A number of factors predict the variation in arthropod species composition. Biotic interactions, environmental filters (e.g., habitat structure), spatial scale, and landscape configuration have been emphasized in the ecological literature (Basset 1996, Lewinsohn et al. 2005, Schaffers et al. 2008). It has been suggested that the relative importance of these factors to species abundance and composition is scale- and taxon-dependent (Steffan-Dewenter et al. 2002, Soininen et al. 2007a). Consequently, differences in habitat characteristics and its spatial distribution should be perceived differentially by animals depending on their behavioral, ecological, and physiological requirements (Crist et al. 2006). However, most studies have been performed at the same scale and with organisms having similar requirements, which limit the applicability of these results to other groups (but see Shurin et al. 2009). Thus, by considering species with different requirements, one can depict general patterns not only shared by different groups, but also idiosyncratic responses of those groups to different factors. For instance, Schaffers et al. (2008) showed that both herbivores and predators responded similarly to plant community composition, but differed in response to other factors such as landscape configuration and abiotic conditions.

The way organisms disperse and acquire food may be a strong predictor of how broad- and fine-scale processes will determine species turnover (i.e., change in the identity of species between two samples, also known as  $\beta$ -diversity: Anderson et al. 2011). At broad-scales, dispersal ability will determine the spatial distribution of species and the probability to find suitable conditions to feed and reproduce (Kisdi 2002). Generally, active dispersal favors the spread of an organism and the propensity to find suitable habitat conditions, whereas passive dispersal is more stochastic and depends, for example, on weather conditions (Soininen et al.

2007b). As a result, at broad spatial scales it is expected that species turnover of passive dispersers will be higher than the turnover of active dispersers, which suggest that dispersal mode is related to  $\beta$ -diversity (Tuomisto et al. 2003, Soininen et al. 2007b). Conversely, dispersal does not limit species distribution at finer scales and thus other local ecological factors would determine species turnover (Brehm et al. 2003, Schaffers et al. 2008, Gonçalves-Souza et al. 2010). Hence, by testing how species turnover varies in response to broad-scale (e.g., species turnover among sites over a Neotropical latitudinal gradient) and fine-scale processes (e.g., species turnover in different microhabitats) could elucidates a variety of mechanisms that drive species distribution.

A variety of local ecological factors are known to affect species turnover (e.g., habitat structure, plant traits and composition), although it depends on taxon (Crist et al. 2006). One way it could happens is that the effect of plant species could be more intense to organisms that feed directly on plant tissues, such as herbivores (Schaffers et al. 2008). Thus, plant species composition may have a strong influence on herbivore beta-diversity (Prado & Lewinsohn 2004, Schaffers et al. 2008, Müller et al. 2011). Several authors have explained the ecological and evolutionary pressures affecting the narrow niche breath of herbivore insects (reviewed in Coley & Barone 1996), such as lepidopteran caterpillars. It has been suggested that plant defenses are the main factors driving host-specificity in herbivores (Coley & Barone 1996). For instance, Ehrlich & Raven (1961) showed that lepidopteran caterpillar eat a narrow range of plant chemical compounds. As a result, lepidopterans are generally specialized in fewer plant species, genera, or families (Dyer et al. 2007).

Conversely, ants, cockroaches, and spiders do not feed directly on live plant tissues. As a result, the effect of plant species should be less apparent as in herbivores (Basset 1992 and

references therein). However, it does not mean that plant species will not affect distributional patterns of non-herbivorous arthropods. Indeed, it has long been demonstrated that plant species composition and architecture affect the richness and composition of spiders (Halaj et al. 2000, Haddad et al. 2001, Gonçalves-Souza et al. 2010). However, few studies have tested whether plant variables affect the richness and composition of omnivores such as ants. A previous study (Johnson et al. 2006) suggested that plant genotype diversity affect positively omnivorous and predators. The same authors argued that plants were more important than indirect trophic interactions to both omnivorous and predators. The effect of plants on detritivores such as cockroaches received much less attention. For instance, Siemann et al. (1998) showed that detritivores were the only vegetation-dwelling trophic group not affected by plant species richness, indicating that changes in plant communities have little or no effect at all on detritivore communities. Broadly speaking, we expect that the relevance of plant species to  $\beta$ -diversity patterns will be higher to lepidopteran caterpillars, followed by spiders, ants, and cockroaches.

We aimed to assess whether  $\alpha$ - and  $\beta$ -diversity of multiple vegetation-dwelling arthropods vary according to different spatial scales (i.e., within and among sites over the latitudinal gradient) and different plant species. In addition, we deemed ants (via reproductive female flight), caterpillars (via adult flight), and cockroaches as active dispersers (Peeters & Ito 2001, Gillott 2005, Bell et al. 2007), and spiders as passive dispersers (Foelix 2010). Specifically, we asked whether plant architecture and the latitudinal gradient cause different  $\beta$ -diversity patterns among ants, caterpillars, cockroaches, and spiders. We predict that: (i)  $\beta$ -diversity pattern among different plant architectures:  $\beta_{\text{cockroaches}} < \beta_{\text{ants}} < \beta_{\text{spiders}} < \beta_{\text{caterpillars}}$ , because  $\beta$ -diversity is possibly related to the specificity of food consumption of each arthropod group and its relation to host plant characteristics (e.g., Novotny & Weiblen 2005). (ii)  $\beta$ -diversity among different sites:  $\beta_{\text{ants}}$

$\beta_{\text{cockroaches}} < \beta_{\text{spiders}} < \beta_{\text{caterpillars}}$ , because active dispersers (ants, cockroaches, caterpillars) are less restricted by geographical distance than passive dispersers (spiders). However, since there is a trade-off between dispersal and host-specificity for lepidopterans (Komonen et al. 2004), we expected that lepidopteran  $\beta$ -diversity will be lower among sites. We divided dispersal mode in two broad-sense categories, i.e., active dispersers that are able to fly and passive dispersers that cannot fly and use for instance wind to disperse (e.g., spider ballooning). Thus, we used an indirect measure of dispersal based on two simple modes determined in the literature (e.g., Shurin et al. 2009).

## METHODS

### Study area

We sampled arthropods in 12 localities embedded in a *Restinga* vegetation along 2,040 km of the Brazilian east coast (Appendix S1, Pag. 81; Prancha 1, Pag. 13). The climatic data for each locality are in the Appendix S1 (Pag. 81). We choose a specific type of *restinga*, called “open *restinga*”, which consists of patchy vegetation surrounded by open areas, covered either with sand or herbaceous vegetation (Scarano 2002). The main plant families in open *restingas* belong to Arecaceae, Bromeliaceae, Malpighiaceae, Myrtaceae, Rubiaceae, and Sapindaceae (Assis et al. 2002; Prancha 1, Pag. 13).

### Plant species

We pre-defined five plant species based on varying differences in their leaf and crown size. Since leaf and crown morphology of each plant were necessarily different, referred to as plant architecture hereafter. Specifically, we choose at each locality a bromeliad (family

Bromeliaceae), a palm (Arecaceae), and three different dicot plants with small, medium, and large leaves (Appendix S1, Pag. 81; Prancha 1, Pag. 13). We replaced palms by another common dicot plant distinct from bromeliads and the three other dicots in four localities without palms. Although we focused on plant architecture, it is inevitable that our communities with architecturally distinct plants also represent differences in terms of plant species composition (e.g., Schaffers et al. 2008). Thus, our results can also be generalized to the effects of plant composition on arthropod communities.

#### Arthropod survey

We collected arthropods on these five plant architectures in each locality between September and November 2009, and June through August 2010. We sampled 20 individual of each plant in 20 plots (30 x 30 m) within each locality, at least 50 m apart from each other. We randomized the order of plot sampling before collecting arthropods. The criterion for choosing these plots was the presence of at least three of the five plant architectures pre-selected. Within each plot, we sampled up to 5 individual plants with one type of architecture. For example, if we found five bromeliads in the first four plots, we did not sample bromeliads in the next plots. We sampled the same plots in both years, but we randomized sampling sequence.

We collected arthropods (Araneae, Blattaria, Hymenoptera: Formicidae, and Lepidoptera - caterpillars) (Prancha 2, Pag. 14) in branches of each plant using the following protocol: (i) we used 100 L transparent plastic bags to pack four to ten branches (depending on branch size), and cut the branches off; (ii) we carefully shook the bag 20 times to release arthropods from branches; (iii) we then removed each branch to check for arthropods in a white tray; (iv) we collected every arthropod visible to the naked eye and conserved them in 75% alcohol. After



carefully collecting arthropods from each branch removed, (v) we weighed (PesolaMedio® precision 10g) all leaves from these branches to determine total leaf biomass. Thus, even plants with different sizes, we were able to test whether total leaf biomass affects arthropod abundance. This method was repeated for each individual plant. We implemented another protocol for bromeliads, without steps i, ii, iii and v. Specifically, we collected arthropods (visible to the naked eye) on the entire plant surface. In addition, we counted the number of leaves and weighed three leaves (the smallest one, one intermediate-sized, and the largest one) to estimate total leaf biomass. Then, we multiplied the number of leaves by the average value of the three weighed leaves.

We considered ants, caterpillars, cockroaches, and spiders respectively as omnivorous, herbivores, generalist detritivores, and predators (Gillott 2005, Bell et al. 2007, Foelix 2010). We excluded from the analysis predatory and fungivorous ants.

### Statistical analyses

We used the Diversity Partitioning method to decompose  $\gamma$  diversity into  $\alpha$  and  $\beta$  components (Lande 1996, Crist et al. 2003). Total ( $\gamma$ ) diversity is partitioned into within ( $\alpha$ ) and among samples ( $\beta$ ) average diversity (Fig. 1; Crist et al. 2003). We performed two different partitions by measuring  $\gamma$  diversity as species richness or Simpson diversity index. The use of different indexes is useful to verify if dominant or rare species affect diversity patterns (Crist et al. 2003). The Simpson index is particularly important, since it gives more weight to dominant species, controlling or alleviating the bias caused by rare species (Lande 1996).

Plant architecture was the lowest hierarchical level. Thus, the average  $\alpha$ -diversity was the value within architecture. The components of  $\beta$ -diversity can be divided into different levels that

reflect different spatial scales (Crist et al. 2003). Since individual plants were nested within five different plant architectures, and plant architectures were nested within different sites, we partitioned  $\beta$ -diversity into two components: among architectures and among sites (Fig. 1). We considered these two  $\beta$ -diversity components as representing fine-scale and broad-scale patterns in species compositional differences. We used an individual-based randomization scheme (that generates 1000 random matrices with fixed rows and column totals) to compare the observed and expected values of the partitioned components. We repeated the diversity partitioning method for each arthropod group. All statistical analyses were performed in R 2.15 (R Development Core Team 2012) with the package *vegan* (Oksanen et al. 2005). Additional details about Diversity Partitioning can be found on Lande (1996), Veech et al. (2002) and Crist et al. (2003).

We also constructed individual-based rarefaction curves to compare the patterns of species richness among groups. The rarefaction method allows the standardization and comparison of different datasets (Gotelli & Colwell 2001).

## RESULTS

We found 856 ants from 48 species, 766 caterpillars from 161 species, 172 cockroaches from 32 species, and 1122 spiders from 172 species. On average, we found 5.3 arthropods per plant. Caterpillars and spiders were the groups with more species by individuals, followed by cockroaches and ants (Fig. 2).

We partitioned  $\gamma$ -diversity using total species richness of arthropod groups. We found that  $\alpha$ -diversity explained only a small proportion (less than 10%) of  $\gamma$ -diversity for ants, caterpillars, and spiders, whereas for cockroaches it was 20%. The turnover among plant architectures ( $\beta_1$ ) contributed more to total diversity ( $\gamma$ ) than  $\alpha$ -diversity for all groups.

Specifically,  $\beta_{1(\text{caterpillars})} < \beta_{1(\text{spiders})} < \beta_{1(\text{cockroaches})} < \beta_{1(\text{ants})}$  (Fig. 2A), which means that omnivorous had the highest turnover among plant architectures, followed by generalist detritivores, predators, and herbivores, respectively. On the other hand, turnover among sites ( $\beta_2$ ) explained a greater proportion (more than 54%) of  $\gamma$ -diversity of all groups, i.e.,  $\beta_{2(\text{cockroaches})} < \beta_{2(\text{ants})} < \beta_{2(\text{spiders})} < \beta_{2(\text{caterpillars})}$  (Fig. 2A).  $\beta_2$  were higher than expected by chance for cockroaches, spiders, and caterpillars ( $P < 0.001$ ), and lower than expected by chance for ants ( $P < 0.001$ ). Two active dispersers (ants and cockroaches) had the lowest turnover among sites, whereas spiders (passive dispersers) and caterpillars (active dispersal via adult flight) had the highest turnover among sites.

We also partitioned  $\gamma$ -diversity using Simpson diversity index. Since this index weighted dominant species, the results from this partitioning reflected the response of  $\alpha$  and  $\beta$  diversity of dominant species at the level of the study area (Lande 1996). Similarly to the partitioning with species richness, the average  $\alpha$  diversity within plant architecture was the lowest component (Fig. 2A, B). However, unlike the partitioning with species richness, the turnover among plant architectures explained a greater proportion (more than 60%) of  $\gamma$ -diversity for caterpillars, spiders, and ants, and 36.8% for cockroaches (Fig. 2B). That is,  $\beta_{1(\text{cockroaches})} < \beta_{1(\text{caterpillars})} < \beta_{1(\text{spiders})} < \beta_{1(\text{ants})}$ , which means that ants (omnivorous) had the highest turnover among plant architectures, followed by predators (spiders), herbivores (caterpillars), and generalist detritivores (cockroaches). The turnover among sites was less important than the turnover among plant architectures when Simpson index was used:  $\beta_{2(\text{spiders})} < \beta_{2(\text{ants})} < \beta_{2(\text{caterpillars})} < \beta_{2(\text{cockroaches})}$  (Fig. 2B). The turnover among sites of passive dispersers was smaller than for active dispersers. The partitioning of Simpson diversity was significantly different from the null expectation for all levels and for all trophic ranks.

## DISCUSSION

Our results revealed that fine-scale changes in habitat characteristics (plant architecture) could be a better predictor of arthropod  $\beta$ -diversity than broad-scale changes (turnover among sites). However, the relative importance of fine- vs. broad-scale processes depended on the consideration of dominant and rare species in the partitioning. When we considered richness, species turnover among sites were the main component of diversity partitioning, whereas when we used Simpson index (that weighted abundant species), species turnover among plant architectures were the main component. These results suggest that rare species dictate the pattern of species turnover among sites (see also Gering et al. 2003), which means that discussing our findings based on this type of bias could lead us to wrong conclusion, because of the statistical weakness in considering rare species (Lande 1996).

In general,  $\beta$ -diversity is negatively related to dispersal ability, because high dispersal homogenizes species spatial distribution (Mouquet & Loreau 2003, Soininen et al. 2007b). However, spiders (that have passive dispersal) were the group with the lowest  $\beta$ -diversity among sites ( $\beta_2$ ), followed by ants, caterpillars, and cockroaches. Shurin et al. (2009) have found lower  $\beta$ -diversity of organisms dispersing passively (e.g., plankton), and suggested that differences in life history and dispersal strategies may generate similar levels of dispersal limitation (Shurin et al. 2009) and, consequently, similar  $\beta$ -diversity among sites (as in the case of  $\beta_2$  of ants, caterpillars, and spiders). Although adult lepidopterans are active dispersers, their mobility is strongly influenced by larval host-specificity (Konomien et al. 2004; see also Kisdi 2002), which would explain why  $\beta_2$  of lepidopterans was higher than for a passive disperser. Some spider genera, by its turn, are strictly associated with specific plant families throughout a large geographic extent (Romero 2006), which can explain the lower  $\beta_2$ . For ants, previous studies

have also shown that  $\beta$ -diversity is less affected by dispersal limitation (Vasconcelos et al. 2009). Surprisingly, the turnover of cockroaches among sites was higher than for the other three groups. Although some species have widespread distribution (especially synanthropic species), Schal et al. (1984) showed that the movement of several species is restricted to a few meters or kilometers. At least at the scale of our study, we found that dispersal mode seems to be a weak predictor of turnover among sites (see also Hájek et al. 2011). Although the four groups differ in dispersal mode, a common alternative explanation found in the literature is that other local ecological factors should be considered to explain broad-scale spatial patterns (Basset 1996, Condit et al. 2002, Krawchuk & Taylor 2003). This result also suggests that species turnover among plant architectures (but within the same site) is independent of the regional richness (see also Gonçalves-Souza et al. unpub. ms., Chapter 3; but see Belmaker et al. 2008).

Additionally, life history aspects may help us to understand how local ecological factors influence species diversity patterns. For instance, trophic rank may be a reliable predictor of arthropod species turnover in relation to fine-scale processes. In our study, plant architecture explained more than 60% of species turnover ( $\beta_1$ ) of ants, spiders and caterpillars, and 36% of cockroaches' turnover. As predicted, cockroaches had the lowest  $\beta_1$ . As generalist detritivores with a broad diet, it has been shown that cockroaches are affected by detritus supplementation (Yang 2006), which suggests that differences in plant architecture are less important than food supply to detritivores. Vegetation-dwelling cockroaches have seasonal shifts in vegetation strata in response to food and biotic interactions (Schal et al. 1984), and it has probably contributed to decrease species turnover among plants. Nevertheless, 36% of total diversity was explained by turnover among plants. Bell et al. (2007) reviewed the common habitats of cockroaches and found that the most habitat-specialized groups occur in bromeliads. As we collected on these

plants, it is possible that bromeliads contributed more intensely to the turnover among plants. Thus, even for detritivore communities, fine-scale variations in plant architecture are an important predictor of species turnover.

Almost 60% of changes in lepidopteran species composition were explained by host plant. Previous studies have demonstrated a very large specificity of lepidopterans to their host plant (Novotny et al. 2004, Dyer et al. 2007) as a response to plant chemical compounds (reviewed in Thompson & Pellmyr 1991). For instance, Novotny et al. (2004) showed that caterpillars have more than 90% of probability to have a single host plant. Even though caterpillars are more affected by plant chemical compounds (Thompson & Pellmyr 1991, Coley & Barone 1996), there is evidence that changes in plant architecture (e.g., leaf shape) could affect the performance (e.g., movement, oviposition) of individual caterpillars (Brown et al. 1991 and references therein). Throughout the evolutionary history, host plant and its architecture could favor the occurrence of species with best performances with specific chemical compounds and architecture and thus fine-scale variations should explain  $\beta$ -diversity patterns. Interestingly, plant architecture was more important to predator turnover than for herbivores. In a meta-analysis, Langelloto & Denno (2004) showed that spiders were the predators most affected by changes in plant architecture (see also Halaj et al. 2000, Gonçalves-Souza et al. 2010, 2011). This result suggests that even for a food-generalist predator, selecting their preferred habitats (e.g., the one that best conduct visual or tactile stimuli) could favor their performance (e.g., foraging, mating), leading to habitat specialization. An increasing number of studies have shown that predator communities are compartmentalized in relation to habitat or microhabitat (e.g., Gonçalves-Souza et al. 2010, 2011), which suggests that future studies should address the mechanisms behind this pattern.

For ants, plant architecture explained more than 70% of total diversity. This is a remarkably high value since we considered ants as omnivorous. Although there is no clear pattern between species turnover of omnivorous ants and plant species composition (e.g., Blüthgen & Stork 2007, Janda & Konecná 2011), Luque & López (2007) showed that different microhabitats attracted different ant species, even when food items and temperature were controlled. These authors argued that differences in vegetation complexity among plants have direct effect on ant movement (Luque & López 2007). Taken together, our results suggest at least two implications for future studies: first, by deconstructing diversity at different scales we can unravel interesting patterns that could not be found if we consider one or the other scale (e.g., Levin 1992). Second, trophic rank and life history seem to be stronger predictors of both fine- and large-scale diversity patterns than dispersal mode. Although dispersal mode influences habitat choice (e.g., Pulliam & Danielson 1991), habitat structure could provide reliable information about food quality and quantity. Thus, trophic rank and life history together will probably determine if an organism will succeed in a habitat.

By partitioning  $\beta$ -diversity patterns in two different scales, we were able to understand how arthropod species turnover could be explained by fine- and broad-scale. However, we showed that fine-scale variation in habitat structure is a key element to  $\beta$ -diversity patterns of vegetation-dwelling arthropods and this effect could be more important to local community structure than broad-scale processes. In addition, it seems that differences in species' life history could explain the relative importance of fine- and broad-scale processes to species diversity patterns. Our study concurs with others showing that fine-scale changes may be equivalent or more important than broad-scale processes (e.g., Basset 1996, Krawchuk & Taylor 2003) in determining community structure. Consequently, we suggest that studies could use cross-scale

comparisons (Levin 1992) and groups from different arthropod groups to best understand how communities are assembled. Consequently, future theoretical and applied ecological studies could integrate information on species' life history.

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**Figure captions:**

**Figure 1.** Schematic drawing of the study design with the two scales of  $\beta$ -diversity comparisons. The fine-scale considers arthropod species turnover among different plant architecture ( $\beta_1$ ). Different tree-like symbols illustrate plants with distinct architecture. The broad-scale considers species turnover among different sites (grey rectangles). Average diversity within each architecture represents  $\alpha_1$ . We partitioned total diversity ( $\gamma$ ) as implemented by Crist et al. (2003) (formula at the bottom of the figure).

**Figure 2.** Individual-based rarefaction curves for ants, caterpillars, cockroaches and spiders communities. The vertical dotted line presents the arthropod community with the smaller number of individuals (cockroaches = 172 individuals).

**Figure 3.** Percentage of total arthropod species richness (A) and diversity (B) partitioned into  $\alpha_1$  (within architecture),  $\beta_1$  (among architectures) and  $\beta_2$  (among sites) components. The observed values of each component of all analyses were significant ( $P < 0.05$ ).

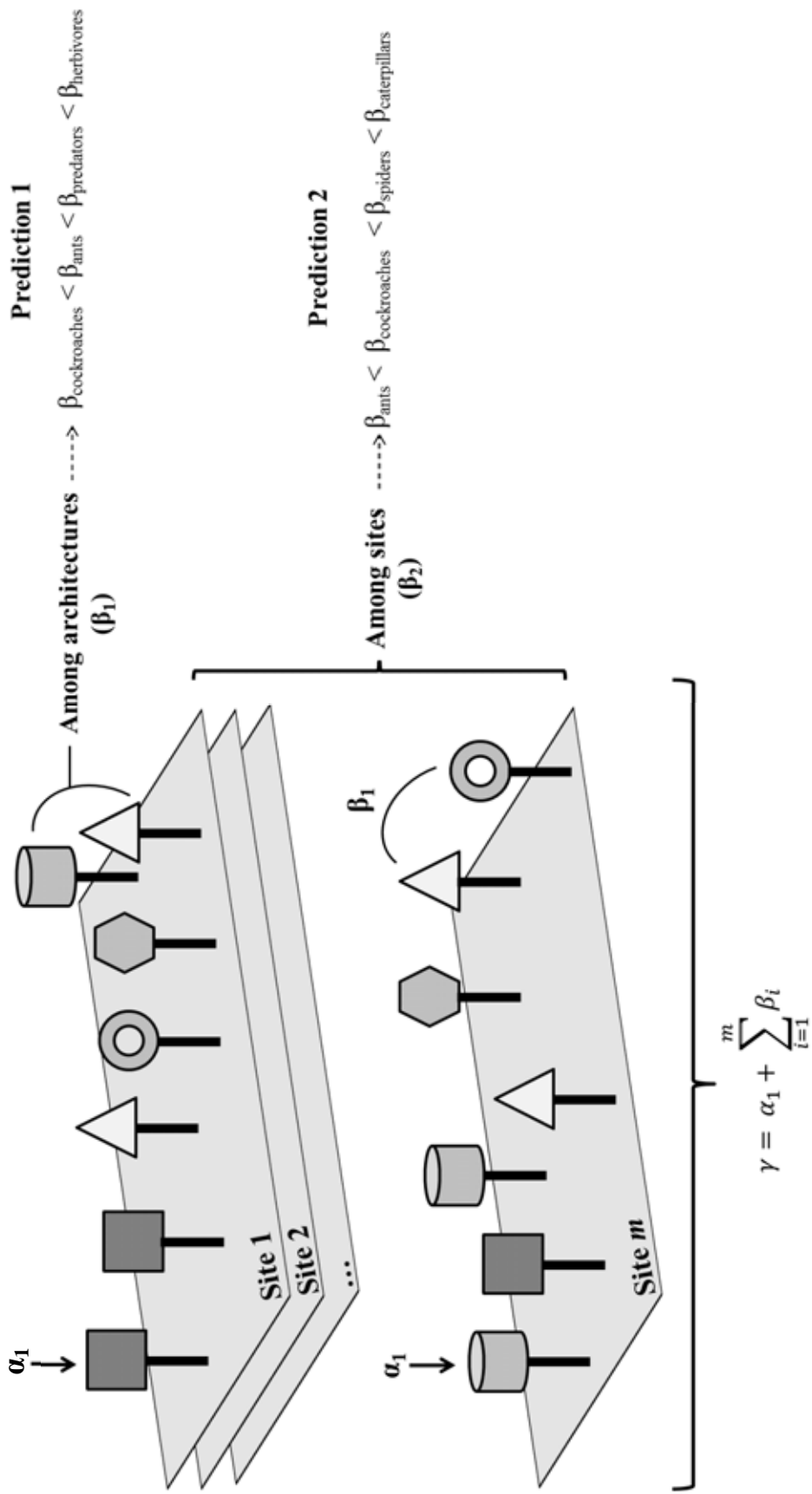


Figure 1



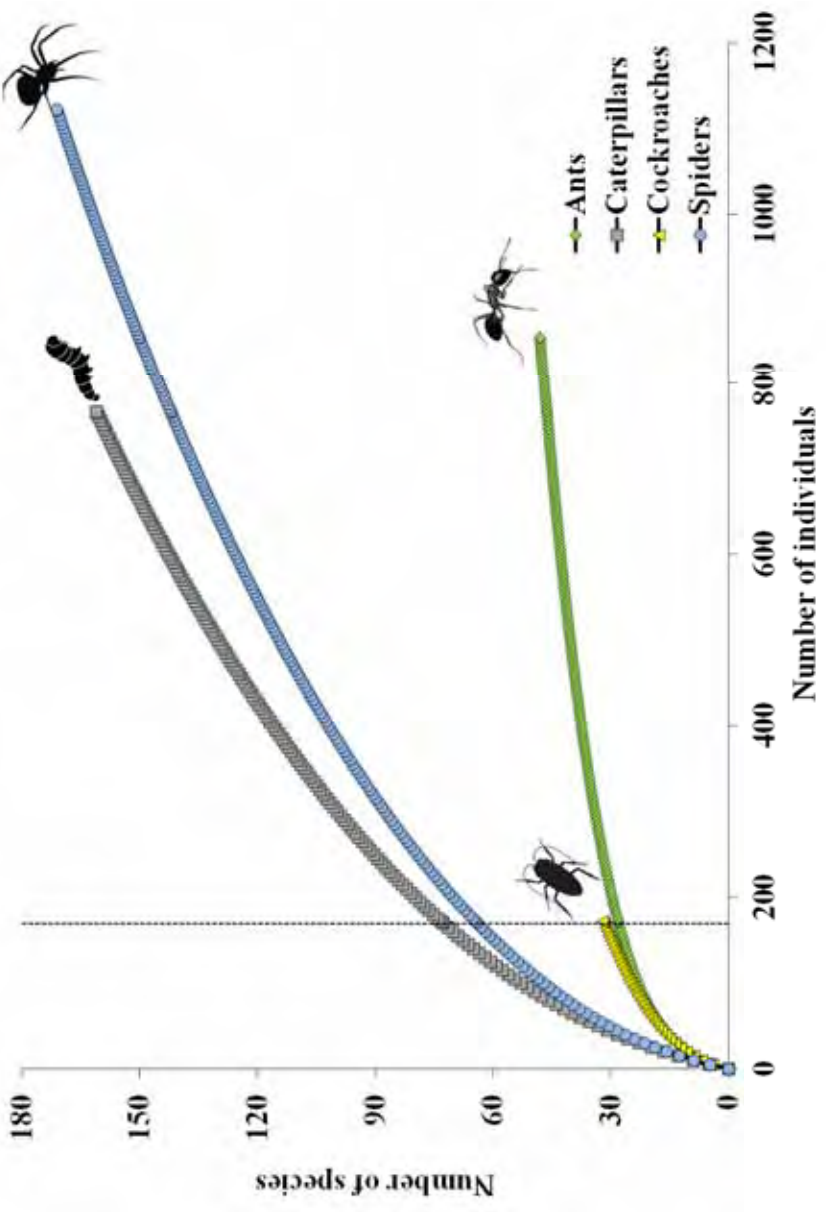
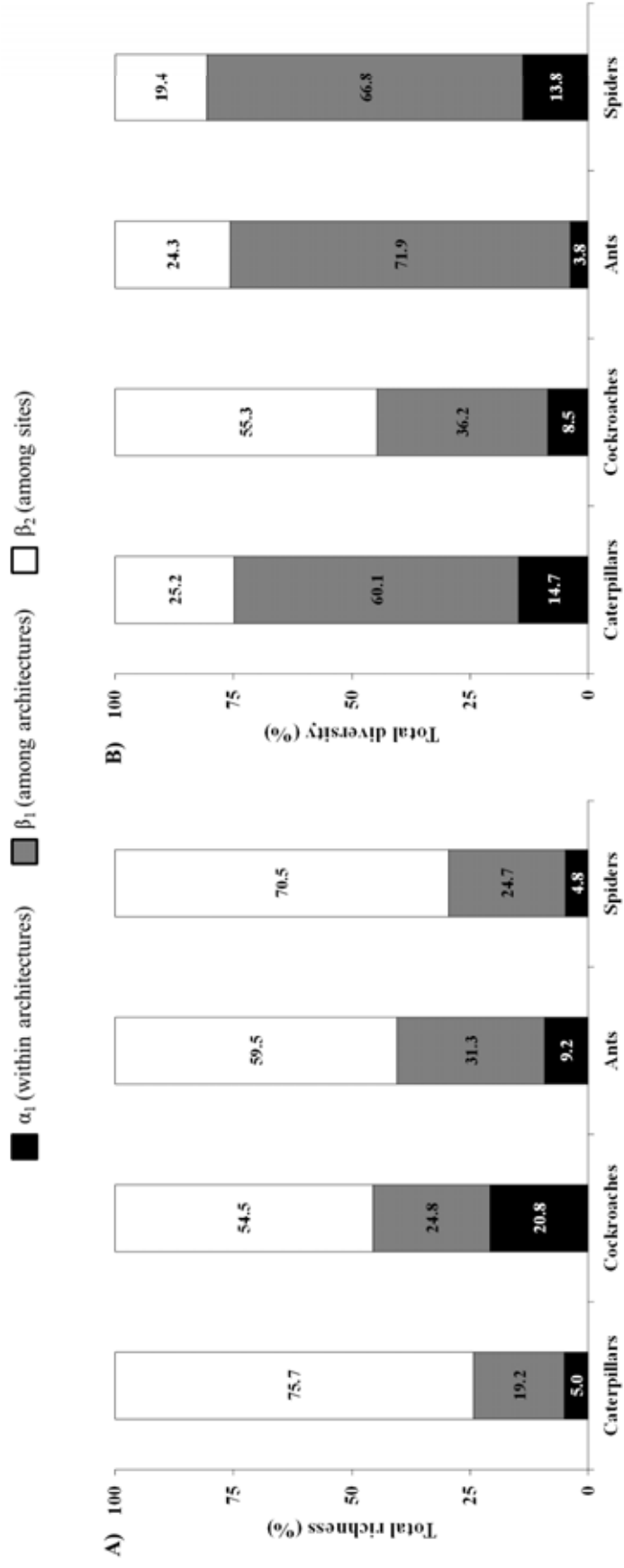


Figure 2



**Figure 3**

## **ARTIGO 4**

# **[INTEGRATING METACOMMUNITY PROCESSES WITH BIOGEOGRAPHY IN THE STUDY OF LATITUDINAL GRADIENTS]**

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## ABSTRACT

We tested the relationship between regional and local communities, and investigated whether plant traits, climate and the latitudinal gradient affect the composition of both local and regional communities. We hypothesized that both lepidopterans and spiders are spatially structured at the latitudinal scale and environmentally structured at local scale. We then predicted that the effect of niche-based processes at the local scale is responsible for the saturation of local-regional richness relationships. We also tested whether dispersal ability explains the spatial structure and the endemism of lepidopterans and spiders, and if these patterns are related to climate. We collected lepidopterans and spiders in 12 localities in a consistent vegetation type along 2,040 km of the Brazilian coast. We sampled the organisms in plant with distinct morphological traits and compared their species composition at local and latitudinal scales. We also evaluated the relationship between local and regional richness. We used redundancy analysis coupled with variation partitioning analysis to estimate the contribution of plant traits and spatial variation to species composition at local and latitudinal scales. We showed that at the latitudinal scale mainly geographical distance explained the variation in the species composition of lepidopterans and spiders. At the local scale, mainly plant and leaf size explained the variation in the species composition of those groups. This result and the relationship between regional and local richness confirm our expectation of saturated communities. We found that dispersal ability is related to climate variability, and that climate stability explains the endemism of spiders. Our results suggested that dispersal- and niche-based processes operate simultaneously, although at different scales, to assemble ecological communities. We argue that communities are assembled by the hierarchical interaction of dispersal processes with speciation, ecological drift and niche-based processes, illustrating that those interactions should be considered in an evolutionary context.

## INTRODUCTION

Since the early observations of Von Humboldt in the 18th century on patterns of species richness from the poles to the equator [1], the latitudinal gradient has challenged ecologists to explain what mechanisms drive large-scale patterns in species richness and composition [2]-[4]. After the contributions of Robert MacArthur to the understanding of large-scale patterns [5], much attention has turned to the relationships between local and regional processes which, in turn, diminished the focus on local interactions *per se* [6]. Thus, the debate between local vs. regional processes is leading us to a balanced view that integrates local processes with global biogeography and the history of life [6], [7]. Traditionally, this resulted in regressing regional and local species richness. In non-interactive communities, the regional species pool affects the local community positively and linearly (unsaturated pattern) [8]. In interactive communities an upper limit will restrict the relevance of the regional species pool, resulting in saturated communities [8]. The authors have speculated that regional richness controls local richness without relying on local processes such as interspecific interactions.

This conceptually very simple approach has been criticized from a metacommunity perspective that considers a set of local communities linked by dispersal of potential interacting species [9]. The metacommunity framework investigates the contribution of both local (e.g., niche) and regional processes in dictating patterns of species richness and composition [10], [11]. Testing the relationship between local versus regional richness, for example, disregards the influence of environmental processes on both local and regional communities [12], [13]. Moreover, recent metacommunity models have shown that dispersal is linked with local competition and habitat heterogeneity/availability [12], which generates interdependence between the dynamics of both local and regional communities.

Based on metacommunity models we predict two distinct patterns at local and regional scales [9], [10]. We considered the local scale as local metacommunities that are isolated from each other, and the regional scale as the combination of all metacommunities (details below). We first predict that if geographical distance among local metacommunities is long enough to limit the dispersal of organisms, compositional similarity will thus be spatially structured at the regional scale (i.e., neutral perspective) [11], [14]. On the other hand, we predict that at the local scale metacommunities are environmentally structured because local (niche-based) conditions such as patch quality or habitat type generally cause strong differences in local demography of species that, in turn, affects local species composition (species sorting perspective) [11]. These predictions of neutral- and niche-based perspectives are not mutually exclusive [10]. Recent works suggest that the relative importance of niche- and dispersal-based processes may change from local to regional communities [15], [16]. In this point of view, the assembly of local ecological communities is determined by the interaction between regional and local processes (Shurin and Srivastava 2005) rather than by the unidirectional effect of regional processes cascading to those local communities (Gonçalves-Souza T, Cottenie K, Romero GQ, unpublished data; Artigo 3, Pag. 99).

In addition, Jocqué *et al.* [17] have suggested a trade-off between dispersal and species' ecological specialization to local conditions as an important driver of large-scale diversity patterns. In this study, Jocqué *et al.* derived three predictions: first, that ecological specialization limits dispersal, since the chance of colonizing suitable habitats for locally specialized species decreases away from the optimal habitat. Second, that longer dispersal distances will be present in more climatically variable environments, since this allows organisms to follow their optimal habitat conditions. Third that higher level of endemism will be present in more stable

environments because of higher speciation rates. The rationale of Jocqué et al. predictions thus predicts that metacommunity processes could be integrated into the latitudinal gradient theory. We thus performed a formal test of two of Jocqué et al. predictions (see below).

Several studies have investigated local versus regional processes from a metacommunity perspective [10], [15], [18]. However, as far as we know no empirical studies have tested the relative contribution of environmental and spatial processes to both local and regional communities and the effect of those processes in the formation of the latitudinal gradient. To investigate how niche- and dispersal-based processes affect species composition at local and regional scales, and to test the potential combinations of the five predictions outlined above, we studied two vegetation-dwelling arthropod groups along 2,040 km of the Brazilian east coast, between -12 and -28 latitude. We selected 12 localities of *restinga* vegetation ranging from Northeast to South of the continent (Fig. 1; Appendix S1). Scarano [19] defined *restinga* vegetation as plant communities that grow in sandy plains (formed in the late Quaternary) occupying stretches between the sea and the Atlantic Rainforest. This vegetation covers about 18,000 km<sup>2</sup> of the Brazilian coast and the climate ranges from tropical to subtropical [20]. Thus, we performed environmental comparisons at a latitudinal scale, but comparing the same vegetation type. The selection of this type of similar habitat removed as much as possible differences in environmental heterogeneity between different latitudes (see, e.g., [21]).

We selected lepidopterans and spiders because both groups are common over vegetation; as well, those groups have different biology and dispersal capabilities that are important to test our predictions. For instance, lepidopterans are phytophagous and mostly specialized to a single plant family [22]. Thus, plant families with distinct traits (e.g., leaf size) will affect lepidopteran community composition. Their adults are good dispersers and can fly actively over extensive

areas. In addition, ballooning caterpillars (larval phase) can move to a new host plant if the quality of their “old” plant is declining [23]. Spiders, in turn, are generalist predators and most individuals are able to weave webs, which makes habitat structure a noteworthy feature of their life history [24], [25]. Spiders have been considered poor dispersers because they depend on passive movement (ballooning) to reach new localities with suitable conditions [23]. In fact, the dispersal of spiders is considered a high-risk activity, because in cases that spiders land in unfavourable localities, individuals will not be able to reproduce [26]. Thus, the composition of lepidopterans and spiders could be affected by both environmental (niche-based) variation and distance among suitable habitats (i.e., dispersal-limited), although the relative importance of dispersal-based processes probably vary among these organisms. For instance, broad- and fine-scale spatial structures probably affect more intensely poor dispersers such as spiders.

We evaluated the relationship between local (plant traits) and regional (latitudinal gradient) richness (saturated vs. unsaturated tests), and employed the variation partitioning method at the local and latitudinal scales to test four of the five predictions (except for the Jocqué’s prediction about ecological specialization limiting dispersal) outlined below. This approach adopts an important recommendation from Weiher et al. [27]: combining community ecology with biogeography. We expected (1) that lepidopterans and spiders will be spatially structured at the latitudinal scale, but that spiders will be stronger affected by broad and fine-scale spatial structure; and (2) strong environmental structures for both lepidopterans and spiders at the local scale. Spiders are influenced by habitat structure and lepidopterans by the phylogenetic similarity of their host plant (which is a good proxy of architectural differences in the studied plants); therefore we expected that plant traits would affect lepidopterans and spiders similarly at the local scale. Indeed, as we expect a strong environmental structure at the local



scale for both groups, we also predict a saturated relationship between local and regional species richness for lepidopterans and spiders; (3) since lepidopterans are good (active) dispersers, they will be less spatially structured in more climatically variable localities [17]; and (4) since spiders are poor (passive) dispersers, the number of endemic species will be higher in climatically stable localities [17].

## METHODS

We propose a new approach to combine metacommunity ecology with biogeography by expanding the traditional way to test the relationship between regional and local richness. We conceptually substituted regional richness with more specific proxies of regional processes, and local species richness with more specific proxies of local ecological patterns in the analyses that we outline below. For example, we used climate variability as a regional process and average local species richness, endemism and variation components as local ecological patterns.

### *Study area and sampling*

In this study we choose a specific type of *restinga*, called “open *restingas*”, which are characterized by patchy vegetation surrounded by open areas covered either with sand or herbaceous vegetation [28]. The main plant families found in open *restingas* belong to the families Arecaceae, Bromeliaceae, Malpighiaceae, Myrtaceae, Rubiaceae and Sapindaceae [28]. Because the selected *restingas* occur at regions with contrasting climate regimes, we summarized climatic information in Figure S1 and Table S1 (Appendix S1). We selected 12 localities of *restinga* vegetation along 2,040 km of the Brazilian coast (Prancha 1, Pág. 13). The average distance among localities is 811 km (max = 2,040 km, min = 14.7 km).

We considered each plant species as a habitat type (i.e., discrete variable) and we chose each plant species based on their traits (i.e., values related to plant and leaf size). Specifically, we chose at each locality a bromeliad (family Bromeliaceae), a palm (Arecaceae), and three different dicot plants species with small, medium and large leaves (Tables S2 and S3, Appendix S1). These five plant species present different traits based on canopy and leaf size and shape. In localities without palms (four localities), we substituted for them another common dicot plant with an architecture distinctive from bromeliads and the three other dicots. To standardize across localities, we used differences in plant trait variation (e.g., variation in leaf length among plants) to test their effect on species composition (see below).

We collected arthropods occurring on five different plant species in each of the 12 localities between September and November of 2009, and June and August of 2010. We selected 20 plots (30 x 30 m) at least 50 m apart within each locality; we randomized the order of plot sampling. The criterion for choosing these points was the presence of at least three of the five traits; from each trait, we sampled 20 individual plants. Within each plot, we sampled up to 5 individual plants of each species. For example, if we found five bromeliad individuals in each of the four first plots, we did not sample bromeliads in the next plots. This protocol was repeated in each locality and in both years. The plots we chose in the first year were the same in the second year, but new randomizations were performed to decide the order of sampling. To control for the possible effect of different samplings, we used year as a factor in RDA analyses (see below). All necessary collect permits were obtained for the described field studies and were licenced by “Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis”/ IBAMA (proc. n. 14894).

We collected arthropods (lepidopterans and spiders) in the branches of each plant using the following protocol: (i) we used 100 L transparent plastic bags to pack four to ten branches (depending on branch size), and cut the branches off; (ii) we carefully shook the bag 20 times to release the arthropods from the branches; (iii) we then removed each branch to check for arthropods in a white tray; (iv) we collected every arthropod visible to the naked eye and conserved them in 75% alcohol. After carefully collecting the arthropods from each branch removed, (v) we weighed (PesolaMedio® precision 10g) all the leaves from these branches to determine total leaf biomass. Thus, even from plants of different sizes, we were able to test whether total leaf biomass affects arthropod abundance. This method was repeated for each individual plant. For bromeliads, however, we did not follow steps i, ii, iii and v; instead, we collected the arthropods (visible to the naked eye) present over the entire plant surface. In addition, we counted the number of leaves of the plant and weighed three leaves (the smallest, one intermediate-sized, and the largest) to estimate total leaf biomass. Then, we multiplied the number of leaves times the average value of the three weighed leaves.

Detailed information about the definition of latitudinal and local scales, as well as how we obtained local and regional richness can be found on Appendix S2.

### *Environmental variables*

We measured plant traits such as tree canopy height, plant biomass, the longest and shortest length of tree canopy variables at the plant level, and leaf length, leaf width, distance between the second and third leaf, and the ratio between leaf width and length at the leaf level. In addition, we extracted macroclimatic variables at 1 km<sup>2</sup> resolution from WorldClim [29].

Detailed information about the variables used and the procedure to control autocorrelation can be found on Appendix S3.

### *Spatial variables*

We calculated the latitudinal range size for each lepidopteran and spider species as the maximum and minimum latitudes (considering the 12 localities) of their occurrence. We attributed the value 1 to the most northeast locality (i.e., latitude -12), value 2 to the second one, and so on. Thus, the most southern locality (i.e., latitude -28) received value 12. For example, the range size of one species that occurs in the whole latitudinal gradient is 11, but the range size of one species that occurs only in one locality is 0. Species with a range size of 0 are thus considered endemics.

We analyse spatial patterns by using Moran's eigenvector maps (MEMs) [30] based on Gabriel graphs [31], [32]. We retained only MEMs with significant values; we also grouped the MEMs as those corresponding to broad (positive autocorrelation) and fine (negative autocorrelation) spatial scales [31]. This technique is suitable for studying the variation of species composition at multiple scales [31]. Thus, we used as spatial predictors in RDA analyses MEMs presenting broad and fine-scale patterns. Figures S2-2 and -3 (Appendix S2) show the spatial pattern of those significant spatial components, grouped as broad and fine scale spatial predictors.

### *Statistical analyses*

To test the relationship between regional (RSR) and local species richness (LSR) we used the log-ratio transformation method (hereafter log-ratio method) proposed by Szava-Kovats et al.

[33] to compare RSR and LSR. First, we log transformed the RSR; second, we transformed the LSR by the additive log-ratio function with  $y = \ln(\text{LSR}/(\text{RSR}-\text{LSR}))$ . We then used ordinary least square regression to test the relationship between RSR and LSR. Results of this regression without change in RSR-LSR ratio represent an unsaturated pattern, while significant negative slope presents saturated pattern [33]. We use the log-ratio method instead of the traditional method (i.e., regressing LSR against its RSR) because the former circumvent some statistical artifacts of the last (Appendix S2).

We tested predictions (1) and (2) based on the metacommunity framework by estimating the relative importance of environmental (plant traits) and spatial variables (broad and fine-scale MEMs) to arthropod species composition with a Redundancy analysis (RDA) coupled with a Variation Partitioning analysis [34]. The RDA decomposes the total variation in species composition into environmental ( $E$ ) and spatial components ( $S$ ). In addition, we partitioned the total variation into the variance explained exclusively by environmental and spatial variables. We used the unbiased Variance Partitioning method proposed by Peres-Neto et al. [35], which computes the adjusted coefficients of variation for each component. Details of calculation of fractions can be found in Peres-Neto et al. [35] and a comment to recent criticism about variance partitioning method in Appendix S2. We implemented this analysis for each locality (local scale analysis,  $\text{RDA}_{\text{local}}$ ) and compared all localities (latitudinal scale analysis,  $\text{RDA}_{\text{latitudinal}}$ ). Prior to  $\text{RDA}_{\text{local}}$  analyses we calculated the variance inflation factor and removed plant trait variables with values higher than 10 [36]. We added year to the  $\text{RDA}_{\text{local}}$  models as a factor to control for possible differences of species composition between years. According to prediction 1 (spatial structure), the pure spatial component of the  $\text{RDA}_{\text{latitudinal}}$  will be higher than the pure environmental component for both lepidopterans and spiders, but the relative importance of S|E

will be higher for spiders than for lepidopterans. According to prediction 2 (environmental determinism), the pure environmental component of the  $RDA_{local}$  will be higher than the pure spatial component for both lepidopterans and spiders.

To test whether macroclimate variables affect local environmental and spatial processes, we performed another RDA analysis ( $RDA_{climate}$ ) using the variation explained by each  $RDA_{latitudinal}$  fraction (Appendix S2) against the four scores obtained by the PCA of macroclimate variables (Appendix S3). In this analysis it is possible to test whether macroclimate variables at the latitudinal scale predict the variation of each component of arthropod species composition. The  $RDA_{climate}$  was done only at the latitudinal scale because at the local scale the resolution of climate data is not fine enough to show differences among plots. To test whether macroclimate variables explain species richness gradients at the latitudinal scale, we regressed species richness values of each locality against the scores of the PCA analysis obtained from macroclimate variables. We implemented these four analyses ( $RDA_{local}$ ,  $RDA_{latitudinal}$ ,  $RDA_{climate}$  and regression) for both lepidopterans and spiders.

To test prediction 3 (dispersal vs. climatic variability) of Jocqué *et al.* [17] we used the component S|E (pure spatial) obtained from each arthropod group and regressed it against the scores obtained by the PCA of the macroclimatic variables (Appendix S3). The higher the values of S|E and PCA scores, respectively, the higher will be the importance of the spatial component (e.g., dispersal limited) and the variability in climate. To test prediction 4 (endemism vs. environmental stability) we regressed the number of endemic species of each locality against the PCA scores representing the macroclimate variables (Appendix S3). The lower the value of these variables, the lower is the stability of the environment.

We used R-language environment [37] and the packages `ade4`, `fields`, `fossil`, `spacemaker`, `rich`, and `vegan` to perform all analyses.

## RESULTS

We collected a total of 333 arthropod species and 1890 individuals in the twelve localities, of which there were 161 species (average richness by locality =  $26 \pm 8.67$  SD) and 766 individuals of lepidopterans (average abundance by locality =  $63.8 \pm 26.3$  SD), and 172 species ( $27.7 \pm 9.87$ ) and 1124 individuals of spiders ( $93.6 \pm 32.8$ ). The range of species along the Brazilian coast was similar between lepidopterans and spiders. Only three species of lepidopterans and one species of spiders occurred along the whole latitudinal gradient, and the majority of species (95 for lepidopterans and 104 for spiders) occurred only at one locality (Fig. 2). That is, 59% and 60% of lepidopterans and spider species, respectively, are endemics.

We found that at the latitudinal scale the composition spiders were mainly explained by broad ( $R_{adj}^2 = 0.141$ ) and fine spatial scale structures ( $R_{adj}^2 = 0.016$ ), and the composition of lepidopterans was explained only by broad spatial structure ( $R_{adj}^2 = 0.061$ ). Indeed, the variance explained by the spatial components were higher for spiders (15.7%) than lepidopterans (6.1%) (Table 1), as expected in prediction 1. At this scale there is a small, but significant, environmental effect on lepidopterans ( $R_{adj}^2 = 0.023$ ) and spiders ( $R_{adj}^2 = 0.011$ ). As expected in prediction 2, at the local scale the average (i.e., mean value of 12 localities) total variation explaining species composition of lepidopterans was 11.2% ( $\pm 8.9$  SD), of which plant traits (E|S) explained 9.2% of the variation ( $P < 0.05$  in 8 of 12 localities) and spatial variables (S|E) explained only 0.6% ( $P < 0.05$  in 3 of 12 localities; Table 1). For spiders, the average (i.e., mean value of 11 localities) total variation explaining species composition was 10.6%, of which 8.3% was explained by plant traits (E|S;  $P < 0.05$  in 10 of 11 localities) and only 1.5% was explained

by spatial variables (S|E;  $P < 0.05$  in 6 of 11 localities; Table 1). On average (12 lepidopteran comparisons and 11 spider comparisons), plant traits explained 8.8% (significant in 18 of 23 comparisons) of the variation in those arthropod species composition at the local scale, while spatial variables explained 1.1% (significant in 9 of 23 comparisons) (see also Appendix S4). Indeed, the components related to plant traits and space (Appendix S2) were not significantly related to bioclimatic variables measured by PCA scores for both lepidopterans (permutation test for RDA:  $F = 1.302$ ,  $P = 0.34$ ) and spiders ( $F = 0.763$ ,  $P = 0.67$ ). In summary, spatial structure predominates at the latitudinal scale and environmental structure at the local scale for both lepidopterans and spiders. The importance of local environmental variation is reinforced by the relationships between regional and local richness. We found that lepidopteran ( $LSR = -0.214 - 0.841 * RSR$ ;  $R_{adj}^2 = 0.896$ ,  $P < 0.0001$ ) and spider communities ( $LSR = 0.114 - 0.942 * RSR$ ;  $R_{adj}^2 = 0.978$ ,  $P < 0.0001$ ) are saturated.

The spatial component (a proxy of dispersal limitation) associated with lepidopteran species composition was negatively related to climatic variability ( $F = 18.41$ ,  $P = 0.002$  for PCA3), as in prediction 3. The PCA3 axis was positively related to precipitation seasonality and negatively related to mean temperature diurnal range. Climate variability positively affected the number of endemic spider species ( $F = 6.57$ ,  $P = 0.037$ ; significant for PCA1) but did not affect lepidopterans' endemism ( $F = 1.69$ ,  $P = 0.246$ ), as in prediction 4. The PCA2 axis was negatively correlated to mean temperature diurnal range, maximum temperature of the warmest month, and precipitation of the wettest month. Thus, the latitudinal richness of lepidopterans scales positively with temperature and precipitation. PCA1 was positively related to temperature seasonality and annual range and negatively related to isothermality. Therefore, spider endemism was higher at localities with lower isothermality (i.e., lower temperature diurnal range compared



to annual temperature range: Hijmans et al. [19]) and lower temperature seasonality, as expected in prediction 4.

## DISCUSSION

The growing evidence that neither dispersal-based nor niche-based processes exclusively explain by the patterns of similarity among communities [38]-[40] illustrates that these processes operate simultaneously to assemble communities [41]. We found that, at the latitudinal scale, mainly the geographical distance explained the variation in the species composition of lepidopterans and spiders. We also found that the relationship between RSR and LSR is saturated for lepidopterans and spiders, which suggest that local processes determine local species composition. In addition, we showed that plant traits are the main predictors of the variation in the species composition of lepidopterans and spiders at the local scale, which reinforces that local processes are pervasive in determining local scale patterns. Thus, although the regional species pool influenced the local communities, differences in habitat preferences among species (or other selection factors) may also determine the local distribution of species.

As we expected from prediction 1, lepidopteran and spider communities were spatially structured, which suggests that geographic distance (i.e., latitudinal gradient) is constraining the distribution of terrestrial arthropods. Under dispersal limitation at a latitudinal scale, this spatial pattern may arise from change in species abundance throughout the evolutionary history determining the composition of these arthropod communities along the latitudinal gradient. Speciation has been considered fundamental to explain the assembly of regional species pool [42], [43]. For example, we found two spider species from the genus *Psecas* (Salticidae) occurring only on bromeliads, while *Psecas* sp1 occurs from latitude -18 to -21, and *Psecas* sp2 from latitude -25 to -27. The distinct spatial distribution of these two species between these

regions coincides with the divergent distribution of endemic anurans from the genus *Rhinella*, in which genetic breaks in their phylogeny were spatially concordant with geographic barriers (e.g., rivers) in the Atlantic Forest [44]. These barriers could limit dispersal and therefore isolate species in different metacommunities, reduce gene flow and increase allopatric speciation [17]. Thus, speciation may interact with dispersal to generate and maintain richness along the latitudinal gradient.

As expected in prediction 2 and confirmed by the saturated pattern, we showed that at the local scale plant traits explain the variation in species composition of lepidopterans and spiders. Plant traits (i.e., leaf width and canopy height) affected local lepidopteran and spider communities at different latitudes. This does not mean that the mechanisms affecting the composition of lepidopterans and spiders are the same (e.g., plant phylogeny has been considered important for lepidopterans and plant traits for spiders: [22], [25]), though. These results highlight that the interpretation of local and regional processes based on saturated and unsaturated patterns needs to be reassessed [12], [33]. We suggest that regional processes (dispersal and speciation) act together with selection (e.g., typically local processes such as habitat preferences) in determining the composition of local metacommunities (Fig. 3) [43], [45]. In addition, these results also indicate that dispersal-based processes determine how much of the regional pool will occur locally [45].

In addition, we have shown that ~91% of the variation in species composition at the local scale was unexplained, even after taking into account spatial and environmental variation (i.e., plant traits plus macroclimate variables). While this 10% explained variation is well within the range of explained variation [46], [47], we did not include other known drivers of spider and lepidopteran community composition such as shading gradient for spiders [48] and plant

secondary chemical components for lepidopterans [49]. However, some studies have emphasized that plant species composition and their morphological traits are the main drivers of those communities [50], [51]. In addition, we speculate that the unexplained variation could be also be attributed to neutral processes (via ecological drift) [52] acting at the local scale. Each local arthropod metacommunity could be organized by plant trait variation, but the relative importance of plant traits depends on the species (from regional/latitudinal pool) that disperse to each locality. Thus, the presence of certain species in the region does not mean that organisms of this species will necessarily disperse to all local communities and find their preferred habitats, which may explain the 91% of randomness in species composition. For example, the bromeliad-living spider *Psecas* sp. did not occur at the Trancoso's *restinga* (Fig. 1) although its microhabitat (bromeliad) is densely distributed in this locality. Taken together, high latitudinal spatial structure, local determinism and the remaining 91% of unexplained variation illustrate that regional and local processes are not mutually exclusive [12] and probably interact to assemble local metacommunities. Evolution could determine which species occur at the latitudinal gradient and interact with environmental determinism and ecological drift to assemble local metacommunities.

In addition, differences in dispersal capabilities among organisms can also affect both the species available along the latitudinal gradient and the response to climate variability. For example, for lepidopterans we found longer dispersal (i.e., low importance of pure spatial component) in localities with more variability in mean temperature diurnal range, as expected in prediction 3; however, for lepidopterans, dispersal was related to precipitation stability. On the other hand, the number of endemic spiders was higher in climatically stable localities (i.e., lower isothermality and precipitation seasonality), as expected in prediction 4. We suggest that

differences in dispersal between adult lepidopterans and spiders may explain the differential effects of climate on their regional richness and endemism. On the one hand, lepidopterans (adults) are dispersers that actively choose the locality and the host plant to oviposit, resulting in a “deterministic” occurrence. These adults may occur, for example, in localities with a specific range of temperature [53] through direct active choice. In fact, in localities with more instability in temperature, lepidopterans were more dispersal-limited. On the other hand, the majority of spiders disperse passively using silk threads, resulting in a “stochastic” occurrence. Thus, in localities with suitable climatic conditions there will be more species of lepidopterans because these organisms can actively choose the best quality localities. However, in those suitable localities we can find more endemic spiders because in localities with unsuitable conditions (e.g., unstable climate) few spider species will survive. These results highlight the importance of considering differences in dispersal abilities among species to obtain a more predictive metacommunity model to explain large-scale patterns, as the latitudinal gradient (e.g., Jocqué et al. [17]).

By integrating processes that operate at different scales, we showed that dispersal and speciation processes at the latitudinal scale, coupled with plant traits and ecological drift at the local scale, may explain the relationship between regional and local communities. Although the local patterns are the same, the latitudinal patterns depend on the dispersal capabilities of the taxonomic groups. We successfully combined metacommunity processes with biogeography to improve our understanding of the scale dependence of processes such as dispersal and its association with speciation and “evolutionary drift”, and the association of dispersal with niche-based explanations and ecological drift. Future work can then build on this approach to explicitly

integrate the evolutionary history of organisms to explore, for example, the evolutionary origin of regional species pools, i.e. “evolutionary drift”.

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**Author contributions:** T.G-S. and G.Q.R. conceived the initial idea; T.G-S. collected the data; K.C. contributed to further development of the idea; T.G.S. and K.C. analysed the data; and T.G.-S., G.Q.R. and K.C. wrote the manuscript.

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**Table 1.** Explained variation of each component of the partitioning of arthropod species composition (Araneae and Lepidoptera). [E] and [S] represent the environmental and spatial components without control for the autocorrelation. [E|S] represents pure environmental (plant morphology) effects. [S|E] represents pure spatial effects. The spatial variation presenting broad and fine scale spatial variation was significant only for spiders. Bold values indicate significant values ( $P < 0.05$ ) of each pure fraction. For Praia do Forte (only spiders) we do not have enough data to perform variance partitioning.

	<b>Total</b>	<b>[E]</b>	<b>[S]</b>	<b>[S<sub>broad</sub>]</b>	<b>[S<sub>fine</sub>]</b>	<b>[E S]</b>	<b>[S E]</b>
<b>CATTERPILLARS</b>							
<b>Latitudinal scale</b>	0.111	0.049	0.087	-	-	<b>0.023</b>	<b>0.061</b>
<b>Local scale (mean)</b>	0.112	0.106	0.020	-	-	0.092	0.006
Praia do Forte	0.325	0.287	0.052	-	-	<b>0.272</b>	<b>0.038</b>
Salvador	0.012	0.016	-0.004	-	-	0.017	-0.003
Trancoso	0.111	0.064	0.060	-	-	<b>0.051</b>	<b>0.047</b>
Barra Nova	0.155	0.181	-0.003	-	-	<b>0.158</b>	-0.026
Setiba	0.028	0.054	-0.003	-	-	0.032	-0.025
Praia das Neves	0.199	0.145	0.085	-	-	<b>0.114</b>	<b>0.054</b>
Iquipari	0.084	0.081	0.029	-	-	<b>0.055</b>	0.003
Massambaba	0.118	0.118	0.019	-	-	<b>0.099</b>	0.001
Maricá	0.066	0.067	0.019	-	-	<b>0.047</b>	-0.001
Ilha do Cardoso	0.124	0.127	-0.003	-	-	<b>0.127</b>	-0.002
Dunas dos Ingleses	0.121	0.087	0.013	-	-	<b>0.107</b>	0.033
Dunas de Joaquina	0.006	0.047	-0.026	-	-	0.031	-0.042
desvpad	0.089	0.073	0.032			0.072	0.031
<b>SPIDERS</b>							
<b>Latitudinal scale</b>	0.177	0.027	0.161	<b>0.141</b>	<b>0.016</b>	<b>0.011</b>	<b>0.157</b>
<b>Local scale (mean)</b>	0.107	0.092	0.024	-	-	0.083	0.015
Praia do Forte	-	-	-	-	-	-	-
Salvador	0.045	0.039	0.016	-	-	0.028	0.005
Trancoso	0.118	0.124	0.015	-	-	<b>0.103</b>	-0.006
Barra Nova	0.066	0.065	-0.003	-	-	<b>0.069</b>	0.001
Setiba	0.177	0.149	0.041	-	-	<b>0.136</b>	<b>0.029</b>
Praia das Neves	0.136	0.124	0.022	-	-	<b>0.114</b>	<b>0.012</b>
Iquipari	0.087	0.084	0.008	-	-	<b>0.079</b>	0.003
Massambaba	0.084	0.082	0.005	-	-	<b>0.078</b>	0.001
Maricá	0.085	0.047	0.052	-	-	<b>0.033</b>	<b>0.037</b>
Ilha do Cardoso	0.045	0.024	0.015	-	-	<b>0.028</b>	<b>0.020</b>
Dunas dos Ingleses	0.188	0.143	0.060	-	-	<b>0.128</b>	<b>0.045</b>
Dunas de Joaquina	0.150	0.127	0.029	-	-	<b>0.120</b>	<b>0.022</b>

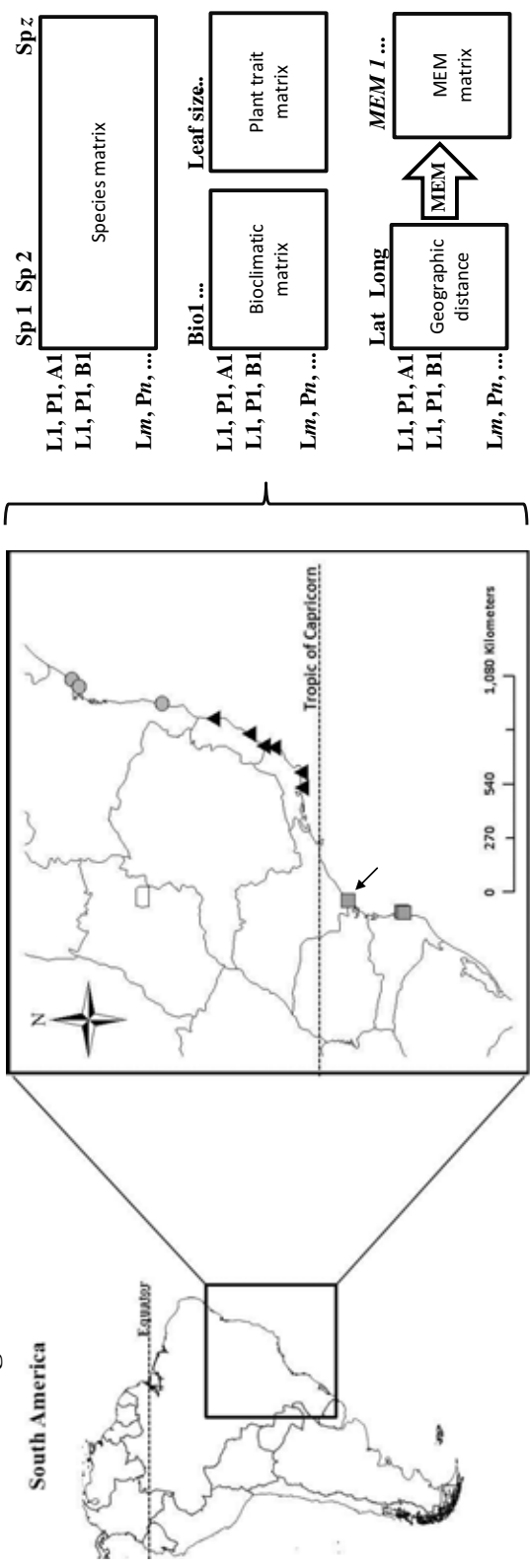
## Figure legends

**Figure 1.** A) Map of South America (left) and the geographical range of the study (middle). The symbols present each 12 sampled localities; localities with similar symbols (grey squares, black triangles and grey circles) have similar climatic characteristics (Appendix S1, Fig. S1). From Northeast to South, the order of the sampled localities is the same as in Table 1 (see below). Although *Ilha do Cardoso* (arrow) is at the Southeast of Brazil, our analysis (see Appendix S1) showed similar climate characteristics shared with the two localities at the South region (grey squares). At the regional scale (1A, middle), we used a species matrix (including all localities), two groups of environmental variables (climate and plant architectural features), and the distance among plots to perform the  $RDA_{\text{regional}}$  (right); thus, we ran one  $RDA_{\text{regional}}$  for each arthropod group. Each row of the regional matrix presents the locality ( $L_m$ ), the plot ( $P_n$ ), and the individual plant (A, B, C, D or  $E_{1 \text{ to } 20}$ ) (1A, right). We sampled up to 20 individual plants per plant species in each locality. B) Representation of sampling procedure showing the distribution of twenty plots (30 x 30 m, grey squares) in the locality  $m$  (left), as well as the minimum distance between plots (i.e., 50 m). We sampled up to five individual plants per plant species (A, B, C, D, and E) in each plot. At the local scale (1B, left), we used a species matrix, only plant architectural features as environmental variables, and the distance among  $n$  plots to perform the  $RDA_{\text{local}}$ ; thus, we ran 12  $RDA_{\text{local}}$  for each arthropod group (see Table 1). Each row of the local matrixes ( $n=12$  per arthropod group) presents the sampled plot ( $P_n$ ) and individual plant (A, B, C, D or  $E_{1 \text{ to } 20}$ ) (1B, right). See additional details about the definition of regional and local scales, as well as the analytical procedure in Methods.

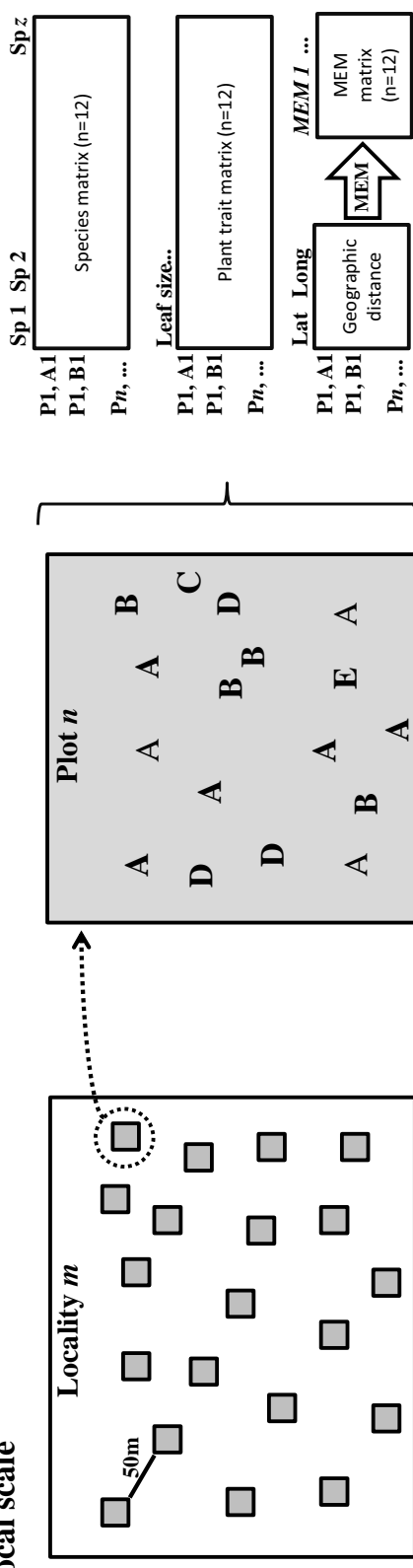
**Figure 2.** Species' range size of lepidopterans and spiders in relation to their distribution along the Brazilian coast. The *X* axis presents the species rank (i.e., species with the greatest range, which occur throughout the whole latitudinal gradient, to species with the smaller range) and the *Y* axis presents species range, i.e., the maximum and minimum occurrences at the latitudinal gradient. Circles present the mean range of each species. Species occurring at one locality (lowest range) are represented by just a circle.

**Figure 3.** Schematic representation of the proposed hierarchical (from latitudinal spatial structure to local environmental determinism) assembly of lepidopteran and spider species composition. Along the latitudinal gradient the “evolutionary drift”, coupled with speciation and dispersal limitation, determines species composition. The latitudinal species pool influences positively the number of species of each local community. The available pool at each region will then interact with local extinctions, selection (e.g., habitat selection) and ecological drift to determine the composition of local communities. See details in Discussion.

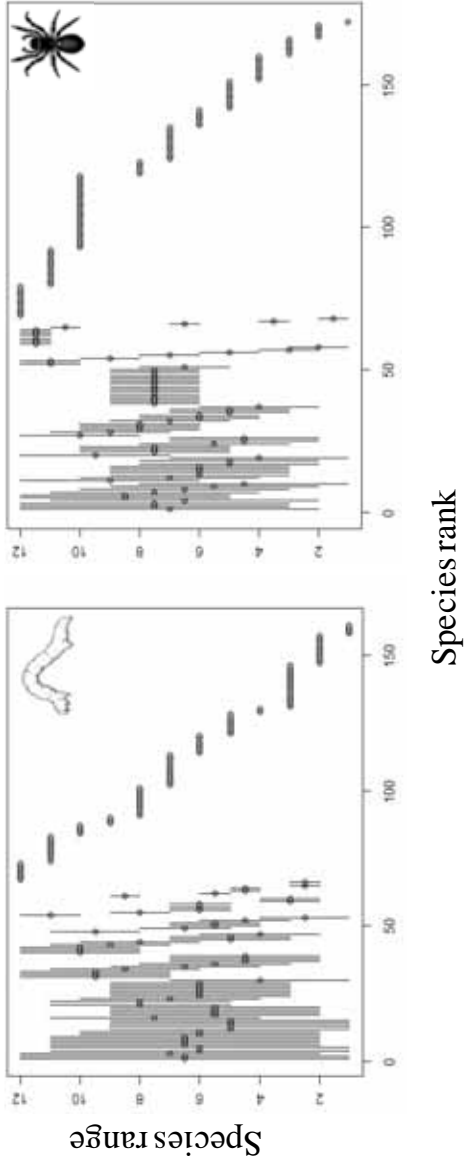
**A) Latitudinal / Regional scale**



**B) Local scale**

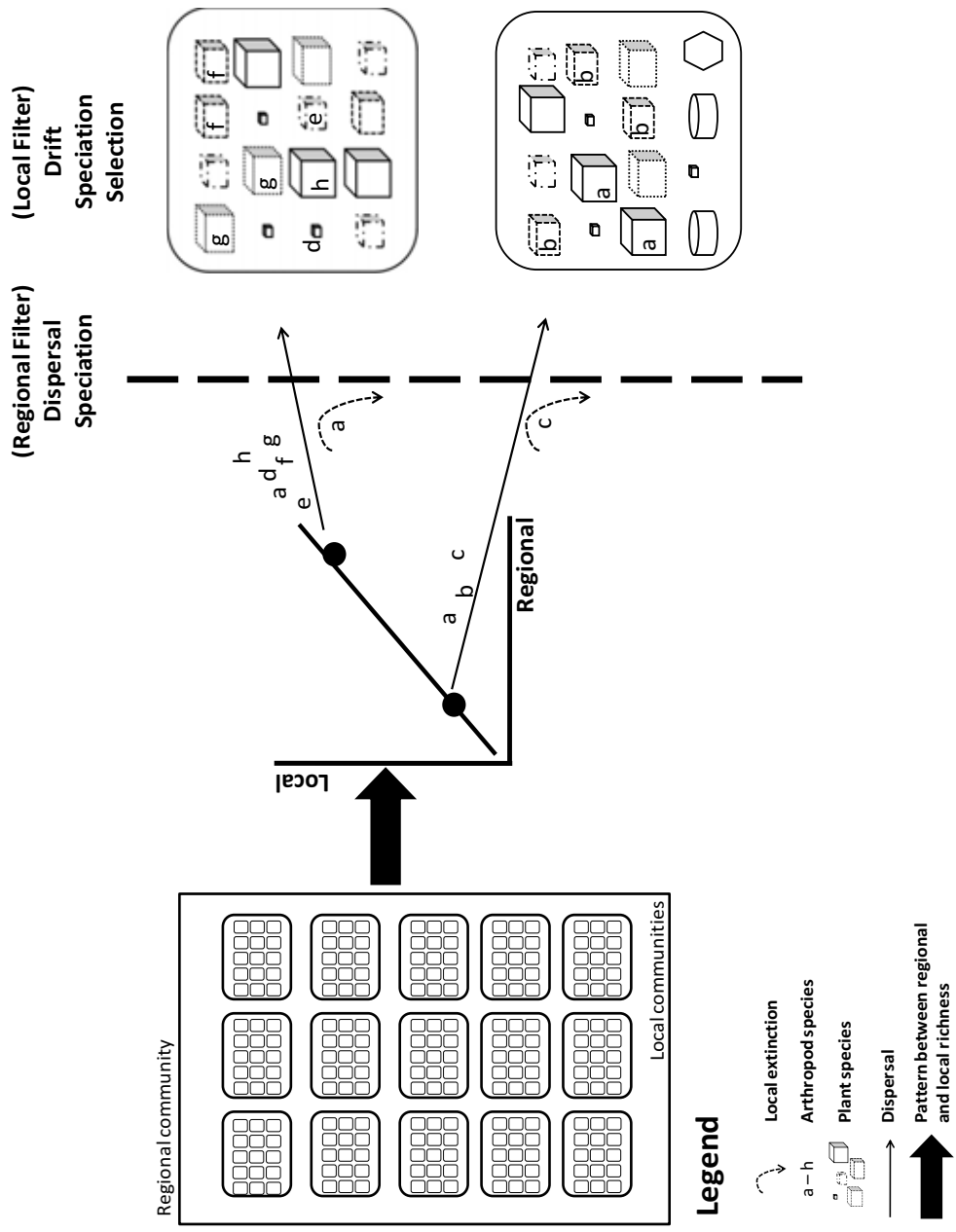


**Figure 1**



**Figure 2**





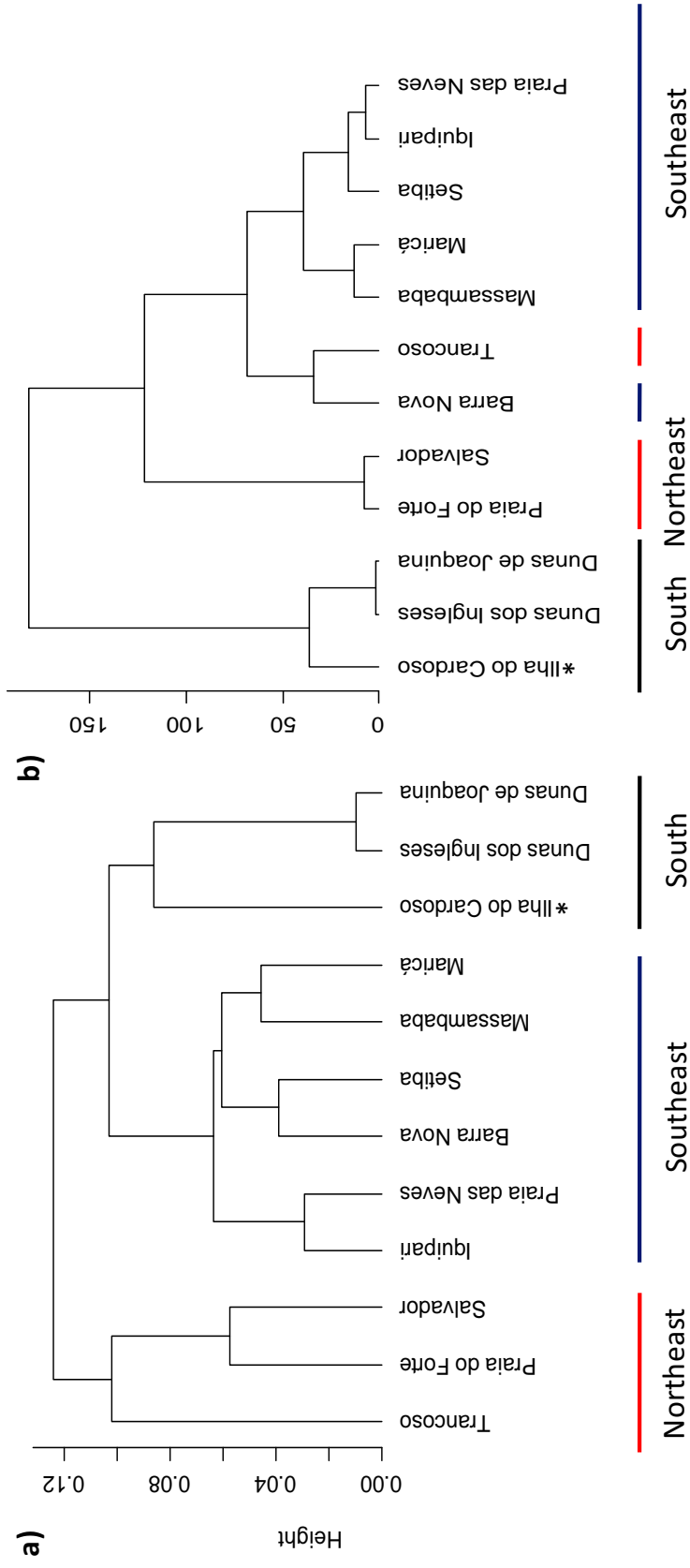
**Figure 3**

### **Appendix S1: Information of macroclimate variables, plant species and families at the 12 sampled sites.**

We conducted this study on 12 *restinga* sites along the Brazilian coast (Fig. 1, Manuscript), ranging from South to Northeast of the continent (Table S1). We used the macroclimate variables obtained from Hijmans et al. (2005). They defined the macroclimate variables as bioclimatic 1 to 19, but we used bio1 (annual mean temperature), bio2 (monthly mean value of maximum – minimum temperature), bio3 (isothermality, which is the ratio between bio2 and bio7), bio4 (temperature seasonality), bio5 (maximum temperature of the warmest month), bio6 (minimum temperature of the coldest month), bio 7 (temperature annual range), bio 12 (annual precipitation), bio 13 (precipitation of the wettest month), bio 14 (precipitation of the driest month), bio 15 (precipitation seasonality) (Hijmans et al. 2005; <http://www.worldclim.org/bioclیم>). These bioclimatic variables are derived from monthly values of temperature and precipitation with 2.5 arc-minutes resolution.

To show the geographic and climatic dendrograms representing the distance among sites, we implemented a Hierarchical Cluster analysis (Figure S1). These clusterings were based in an Euclidian distance matrix for climatic variables and in a Great Circle distance for geographic distance among sites. We used R-language environment (R Development Core Team 2011) and the packages `fields` and `stats`.

We summarized the information about plant architecture sampled at each site and the morphospecies in the Table S2 and S3.



**Figure S1.** UPGMA dendrograms based on (a) climatic and (b) geographic distance among the 12 sites. Mantel statistics ( $r$ ) of the correlation between the distance matrices was 0.575 ( $P = 0.001$ ). (\*) In this analysis, “Ilha do Cardoso” was clustered in the south group, but considering the Brazilian regions, it is from the Southeast region. However, this site is localized in the most southern city from this region.

**Table S1.** Geographic coordinates (Longitude and Latitude) and bioclimatic variables of each site obtained from Hijmans et al. (2005)

method. The code of the bioclimatic variables (bio1-7, bio12-15) is the same suggested by the authors of the original description (Hijmans et al. 2005). See text to detailed information about bioclimatic variables.

Site	Longitude	Latitude	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio12	bio13	bio14	bio15
Praia do Forte	-38.0023	-12.5694	24.66	7.41	66.74	131.41	30.3	19.2	11.1	1749	312	73	51.61
Salvador	-38.3228	-12.9194	24.99	6.44	65.73	117.59	30	20.2	9.8	1275	193	50	45.73
Trancoso	-39.1003	-16.6556	24.46	7.63	65.80	133.62	30.1	18.5	11.6	1477	155	91	18.33
Barra Nova	-39.7387	-18.9573	24.10	8.54	62.35	166.30	31	17.3	13.7	1279	180	55	41.96
Setiba	-40.4164	-20.6054	24.56	7.80	58.65	177.06	31.5	18.2	13.3	1100	172	47	44.71
Praia das Neves	-40.9758	-21.2355	23.33	8.48	59.74	185.23	29.9	15.7	14.2	969	167	27	53.06
Iquipari	-41.0321	-21.7285	23.05	8.55	58.97	189.76	30	15.5	14.5	1022	148	28	46.69
Massambaba	-42.1289	-22.9449	23.03	6.48	56.30	180.86	28.9	17.4	11.5	870	114	39	32.06
Marica	-42.8479	-22.9608	23.35	7.96	55.27	214.49	30.6	16.2	14.4	1182	147	51	36.86
Ilha do Cardoso	-47.9136	-25.0673	22.63	8.60	50.29	297.60	31	13.9	17.1	2469	374	84	46.74
Dunas dos Ingleses	-48.4040	-27.4945	20.04	7.21	47.42	278.83	28	12.8	15.2	1521	198	74	34.13
Dunas de Joaquina	-48.4588	-27.6192	19.65	6.86	45.72	282.57	27.5	12.5	15	1481	203	74	35.61

**Table S2.** Plant species (or morphospecies) selected in each site. The number of plant species varies from 5 to 6. Asterisks denote site that we did not find palm species; thus, we substituted for another dicot species with architecture distinctive from the other dicots.

Site	Bromeliad 1	Bromeliad 2	Palm	Small-leaved dicot	Medium-leaved dicot	Large-leaved dicot
Praia do Forte	<i>Aechmea cf. aquilega</i>	-	<i>Allagoptera</i> sp.	Myrtaceae sp.1	Rubiaceae sp.	<i>Manilkara</i> sp.
Salvador	<i>Hohenbergia litorallis</i>	-	<i>Allagoptera</i> sp.	<i>Byrsonima</i> sp.	Anacardiaceae sp.	Sapotaceae sp.
Trancoso	<i>Aechmea blanchetiana</i>	<i>Bromelia antiacantha</i>	-	Humiriaceae sp.	<i>Matayba discolor</i>	<i>Anacardium</i> sp.
Barra Nova	Bromeliaceae sp.1	<i>Quesnelia arvensis</i>	<i>Allagoptera</i> sp.	<i>Eugenia</i> sp.	<i>Protium</i> sp.	<i>Clusia</i> sp.
Setiba	<i>Aechmea lingulata</i>	<i>Vriesea procera</i>	<i>Allagoptera</i> sp.	<i>Baccharis</i> sp.	Myrtaceae sp.2	<i>Clusia</i> sp.
Praia das Neves	<i>Aechmea lingulata</i>	<i>Vriesea procera</i>	<i>Allagoptera</i> sp.	unidentified	<i>Byrsonima</i> sp.	<i>Clusia</i> sp.
IQUIPARI	<i>Neoregelia cruenta</i>	<i>Aechmea nudicaulis</i>	<i>Allagoptera</i> sp.	<i>Eugenia</i> sp.	<i>Pera</i> sp.	<i>Clusia cf. hilariana</i>
Massambaba	<i>Neoregelia cruenta</i>	-	<i>Allagoptera</i> sp.	<i>Pithecellobium</i> sp.	<i>Byrsonima</i> sp.	<i>Clusia</i> sp.
Marica	<i>Neoregelia cruenta</i>	-	<i>Allagoptera</i> sp.	<i>Pithecellobium</i> sp.	<i>Byrsonima</i> sp.	<i>Clusia fluminensis</i>
Ilha do Cardoso	<i>Quesnelia arvensis</i>	-	<i>Tibouchina clavatum*</i>	Asteraceae sp.1	<i>Dodonaea viscosa</i>	<i>Dalbergia</i> sp.
Dunas dos Ingleses	<i>Aechmea</i> sp.	Bromeliaceae sp.2	Myrtaceae sp.3*	Asteraceae sp.1	<i>Dodonaea viscosa</i>	<i>Clusia criuva</i>
Dunas de Joaquina	<i>Aechmea</i> sp.	Bromeliaceae sp.2	Myrtaceae sp.3*	Asteraceae sp.1	<i>Dodonaea viscosa</i>	<i>Clusia criuva</i>

**Table S3.** Plant species (or morphospecies) and their families.

<b>Species (or morphospecies)</b>	<b>Plant family</b>
<i>Aechmea lingulata</i>	Bromeliaceae
<i>Aechmea nudicaulis</i>	Bromeliaceae
<i>Aechmea</i> sp.	Bromeliaceae
<i>Allagoptera</i> sp.	Arecaceae
<i>Byrsonima</i> sp.	Malpigiaceae
<i>Clusia</i> cf. <i>hilariana</i>	Clusiaceae
<i>Clusia criuva</i>	Clusiaceae
<i>Clusia fluminensis</i>	Clusiaceae
<i>Clusia</i> sp.	Clusiaceae
<i>Dalbergia</i> sp.	Fabaceae
<i>Dodonaea viscosa</i>	Sapindaceae
<i>Eugenia</i> sp.	Myrtaceae
<i>Neoregelia cruenta</i>	Bromeliaceae
<i>Pera</i> sp.	Euphorbiaceae
<i>Pithecellobium</i> sp.	Fabaceae
<i>Protium</i> sp.	Burseraceae
<i>Quesnelia arvensis</i>	Bromeliaceae
<i>Tibouchina clavatum</i>	Melastomataceae
<i>Vriesea procera</i>	Bromeliaceae

## **Literature cited (Appendix S1)**

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

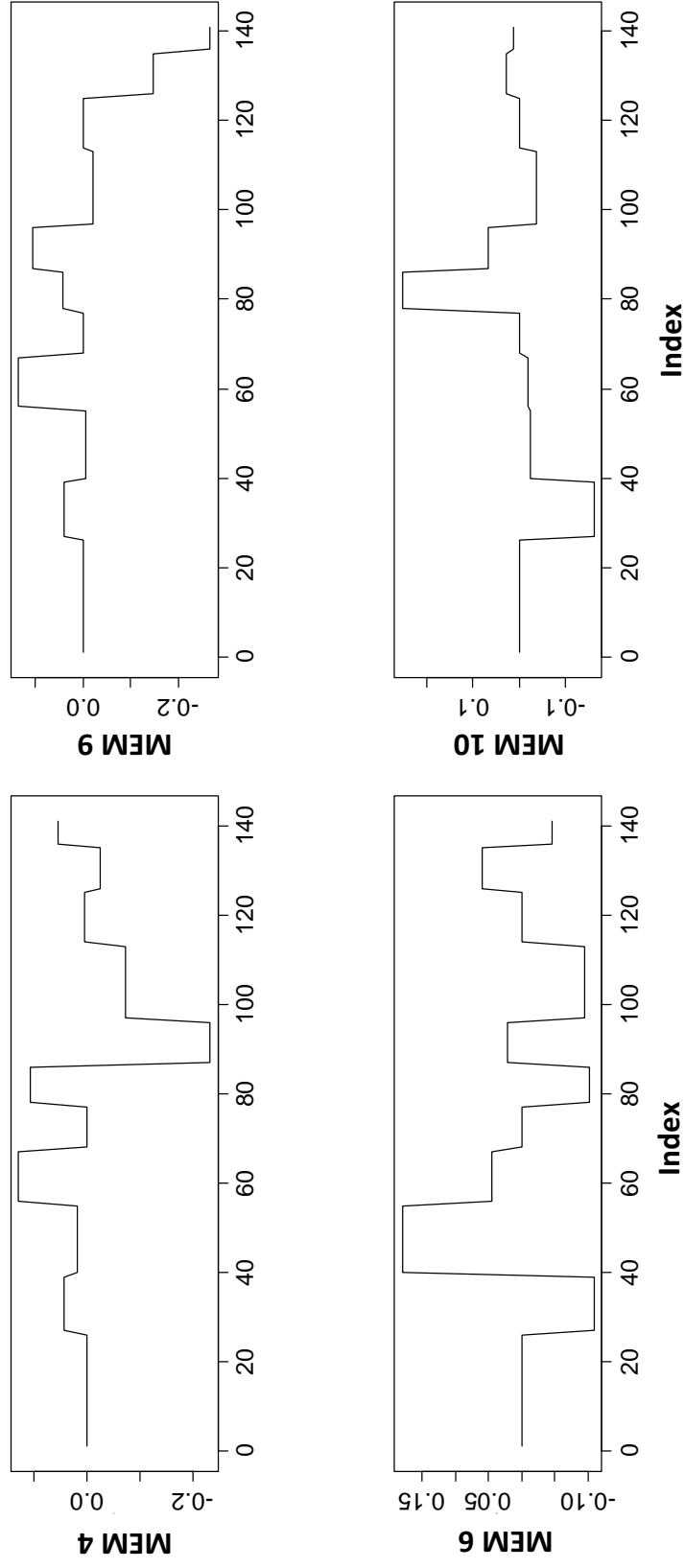
R Development Core Team (2011) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.

## **Appendix S2. Auxiliary description of methods and statistical analyses**

### **1. Spatial patterns and MEM variables**

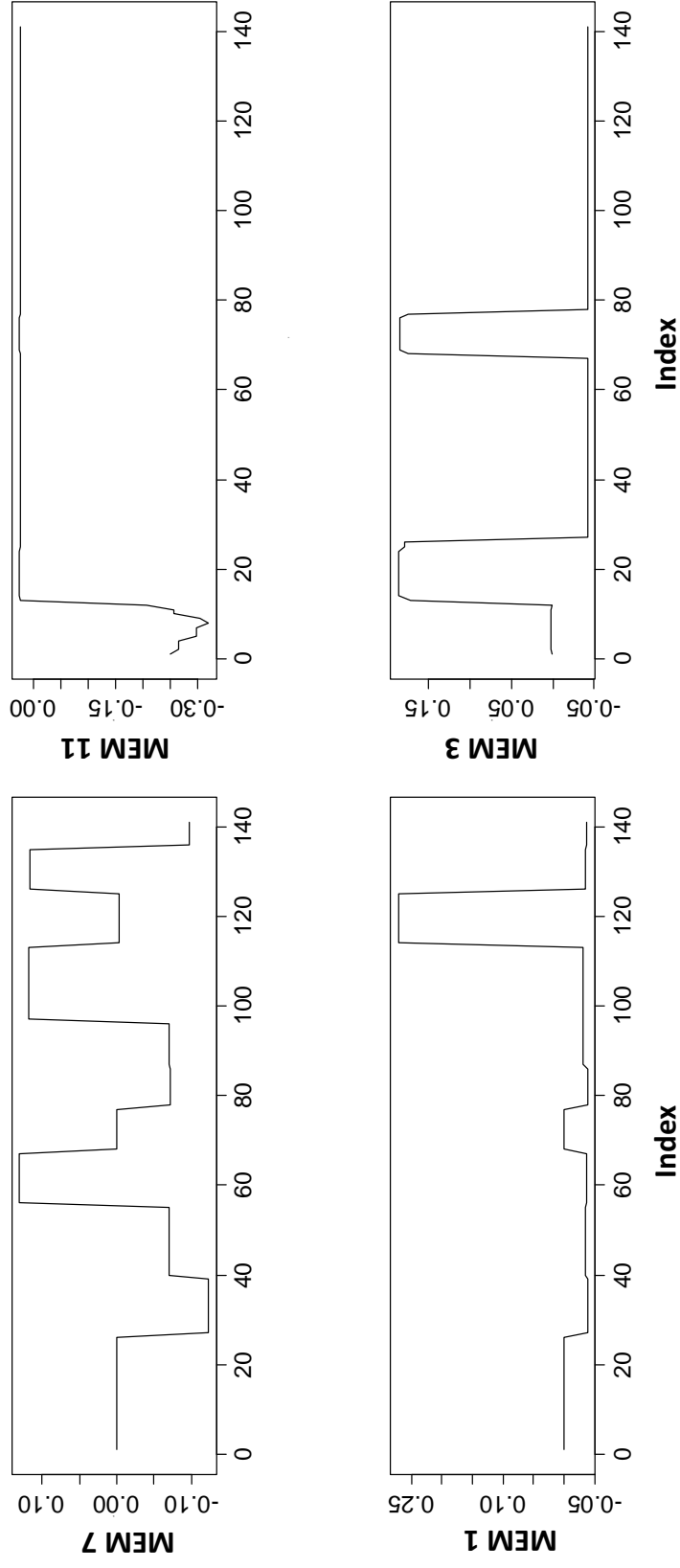
The significant MEM variables presenting broad and fine scale patterns (i) were plotted as a function of each replicate. Thus, patches within localities are plotted in  $y$  axis and significant MEMs (broad and fine scale) in  $x$  axis (see details in main text).

**Fig. S2 – 1.** Broad scale spatial predictors of spider metacommunities. The y axis (index) presents the raw data (replicates – patches – within each locality) of the matrix of coordinates. The values range from south (left: index = 1) to northeast (right: index=140).

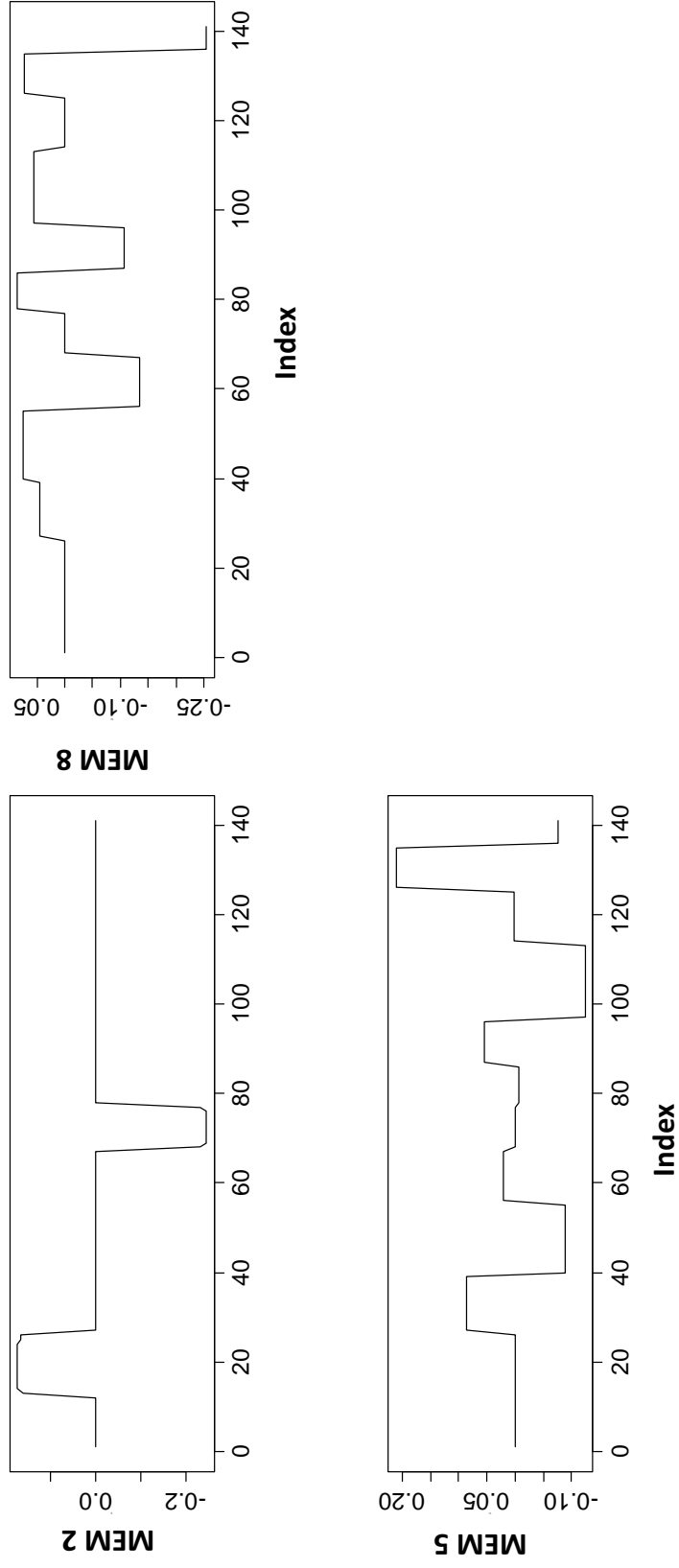




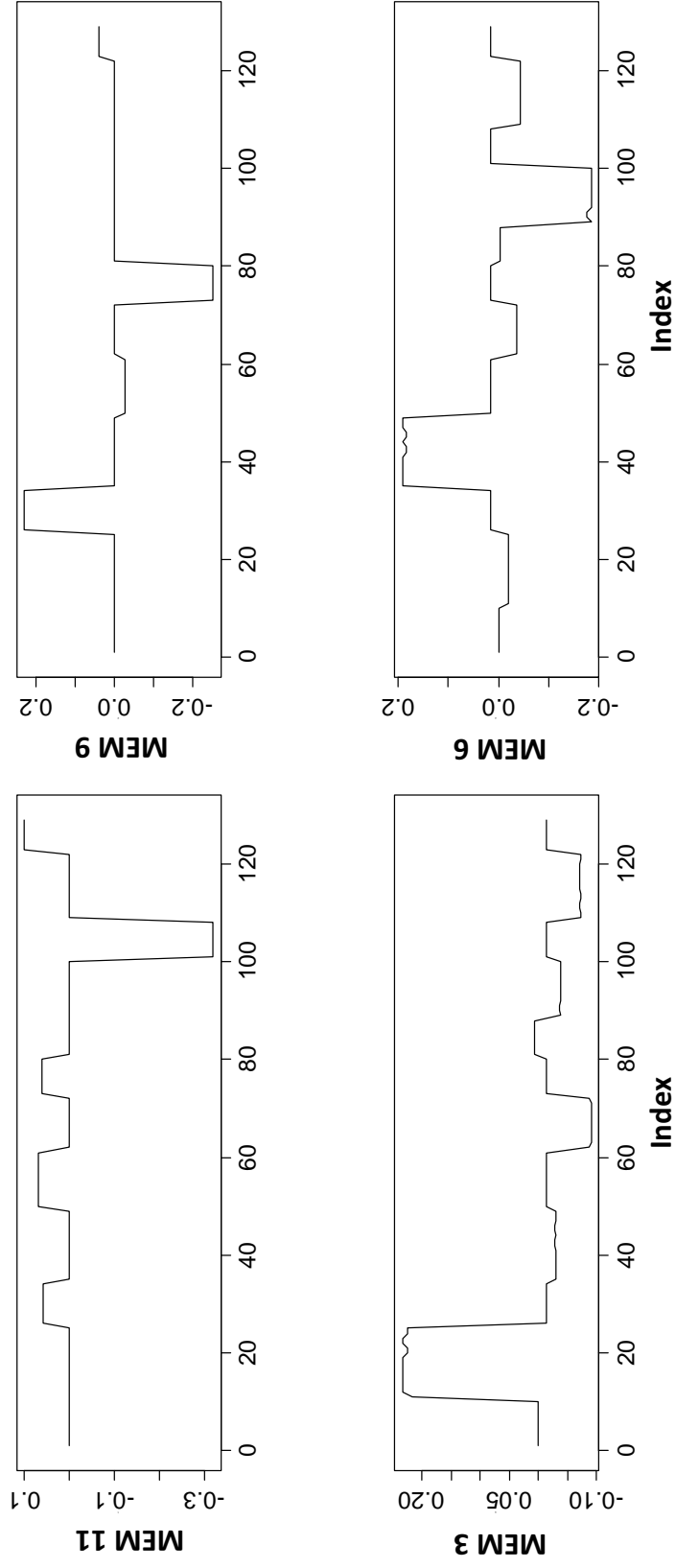
**Fig. S2 – 1.** Broad scale spatial predictors of spider metacommunities. The y axis (index) presents the raw data (replicates – patches – within each locality) of the matrix of coordinates. The values range from south (left: index = 1) to northeast (right: index=140).



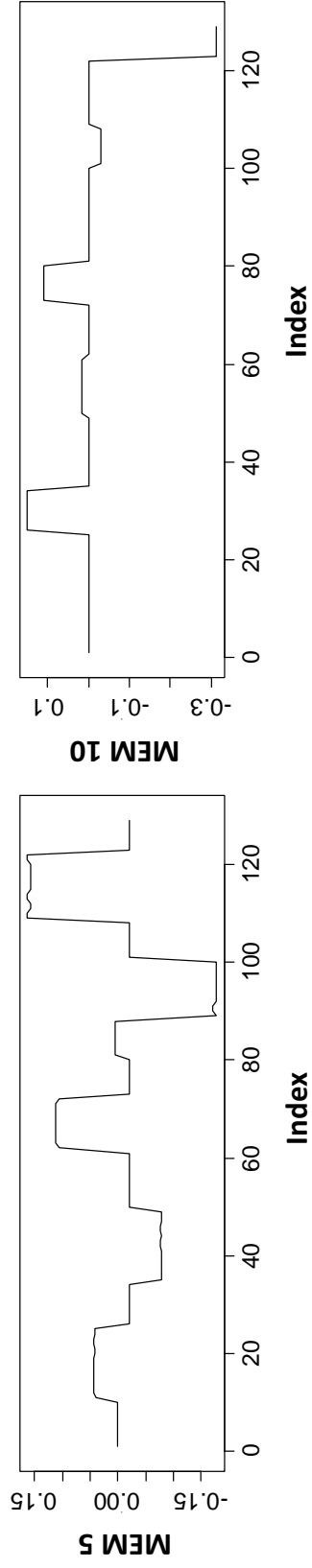
**Fig. S2 – 2.** Fine scale spatial predictors of spider metacommunities. The y axis (index) presents the raw data (replicates – patches – within each locality) of the matrix of coordinates. The values range from south (left: index = 1) to northeast (right: index=140).



**Fig. S2 – 3.** Broad scale spatial predictors of lepidopteran metacommunities. The y axis (index) presents the raw data (replicates – patches – within each locality) of the matrix of coordinates. The values range from south (left: index = 1) to northeast (right: index=140).



**Fig. S2 – 3.** Broad scale spatial predictors of lepidopteran metacommunities. The y axis (index) presents the raw data (replicates – patches – within each locality) of the matrix of coordinates. The values range from south (left: index = 1) to northeast (right: index=140).



## **2. Latitudinal and local scale definition**

The local scale was defined as each locality because they are isolated (i.e., without direct forest connections) from each other. As indicated above, the mean distance among localities is 811 km. Within each locality we calculated the mean richness of spiders (or caterpillars) on each plant species. We then considered the mean value of species richness among five different plant species (20 individuals each) as local species richness (LSR). We considered the whole region from latitudes -12 to -28 (Fig. 1A) as the latitudinal scale. We then defined the total richness (i.e., sum of spiders or caterpillars species sampled on 100 individual plants) of each locality as the regional species richness (RSR). Thus, we used 12 values of regional richness along the latitudinal scale. Each region belongs to the same vegetation type (i.e., *restinga*). We used as response variables in latitudinal-scale analyses species composition and richness.

## **3. Log-ratio method to test the relationship between local richness (LSR) and regional richness (RSR) and the rationale to use this method instead of the traditional method**

To test the relationship between RSR and LSR we used the log-ratio transformation method (hereafter log-ratio method) proposed by Szava-Kovats et al. (2012) to compare RSR and LSR. First, we log transformed the RSR; second, we transformed the LSR by the additive log-ratio function with  $y = \ln(\text{LSR} / (\text{RSR} - \text{LSR}))$ . We then used ordinary least square regression to test the relationship between RSR and LSR. Results of this regression without change in RSR-LSR ratio represent an unsaturated pattern, while significant negative slope presents saturated pattern (Szava-Kovats et al. 2012). We use the log-ratio method instead of the

traditional method (i.e., regressing LSR against its RSR) because the former circumvent some statistical artifacts of the last.

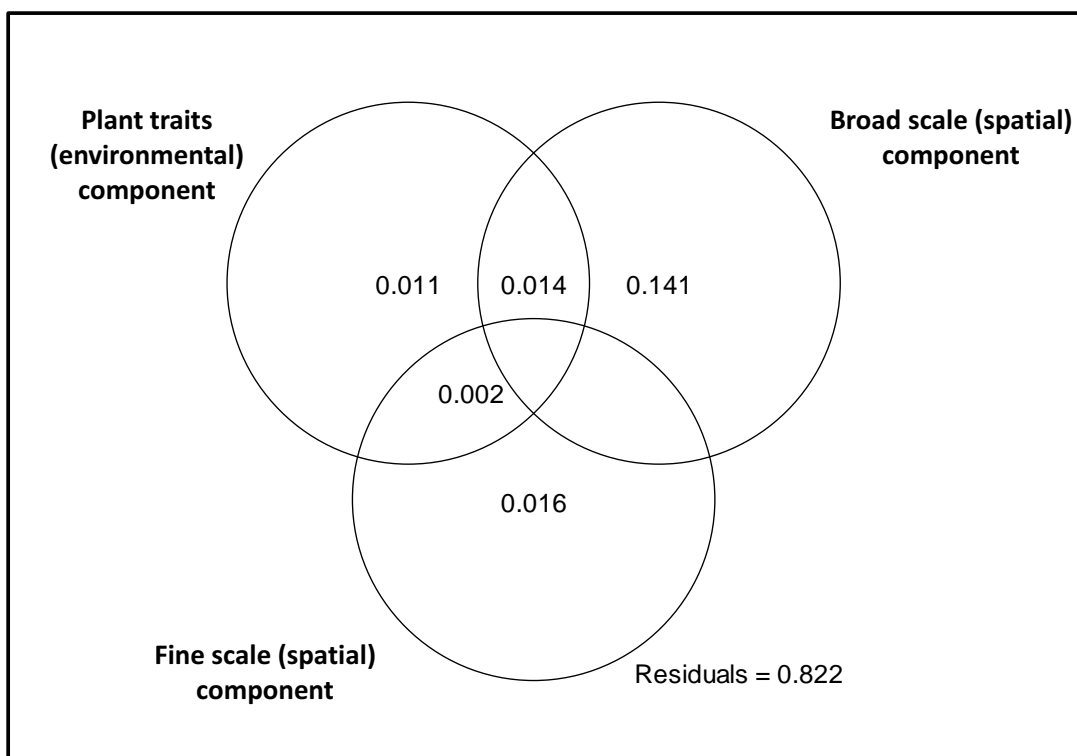
The interpretation of those saturated and unsaturated patterns in the log-ratio method is the same as in the traditional method, i.e., the unsaturated communities are those that local richness is driven solely by regional factors, while in saturated communities local richness is driven by other local (ecological) factors such as species interactions (Srivastava 1999). We did not use the traditional method because it has some statistical artifacts that increase the tendency to linearity (i.e., unsaturated pattern) between LSR and RSR (Srivastava 1999, Szava-Kovats et al. 2012). Conversely, the log-ratio method apparently circumvents some of the potential statistical artifacts of the traditional method (Szava-Kovats et al. 2012).

#### **4. Fractions of the variance partitioning and problems with this method**

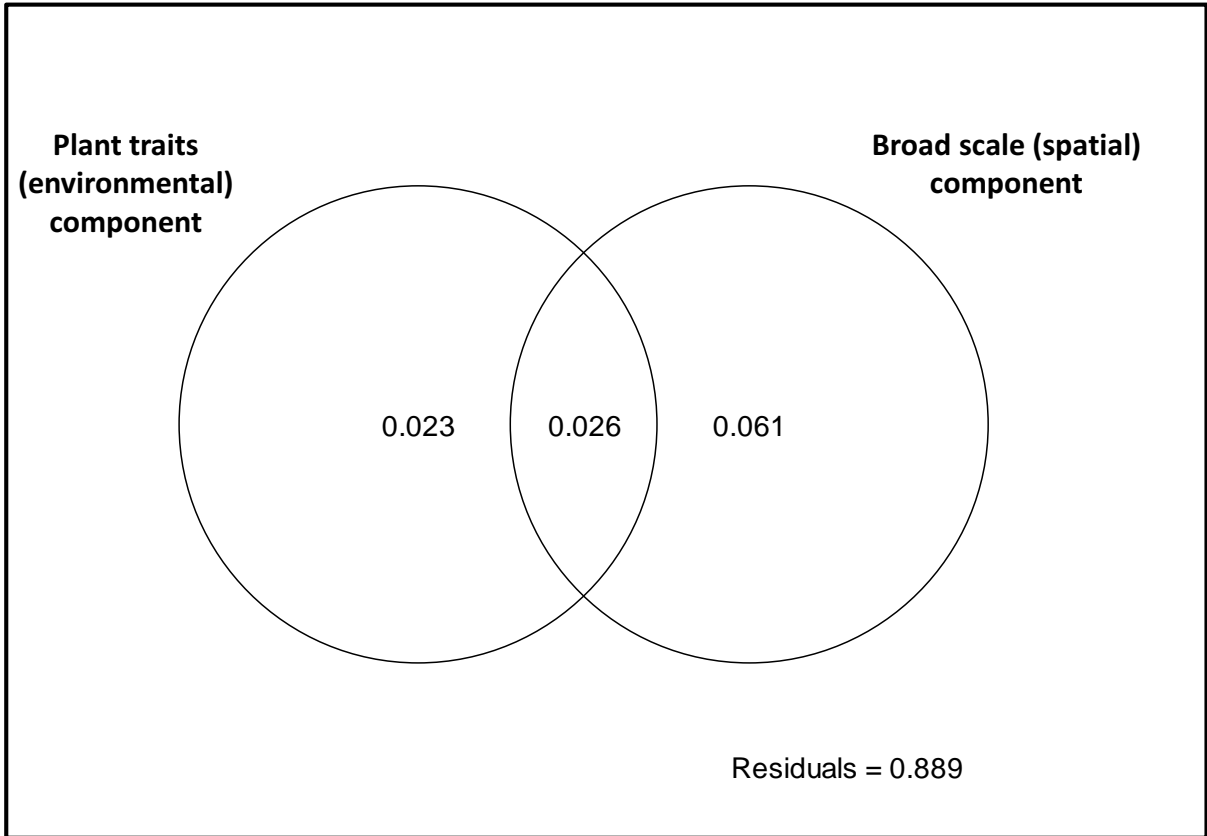
The fractions obtained with the partitioning method were: total explained variation (E+S), environmental (E) and spatial (S) variations. In addition, we obtained pure environmental without the spatial component (E|S), pure spatial without the environmental component (S|E), the shared explanation of environmental and spatial components ( $S \cap E$ ), and the residual variation (Peres-Neto *et al.*, 2006). The variance explained by environmental and spatial (broad and fine) components are plotted below in figures S3-4 and -5.

Despite recent criticism about the accuracy of variance partitioning in disentangling the influence of multiple components in species composition (Gilbert & Bennett, 2010), we believe that our sampling design diminished the problems indicated by these authors. For example, they showed that sampling configuration (e.g., contiguous plots vs. distant plots) affects the estimation of the spatial component (S), and that the linear terms for environmental variables are

insufficient to be tested against the complexity of spatial models. We argue that at the local scale the distance among plots is not dispersal limiting (in fact, the spatial component was not significant; see Results), and at the latitudinal scale, distance among localities is large enough to be detected by the partitioning method (see Results). In addition, by using pre-determined plant traits, the environmental variables (plant traits) were not spatially autocorrelated (see Results). In a recent work, Diniz-Filho *et al.* (2012) showed that the percentage of explained variation of the pure spatial component [c] decreases with the number of non-neutral species in the community. At the latitudinal scale, we showed that the explanation of the pure spatial component was not most important for the composition of arthropods, suggesting that there is indeed a strong local drift of many neutral species associated with each plant trait component.



**Figure S3-4.** Variance partitioning of spider communities (results and *P* values provided in the main text).



**Figure S3-5.** Variance partitioning of lepidopteran communities (results and *P* values provided in the main text).



## References (Appendix S2)

- Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51-68.
- Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical Ecology with R*. Springer, New York.
- Diniz-Filho, J.A.F., Siqueira, T., Padial, A.A., Rangel, T.F., Landeiro, V.L. & Bini, L.M. (2012) Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. *Oikos*, **121**, 201–210.
- Dray, S., Legendre, P. & Peres-Neto, P.R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, **196**, 483-493.
- Gilbert, B. & Bennett, J.R. (2010) Partitioning variation in ecological communities: do the numbers add up? *Journal of Applied Ecology*, **47**, 1071–1082.
- Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, **87**, 2614-2625.
- Szava-Kovats, R.C., Zobel, M., & Pärtel, M. (2012) The local-regional species richness relationship: new perspectives on the null-hypothesis. *Oikos*, **121**, 321-326.

**Appendix S3: Macroclimatic variables used and details of the Principal Components Analysis (PCA) used to control for autocorrelation of those variables.**

We used 11 macroclimatic variables related to temperature and precipitation as predictor variables: (1) annual mean temperature, (2) mean diurnal range (max – min temperature), (3) isothermality (mean diurnal range/temperature annual range), (4) temperature seasonality, (5) maximum temperature of the warmest month, (6) minimum temperature of the coldest month, (7) temperature annual range, (8) annual precipitation, (9) precipitation of the wettest month, (10) precipitation of the driest month, and (11) precipitation seasonality (coefficient of variation) (Hijmans *et al.*, 2005). The variables 1, 3 and 8 present annual trends, while variables 2, 3, 4, 7 and 11, and 5, 6, 9, and 10 present seasonality and extreme environmental factors, respectively (Hijmans *et al.*, 2005). Because the distance among plots in the same locality was not large enough to detect differences in macroclimatic variables at a 1 km<sup>2</sup> resolution, we performed analyses with macroclimatic variables only at the latitudinal scale (see below). Once these bioclimatic variables were strongly autocorrelated, we performed a Principal Component Analysis (PCA) and extracted the first four orthogonal axes (cumulative proportion of 97%) to use as macroclimatic predictor variables (see below). To test the predictions of Jocqué *et al.* (2010) we performed the PCA just with the variables related to climatic variability (seasonality).

## Appendix S4.

**Table S1.** *F* values of the Redundancy analysis (RDA) between species composition and plant traits. To test for the significance of each plant trait we implement 1000 randomizations. We considered tree canopy height (CH), plant biomass (PB), the longer (LLTC) and shorter (SLTC) length of tree canopy as plant level variables, and leaf length (LL), leaf width (LW), distance between the second and third leaf (DBL), and the ratio between leaf width and length (RLL) as leaf level variables. Values of *F* in red mean significant *P* values ( $P < 0.05$ ). The sites were organized in the table from the Northeastern (Praia do Forte or Salvador) to the Southern (Dunas de Joaquina). See Fig. 1 (Pag. 78) for additional geographical details.

Organisms/sites	Plant level				Leaf level				Year
	CH	LLTC	SLTC	PB	LL	LW	HBL	RLL	
<b>Catterpillars</b>									
Praia do Forte	6.098	5.887	-	0.585	-	4.374	1.175	2.585	1.399
Salvador	2.631	1.291	1.084	1.503	-	1.717	0.674	1.289	1.53
Trancoso	1.818	0.985	1.139	1.494	1.219	3.694	0.925	2.423	4.806
Barra Nova	3.888	5.529	-	0.610	1.565	1.479	1.258	1.518	1.292
Setiba	1.652	0.987	1.235	1.166	1.285	-	0.896	1.561	1.348
Praia das Neves	1.775	1.968	0.714	1.041	2.164	2.496	1.767	-	2.445
Iquipari	1.178	1.035	1.112	1.717	1.429	1.475	2.445	0.849	1.221
Massambaba	0.895	1.042	1.442	2.294	-	2.181	1.273	1.944	1.621
Maricá	1.049	1.039	1.862	1.813	2.749	2.257	1.317	0.769	1.178
Ilha do Cardoso	0.613	-	1.365	1.095	1.691	-	3.110	2.377	0.689
Dunas dos Ingleses	1.353	1.225	1.839	1.488	1.186	2.353	1.362	1.731	1.835
Dunas de Joaquina	1.316	0.629	0.859	0.913	-	1.759	1.565	1.460	0.643
<b>Spiders</b>									
Salvador	1.077	1.657	0.659	1.472	-	2.011	0.695	0.888	1.167
Trancoso	2.134	2.282	0.976	1.121	-	1.121	1.624	1.855	1.604
Barra Nova	2.271	-	1.492	1.062	2.888	0.747	1.515	0.641	1.861
Setiba	9.424	-	2.681	0.727	2.813	1.943	1.838	1.228	1.16
Praia das Neves	3.518	4.809	1.988	0.608	-	3.583	1.521	3.511	1.622
Iquipari	1.826	3.235	0.825	1.199	2.902	1.314	1.431	1.950	1.932
Massambaba	2.207	1.264	2.187	0.886	-	1.793	1.326	1.288	1.095
Maricá	1.770	1.268	0.723	0.659	1.466	2.085	1.444	1.094	1.665
Ilha do Cardoso	1.622	1.356	0.877	1.316	-	1.239	1.574	1.111	1.622
Dunas dos Ingleses	3.727	2.202	2.540	0.738	-	4.842	1.927	1.446	1.716
Dunas de Joaquina	3.153	-	1.682	1.125	3.016	2.697	1.543	1.414	1.589

## **ARTIGO 5**

# **[A CRITICAL ANALYSIS OF THE UBIQUITY OF LINEAR LOCAL- REGIONAL SPECIES RICHNESS RELATIONSHIPS]**

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OIKOS (in press)

## **ABSTRACT**

Identifying the relative importance of regional and local processes to local species diversity is a central issue to many questions in basic and applied ecology. One widely-used method is to plot local species richness against its regional richness to infer whether regional or local processes determine local diversity. However, this method increases the tendency to find regional prevalence as suggested by a recent simulation. We reanalyzed studies in the literature with an unbiased method and found no prevalence of either regional or local processes. In addition, almost 40% of the studies and 50% of the ecology textbook examples using the traditional method were misclassified. Our findings reinforce the need of alternative, novel tools identified by for instance metacommunity theory to go beyond the studies of local-regional relationships in the ecological literature that focus on the interdependence of regional and local processes.

## **Introduction**

Since the early development of ecology as a discipline, ecologists have been interested in explaining the processes driving local community richness (Elton 1946, Hutchinson 1959, MacArthur 1965, Ricklefs 1987). This interest started by focusing on local interactions among coexisting species and has been changing to a regional-based approach that considers biogeographical, evolutionary and historical processes as drivers of local richness (Ricklefs 1987, Huston 1999, Srivastava 1999, Harrison and Cornell 2008, Vellend 2010). Some proponents of the regional-historical viewpoint argue that the distribution of local communities in a given point is idiosyncratic and that a more predictive theory should consider the ecogeographic distribution of species throughout the region (Ricklefs 1987, 2004, 2008b). Whether processes acting at regional or local scales predominantly determine local community composition is still subject to much debate in the literature (Ricklefs 1987, Cornell and Lawton 1992, Shurin and Srivastava 2005, Harrison and Cornell 2008, Vellend 2010; but see Cottenie 2005), with important implications for ecological theory and conservation (Huston 1999, Srivastava 1999, Harrison and Cornell 2008, Vellend 2010).

To test the relative importance of regional and local processes, the traditional method consists of plotting local species richness (LSR) against its regional species richness (RSR) (Cornell and Lawton 1992, Srivastava 1999, Hillebrand and Blenckner 2002). When regional processes control LSR, this method predicts that communities will be unsaturated with species, since adding more species to the regional species pool will result in an increase in LSR. On the other hand, when local interactions limit local richness independent of the RSR, communities should be saturated with species and LSR will approach an upper asymptote with increasing RSR (Fig. 1, Ricklefs 1987, Cornell and Lawton 1992, Srivastava 1999).

However, there has been several types of criticisms of LSR-RSR plots to assess the relative roles of regional *versus* local processes. The main criticism is that even in communities under strong local process control (e.g., competition), linear relationships between RSR and LSR can be found (Fox et al. 2000, Loreau 2000, Shurin et al. 2000, Hillebrand 2005, Fox and Srivastava 2006). For example, several studies have found that ‘unsaturated’ zooplankton communities are strongly controlled by local interactions (Shurin et al. 2000), which demonstrate the limited applicability in inferring processes from regressions between LSR-RSR (Shurin et al. 2000, Shurin and Srivastava 2005, Hillebrand and Blenckner 2002, Szava-Kovats et al. 2012). In addition, estimates of LSR and RSR are generally not independent (Loreau et al. 2000), which also increases the predominance of linear relationships, especially in cases where local scale is too large compared to the regional scale (Hillebrand and Blenckner 2002, Shurin and Srivastava 2005). Other criticisms pointed out that the traditional method is sensitive to issues of pseudoreplication, the arbitrary choice of local and regional area, autocorrelation, and body size of the organisms (Griffiths 1999, Srivastava 1999, Loreau 2000, Hillebrand and Blenckner 2002, He et al. 2005, Hillebrand 2005, Szava-Kovats et al. 2012).

The traditional method used to distinguish between unsaturated and saturated communities compares the best fit (generally the largest  $F$ -statistic) of linear and polynomial regression models (Ricklefs 1987, Cornell and Lawton 1992, Srivastava 1999). If the linear regression presents the best fit to the data, the community is considered unsaturated. However, if the polynomial regression presents the best fit, the community is considered saturated (Srivastava 1999), as shown in Fig. 1. It has been suggested that the linear and polynomial regressions used to distinguish between saturated and unsaturated communities may actually have insufficient power to differentiate both communities (Hillebrand and Blenckner 2002). In

addition, the traditional method use a constrained operational space, which increases the correlation between the components to be compared (Szava-Kovats et al. 2012).

To circumvent the statistical artifacts of the traditional method, Szava-Kovats et al. (2012) proposed a method based on log-ratio models (Fig. 1), that uses an unconstrained operational space. This unconstrained behavior enables RSR and LSR to vary independently without correlation (Szava-Kovats et al. 2012). The authors argued that the log-ratio method has the following methodological improvements: (i) the elimination of autocorrelation and spurious correlation, (ii) a null-hypothesis for species saturation, (iii) the use of a single model to distinguish for linearity or non-linearity, and (iv) the mitigation of the effect of arbitrary selection of local and regional area (Szava-Kovats et al. 2012). They compared their model with the traditional model by simulating datasets with different degrees of curvature and LSR:RSR ratio. The results indicated that the log-ratio method successfully reproduced slopes (non-linearity), while the traditional method did not detect non-linearity in the majority of simulations, suggesting that their new method is unbiased and less sensitive than the traditional method.

The advantages of the log-ratio method relative to the traditional method have at least two major implications to studies testing local-regional species richness relationships. First, since the statistical artifacts of the traditional method increase the tendency to linearity between LSR and RSR (Szava-Kovats et al. 2012), studies using this method will be biased towards the conclusion that regional (i.e. historical) processes are the main forces driving local community structure (Ricklefs 1987, 2008b, Cornell and Lawton 1992). Second, the possible misclassifications of studies with the traditional method can lead to incorrect conclusions about the importance of local and regional processes in the ecological literature. The purpose of this paper is not to provide an extensive review to those drawbacks (see, e.g., Cornell and Lawton



1992, Caley and Schluter 1997, Srivastava 1999, Hillebrand and Blenckner 2002, Shurin and Srivastava 2005), but instead we aimed to 1) re-evaluate previous conclusions (i.e., the dominance of unsaturated patterns in the literature) in light of a new, unbiased statistical method, 2) evaluate the potential implications of the statistical drawbacks that the traditional method has to ecology and to studies interested in local-regional species richness relationships, and 3) discuss the interpretative problems of regressing local vs. regional richness to infer processes driving community structure.

## **Methods**

We searched studies in the database of Web of Science (isiknowledge.com) and Google Scholar (scholar.google.com.br/). We used the keywords “local richness AND regional richness AND satur\*”, “local richness AND regional richness AND unsatur\*”, “local diversity AND regional diversity AND satur\*”, “local diversity AND regional diversity AND unsatur\*”. In addition, we examined the references of the main reviews in the topic (Cornell and Lawton 1992, Caley and Schluter 1997, Srivastava 1999, Hillebrand and Blenckner 2002), as well as the articles that cited these four reviews in the Web of Science database. We found 47 studies (one unpublished) that analyzed 113 ecological communities (Table S1). We consider as a metacommunity each data set (provided as figures) in which authors analyzed the relationship between local (LSR) and regional species richness (RSR) with the traditional method.

The inclusion criterion was that the studies should use the traditional method to test for species saturation, i.e., the regression of local species richness (LSR; dependent variable) against its regional species richness (RSR; explanatory variable) (Srivastava 1999). In addition, the plots of LSR-RSR (as in Fig. 1) should be provided. We also obtained predictor variables of the

organisms and system of each study, such as upper taxa (i.e., Kingdom, Phylum or Subphylum, such as cnidarians, invertebrates, plants, protozoan, or vertebrates), trophic position (autotrophs, detritivores, herbivores, predators, saprophages, or suspension), thermoregulation (ecto or homeothermic), adult dispersal type (motile or sessile), realm (aquatic or terrestrial), hemisphere (Northern, Southern or both), study design (experimental, observational, or compiled data set), and scale (small, medium, large, continental, or worldwide). Scale was defined as: (i) “small ” if the studies were performed within the same biome and the distance among their replicates was smaller 500 km; (ii) “medium” as the studies performed within the same biome, but with the distance among their replicates higher than 500 km; (iii) “large ” as the studies performed in different biomes, but that was not as large as the continental scale; (iv) “continental” included studies that presented data in the whole continent; and the (v) “worldwide” scale were studies that collected data in most continents. We obtained those variables because it has been hypothesized that some predictor variables could explain whether some communities are predominantly saturated or unsaturated (e.g., Cornell and Harrison 2013).

We used the R-language environment (R Development Core Team 2012) and the package `digitize` (Poisot 2010) to extract data sets from figures. We tested the reliability of data extraction by comparing our scatterplots with the extracted LSR and RSR values to the original figures. We then regressed the original values against the extracted ones and found  $R^2$  values higher than 0.98. We did not use studies that applied log-log regressions ( $n = 2$ ), residual local richness vs. regional richness ( $n = 4$ ), or other methods ( $n = 4$ ). In addition, we limited our re-analysis to those studies with more than five replicates ( $n = 2$  studies with less than five replicates). Thus, we re-analyzed 113 communities (90.4%) from the 125 found.

We first analyzed the extracted data with the traditional approach by regressing the local species richness ( $y$  axis) against the regional species richness ( $x$  axis). We then reanalyzed the same data set with the log-ratio method proposed by Szava-Kovats et al. (2012): first, the regional richness is partitioned in a component of  $\alpha$ -diversity (LSR) and of  $\beta$ -diversity (RSR – LSR). Then, these components are transformed by the additive log-ratio model  $y = \ln(\text{LSR} / (\text{RSR} - \text{LSR}))$ . The relationship between LSR and RSR is tested by regressing the  $y$  axis ( $\ln(\text{LSR} / (\text{RSR} - \text{LSR}))$ ) on  $\ln(\text{RSR})$  with an ordinary least square regression (Szava-Kovats et al. 2012). The transformations performed by the log-ratio method compared to the conventional  $x$  (RSR) and  $y$  (LSR) axes change the traditional interpretation of saturation (non-linear) and unsaturation (linear) relationships. However, Szava-Kovats et al. (2012) proposed an inverse transformation to compare the result of the log-ratio method with the traditional method: regression results with negative slopes in the log-ratio method will have a saturated trend in the traditional method, while regression results with non-significant slopes will have a linear trend in the traditional method (Fig. 1). Although the  $x$  and  $y$  axis are different between the two methods, it is still possible to re-transform the data in order to access the traditional interpretations of saturation and unsaturation (Szava-Kovats et al. 2012).

Considering that the traditional method has several drawbacks (see Srivastava 1999, Hillebrand and Blenckner 2002, Hillebrand 2005, Szava-Kovats et al. 2012), we consider as “misclassified” those metacommunities which were classified as either saturated or unsaturated in the traditional method, but had the opposite classification with the unbiased log-ratio method. We used generalized linear models (GLM) with binomial distribution to test if the misclassifications are associated to the predictor variables (system features and organism traits). We used GLMs to test if the predictor variables to explain saturated or unsaturated patterns.

## Results and Discussion

Seventy percent of the studies found unsaturated communities, while 30% found saturated communities with the traditional method ( $\chi^2 = 16.66$ ,  $P < 0.0001$ ). The bias toward linearity was pervasive for vertebrates (which 85% of the studies found unsaturated patterns) and plants (75%), for observational (78%) and continental-scale studies (87%), and for both aquatic (73%) and terrestrial realms (68%). Thus, as expected, most studies using the traditional method concluded that regional processes are the main drivers of local richness (Fig. 2, Table S2). The prevalence of unsaturated patterns in the current literature has added more focus on community ecology as a regional/historical science (Ricklefs 1987, 2004, 2008b, Cornell and Lawton 1992). However, we reanalyzed those studies with the log-ratio method and found no prevalence of either unsaturated (53.1% of the results) or saturated (46.9%) communities ( $\chi^2 = 0.44$ ,  $P = 0.501$ ) (Fig. 2). There was no prevalence of one specific pattern when we compared upper taxa, trophic position, thermoregulation, adult dispersal type, realm, hemisphere, study design and scale (Table S2). These results challenge the apparent dominance of unsaturated communities in the literature (Ricklefs 1987, Cornell and Lawton 1992) and emphasize that local and regional processes are probably interacting to determine both local and regional diversity (e.g., Lewinsohn 1991, Lortie et al. 2004, Brooker et al. 2009, Burgess et al. 2010). This view has been voiced in recent studies showing that local processes affect broad-scale ecological patterns (e.g., Greve et al. 2012, Lessard et al. 2012). Furthermore, there has been no predictor variable (e.g., organism's trophic position, realm) that potentially explain saturated or unsaturated patterns (but see explanations of Cornell and Harrison 2013 for a different point of view).

By comparing the results between the traditional and log-ratio methods we found that 38% of the communities that were considered either unsaturated or saturated by the traditional

method were misclassified (Fig. 2) (Supporting Information). Indeed, this misclassification was not related to any predictor variable, such as realm, organism trophic position, thermoregulation, hemisphere, study design, or scale. Besides the bias toward linearity (as shown in our study and simulations of Szava-Kovats et al. 2012), such misclassification obtained in studies using the traditional method has potential negative effects on the current ecological literature, because those biased conclusions have been drawn in almost 40% of the studies (Table S1, S2: Supporting Information). Thus, much of the current ecological thinking concerning local-regional relationships may have been rooted in weak or biased evidence. For instance, Ricklefs (1987) claimed that ecologists should use a regional/historical perspective to resolve many issues in community ecology (see also Ricklefs 2004, 2008b). One of his arguments was that “local diversity bears a demonstrable dependence upon regional diversity”; he used the traditional method and found an unsaturated pattern for Caribbean bird communities. However, when we reanalyzed this data set a saturated pattern was found (Supporting Information). The consequences of the unsaturation bias are also evident in the information brought by four classical ecology textbooks (Ricklefs 1999, Begon et al. 2006, Krebs 2008, Ricklefs 2008a) and has been used in a recent important review of ecological theory (Vellend 2010; see also Cornell and Harrison 2013); 50% of the examples of LSR-RSR plots were misclassified. The statistical drawbacks were seldom considered in those textbooks and the general idea related to LSR-RSR relationships is that unsaturated patterns are the most pervasive in ecological communities. For instance, one of the “Key Concepts” in Krebs (2008) is “Local species richness tends to increase linearly with regional species richness, suggesting that local communities are never saturated with species” (p. 457). The content of four of the most widespread ecology textbooks reinforces

the need of new paradigms concerning the relative importance of local and regional processes in structuring communities.

### **Conclusion and future directions**

While the traditional LSR-RSR relationships have been instrumental in ecology theory to recognize the joint importance of local and regional processes (Harrison and Cornell 2008), Srivastava (1999) also stated that “it is evidently easy to reach the wrong conclusion about species saturation by analyzing local-regional richness plots”. Our review supports this assertion and the conclusions of several studies (e.g., He et al. 2005, Hillebrand 2005, Shurin and Srivastava 2005) that the results of the traditional method should be treated with caution. Moreover, we also removed another argument in favor of using local-regional richness plots: its apparent ubiquity, which at first glance would suggest that important processes are potentially responsible for these results. By reanalyzing 113 LSR-RSR plots from independent studies using an unbiased statistical method (log-ratio transformations), we conclude that almost 40% of the studies that used the traditional method reached wrong conclusions and that neither unsaturated nor saturated pattern are predominant in ecological communities. We argue that instead of a unidirectional effect of regional process cascading to local communities, both regional and local processes interactively influence each other (e.g., Burgess et al. 2010).

Based on our re-analysis and criticisms of previous studies (e.g., Loreau 2000, Shurin et al. 2000, He et al. 2005, Hillebrand 2005), it is not likely that studies of LSR-RSR relationships using the traditional method enable an unbiased test of relative importance of local and regional processes. Maybe more importantly, even when using a potential improved and unbiased method, the main concern about local-regional species richness plots makes the inference of

ecological processes unwarranted (Shurin et al. 2000, Hillebrand and Blenckner 2002, He et al. 2005). We speculate that the main reason for the lack of reliable conclusions from LRS-RSR relationships is actually caused by the not including relevant information on these local and regional processes into the analyses. We suggest that, instead of focusing solely in local-regional richness plots to infer processes from patterns, additional approaches should be used to really understand the drivers of local community structure. Metacommunity theory provides a much more powerful framework to disentangle both local and regional influences on local community structure (Cottenie 2005, Holyoak et al. 2005, Harrison and Cornell 2008; see also Lewinsohn 1991). For instance, Cottenie (2005) provided one way to test these metacommunity predictions with observational data with actual information on local environmental and dispersal processes included in the analyses. While the statistical issues surrounding this methodology are still hotly debated (see e.g. Gilbert and Bennett 2010), this test is flexible enough to add more specific information on environmental and dispersal variables and thus illustrates that metacommunity theory and its applications are a powerful approach to study and model local and regional dispersal processes (Logue et al. 2011).

Interestingly, recent theoretical developments on the evolutionary aspects of metacommunity theory (Jocqué et al. 2010) illustrated the potentially important reciprocal relationships between local and regional diversity. They thus proposed that conceptually the axes in LRS-RSR relationships can also be flipped around. Local processes (for instance, trade-offs between ecological specialization and dispersal) could be an important driver of regional diversity patterns. To incorporate evolutionary aspects of regional processes into metacommunity theory is the next big step in this research program in community ecology. Peres-Neto et al. (2012), for instance, suggest one way to use evolutionary information when

studying spatial and environmental processes. Their proposed methodology is obviously more data intensive and computationally demanding compared to LSR-RSR plots, but the inferences will be much richer and more detailed as well. While these ideas are currently actively developed, we hope that they will soon make their way into standard ecology textbooks, and replace the potential biased methods and concepts that are still part of the standard ecological curriculum.

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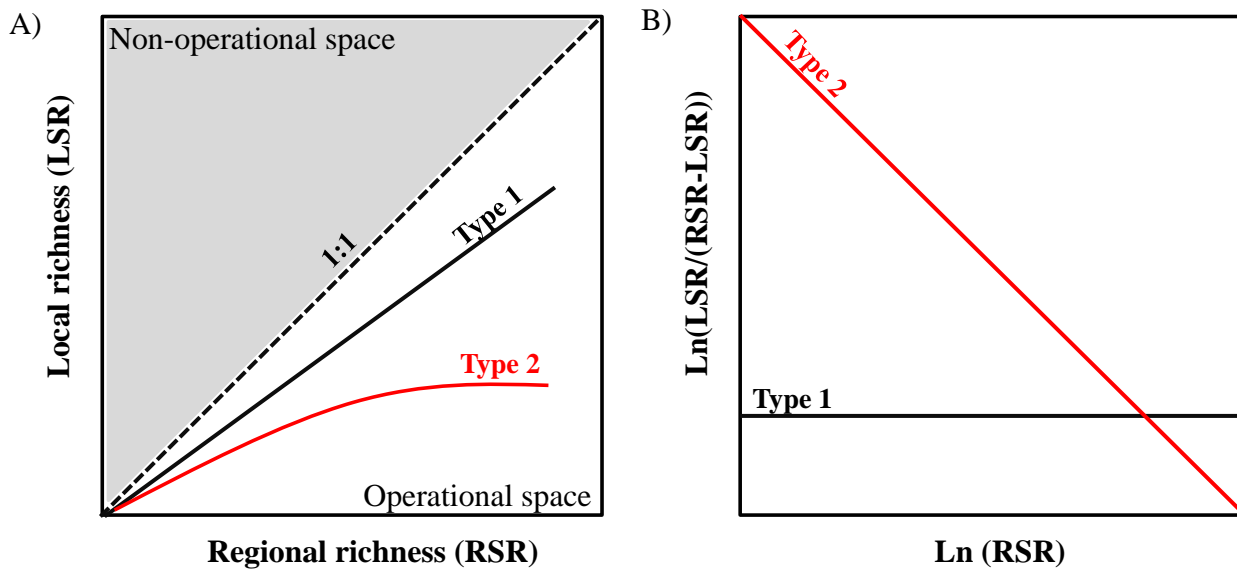


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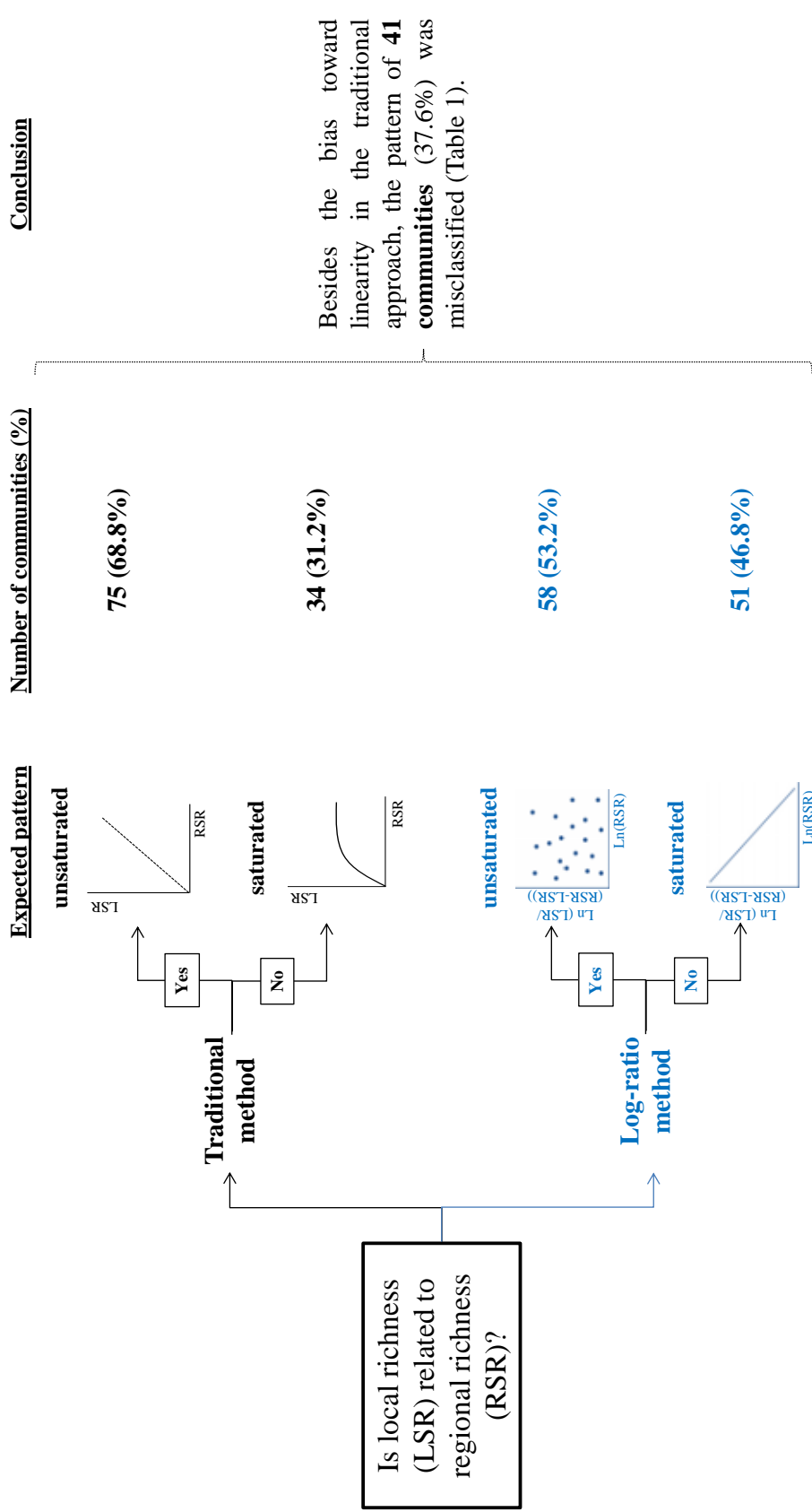
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**Figure 1.** Theoretical curves obtained by regressing local versus regional species richness in the traditional method (A) and regressing  $\ln(\text{RSR})$  against  $\ln(\text{LSR}/(\text{RSR}-\text{LSR}))$  in the log-ratio model (B). In communities fitted by Type 1 models (unsaturated), local richness is dependent of the regional richness and other local ecological factors are weak or absent. In communities fitted by Type 2 models (saturated), local richness is independent of the regional richness, which means that local biotic interactions as well as other ecological factors limit local species richness. The transformations performed by the log-ratio method compared to the conventional  $x$  (RSR) and  $y$  (LSR) axes change the traditional interpretation of saturation (non-linear) and unsaturation (linear) relationships (1B). However, Szava-Kovats et al. (2012) proposed an inverse transformation so that one can compare the result of the log-ratio method with the traditional method. The 1:1 line presents the boundary in which local richness equals regional richness. In the traditional method, values above and below this line present, respectively, non-operational and operational spaces. In the log-ratio method there is no operational space

(see text for details about the operational space). Adapted from Griffiths (1997) and Szava-Kovats et al. (2012).



**Figure 2.** Comparison of the results of local-regional richness plots of 47 studies (113 metacommunities) that used the traditional method with the results reanalyzed with the log-ratio method.

## **Supporting Information (Glossary, Tables S1 and S2)**

### **A critical analysis of the ubiquity of linear local-regional species richness relationships**

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**Table S1** – provided as a .xlsx file. Can be accessed at <[http://bit.ly/tableS1\\_cap3](http://bit.ly/tableS1_cap3)>



## 1. GLOSSARY

**Local scale:** refers to small scales in which predation and competition (and other ecological processes) predominate (Cornell and Lawton 1992).

**Regional scale:** refers to processes such as dispersal and speciation that act at large (biogeographic) scales (Cornell and Lawton 1992).

**Local species richness (LSR):** is the number of species in an area small enough that all the species could interact with each other along the ecological time (Srivastava 1999). “Local” refers to the spatial scale in which ecological processes such as predation, parasitism, and competition act. The scale of local habitat depends on the taxon biology (Cornell and Lawton 1992).

**Regional species richness (RSR):** is the number of species in a region (i.e., the regional species pool). “Regional” refers to the spatial scale that all species are able to disperse to the local communities (Hillebrand and Blenckner 2002).

**Unsaturated communities (Type 1 curve):** When LSR increases positively and linearly with RSR. This pattern, called “regional enrichment” or “proportional sampling”, suggests that local interactions are weak or absent (Cornell and Lawton 1992). This definition is based on the traditional method (Supplementary Text 1.2).

**Saturated communities (Type 2 curve):** Local ecological processes such as predation, competition, and niche packing may limit the number of coexisting species. Thus, even if RSR increases, the LSR has an upper limit (Fig. 1, Supplementary Text 1.2). This definition is based on the traditional method (Supplementary Text 1.2).

**Table S2.** Comparison of the results obtained by using the traditional and log-ratio methods. We compared the prevalence of either saturated or unsaturated pattern with a chi-square. The asterisks denote statistical significance ( $P < 0.05$ ) and thus represent the most common pattern. There is no prevalence of either saturated or unsaturated pattern by using the log-ratio method.

	<b>Traditional method</b>		<b>Log-ratio method</b>	
	saturated	unsaturated	saturated	unsaturated
<b>Upper taxa</b>				
cnidarians	0	3	0	3
invertebrates	22	30	25	27
plants	7	20*	15	12
protozoan	1	1	0	2
variety	0	2	0	2
vertebrates	4	23*	13	14
<b>Trophic position</b>				
autotrophs	8	21*	15	14
detritivores	2	3	1	4
herbivores	4	9	5	8
parasitoids	0	3	0	3
predators	6	5	5	6
saprophagous	0	1	1	0
suspension	0	3	0	3
variety	14	34*	26	22
<b>Thermoregulation</b>				
ectothermic	30	66*	44	52
homeothermic	4	11	9	6
variety	0	2	0	2
<b>Adult dispersal type</b>				
motile	26	56*	39	43
sessile	8	21*	14	15
variety	0	2	0	2
<b>Realm</b>				
aquatic	10	27*	15	22
terrestrial	24	52*	38	38
<b>Hemisphere</b>				
both	1	14*	4	11
North	27	49*	38	38
South	6	16*	11	11

<b>Study design</b>				
compiled dataset	10	27*	16	21
experimental	14	17	17	14
observational	10	35*	20	25
<b>Scale</b>				
continental	2	13*	4	11
large	3	13*	9	7
medium	4	19*	10	13
small	21	29*	24	26
worldwide	4	5	6	3

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## SÍNTESE

### 1. Artrópodes sobre plantas: aspectos ecológicos

Mostramos que a mudanças na arquitetura das plantas têm papel fundamental na distribuição de artrópodes que vivem na vegetação. Mesmo comparando comunidades em regiões diferentes (e com espécies de plantas diferentes), a arquitetura da planta tem forte efeito sobre a substituição de espécies. Em geral, a arquitetura das plantas determina a formação de comunidades compartimentalizadas (i.e., comunidades de artrópodes exclusivas de cada arquitetura). Um fator importante a ser considerado é a história de vida e o grupo trófico dos artrópodes. Como esses grupos têm diferentes requerimentos ecológicos, é importante considerar essas diferenças em modelos teóricos, por exemplo.

Mostramos também que processos ambientais e espaciais atuam conjuntamente (apesar de que atuam em diferentes escalas) na montagem de comunidades de aranhas e lepidópteros. Sugerimos que os debates entre proponentes da teoria neutra e do nicho deveriam considerar um cenário em que ambas explicam a distribuição de espécies, apesar de que a importância relativa deve mudar com a escala.

Além disso, reavaliamos os estudos que testaram a relação entre riqueza regional e local. Antes do nosso estudo a conclusão geral presente na literatura é de que comunidades são principalmente estruturadas por processos regionais e que aparentemente interações em escala local não contribuíam para padrões em ampla escala. Porém, ao utilizar um método potencialmente não enviesado não achamos diferenças no número de estudos suportando processos regionais ou locais como determinantes para a riqueza local de espécies.

## **2. Artrópodes sobre plantas: aspectos evolutivos**

Uma vez que plantas com arquiteturas distintas geram comunidades compartimentalizadas de artrópodes, entender se ao longo do tempo essa compartimentalização pode influenciar a evolução das espécies pode nos auxiliar a compreender melhor a associação entre artrópodes e plantas.

Encontramos que aranhas que ocorrem em bromélias são maiores e mais achatadas do que aranhas que ocorrem em plantas ao redor de bromélias. A diferença entre o tamanho das aranhas entre as plantas foi explicada pela informação filogenética das aranhas. Porém, o achatamento dessas aranhas parece ser uma adaptação para a vida em bromélias, uma vez que essas plantas possuem espaços muito pequenos entre folhas e, desse modo, organismos achatados seriam favorecidos.

Ainda, verificamos que o atributo das aranhas está estruturado de maneira heterogênea na árvore filogenética (i.e., presença de sinal filogenético). Porém, a filogenia aparentemente não é o único preditor da diversidade de atributos das aranhas. Desse modo, a arquitetura da planta se mostrou novamente como um forte filtro para atributos de aranhas. Além disso, a localidade de ocorrência das plantas também funcionou como um filtro de atributos. Por fim, mostramos que aranhas que constroem teia têm atributos mais conservados e aranhas errantes atributos mais lábeis, sugerindo a utilização de teia tem papel fundamental na evolução de aranhas.

Em linhas gerais, argumentamos que a história de vida, fatores ecológicos locais e processos em escala ampla como biogeográficos e evolutivos provavelmente interagem para determinar a montagem das comunidades e a evolução dos atributos das espécies.

### **Custos estimados para amostragem dos artrópodes**

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Os custos acima não incluem despesas com taxonomistas, técnicos e auxiliares que voluntariamente identificaram todos os artrópodes aqui coletados: 172 baratas adultas distribuídas em 32 espécies, 856 formigas distribuídas em 48 espécies, 766 lagartas de Lepidoptera distribuídas em 161 espécies, e 1122 aranhas adultas distribuídas em 172 espécies. O valor de R\$ 1,19 é menor do que o real, uma vez que não foram incluídas despesas com taxonomistas e de triagem do material coletado em laboratório.