UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

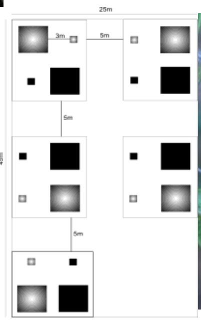
Estrutura e Composição de Assembleias de Aranhas em Manchas de Vegetação na Porção Austral da Mata Atlântica

RONEI BALDISSERA

Tese de Doutorado

Orientação:

Profa. Dra. Sandra Maria Hartz



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Beta Diversidade, Seleção de Microhábitats e Taxas de Colonização

RONEI BALDISSERA

Tese apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Sul como um dos pré-requesitos para obtenção do título de Doutor em Ciências – ênfase em Ecologia

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RESUMO

A fragmentação de hábitats é um dos fatores mais importantes que afetam a biodiversidade em nível mundial. Os estudos da fragmentação, nos seus inícios, baseavam-se nas premissas e predições da Teoria de Biogeografia de Ilhas, a qual procura explicar a diversidade em ilhas oceânicas pelo balanço de colonizações e extinções baseadas nos seus tamanhos e isolamentos. A partir do início do século, houve o desenvolvimento do conceito de metacomunidades, juntamente com um olhar sobre o mosaico de manchas na paisagem, como um conjunto de comunidades locais ligadas pela dispersão de espécies que tem o potencial de interagir. Esse conceito expande a visão da ecologia de comunidades do nível local para diferentes escalas e considera, simplificadamente, que existem quatro tipos de metacomunidades: dinâmica de manchas, seleção de espécies, efeito de massa e neutralidade. Esses quatro modelos assumem diferenças na resposta dos atributos funcionais das espécies, desde a equivalência ecológica até forte capacidade competitiva.

Esta tese teve como objetivo geral “avaliar a resposta da diversidade de espécies, de características comportamentais de seleção de habitat e da composição de espécies de assembleias de aranhas em manchas de vegetações florestais e experimentais a fatores ambientais e espaciais”. Os objetivos específicos foram: 1) Analisar a influência relativa de variáveis ambientais e espaciais nos padrões de variação da composição de espécies de aranhas de teia entre remanescentes florestais da Mata Atlântica no sul do Brasil. 2) Avaliar o padrão de seleção de microhabitats de aranhas de teia em remanescentes de Mata Atlântica no sul do Brasil e sua relação com variáveis ambientais. 3) Acessar os padrões de variação nas taxas de colonização da comunidade de aranhas em relação à manipulação da área e da diversidade de habitats em manchas de vegetação em uma paisagem experimental.

As coletas de dados em campo foram realizadas em remanescentes florestais de Mata Atlântica no município de Torres, RS e em uma paisagem experimental com manchas de vegetação inseridas em uma matriz campestre na mesma localidade. Em uma paisagem de aproximadamente 26 km^2 foram selecionados 16 remanescentes florestais. Foram realizadas amostragens proporcionais aos tamanhos dos remanescentes. Coletas manuais de aranhas de teia foram feitas em parcelas de 12 × 2 ×

2 m, e também foram realizadas medidas de utilização de habitat de cada indivíduo coletado entre março e agosto de 2009. Adicionalmente, foram realizadas medidas da estrutura da vegeatação de cada mancha. A área, isolamento e forma dos remanescentes foram calculados a partir de um arquivo *shape* em software ArcView 3.0.

A paisagem experimental foi formada com cinco blocos contendo quatro manchas de vegetação. Para cada mancha, foram aleatorizados dois níveis de dois tratamentos: tamanho (grande e pequeno) e diversidade de habitats (mais e menos diverso). As manchas consistiram em grupos de mudas de três espécies lenhosas nativas e uma espécie artificial. Foram realizados censos, com frequência média de 28,2 dias, ao longo de oito intervalos de tempos de todas as aranhas encontradas nas manchas.

A amostragem nos remanescentes coletou 3852 aranhas de teia, distribuídos nas famílias Araneidae (N = 588), Hahniidae (9), Linyphiidae (39), Mysmenidae (4), Nephilidae (2), Tetragnathidae (1647), Theridiidae (1027) e Uloboridae (838). A abundância de adultos foi de 254 indivíduos, identificados em 55 espécies. A riqueza rarefeita e a abundância de aranhas de teia não responderam significativamente às variáveis ambientais (vegetação e paisagem). Nenhum modelo de relação espécies-área foi significativo para a metacomunidade.

Três variáveis ambientais e duas variáveis espaciais influenciaram a diversidade beta de aranhas de teia nos remanescentes. Em torno de 15% da variação (valor de R ajustado) na diversidade beta foi explicada pela combinação de variáveis ambientais e espaciais. A maior parte dessa variação (12%) correspondeu à variação ambiental e a variação ambiental espacialmente estruturada.

Duas variáveis de seleção de hábitat maximizaram a divergência e uma variável maximizou a convergência para o padrão de montagem da metacomunidade ao longo do gradiente ambiental. Os valores de entropia quadrática de Rao (divergência) aumentaram ao longo das comunidades locais associados com o aumento da diversidade de uso das manchas nos entornos dos fragmentos. A utilização de ramos de trepadeiras pelas aranhas de teia foi negativamente correlacionada com a quantidade de arbustos nos fragmentos.

O tamanho e a diversidade de manchas de vegetação não influenciaram nas taxas de colonização. Apesar disso, houve diferenças significativas nas composições das comunidades ao longo do tempo. A riqueza e a abundância de adultos variaram temporalmente, mas não houve efeitos significativos dos tratamentos. A abundância total foi maior em manchas maiores e manchas menos diversas.

Pode-se inferir que a metacomunidade em nível de paisagem não é limitada pela dispersão (isso foi corroborado no experimento manipulativo). Dessa forma, o que influencia a chegada em uma mancha, em nível regional, é a amostragem passiva, que determina um filtro para manchas irregulares (menos impactadas) com sub-bosque denso e o tamanho da mancha na menor escala (experimental). Uma vez em um remanescente florestal (comunidade local), a escolha que as espécies fazem das estruturas de habitat para fixação das teias determina se a convergência ou divergência de estruturas vegetais de fixação das teias. No primeiro caso, as espécies escolhem as mesmas estruturas vegetais: ramos de trepadeiras em remanescentes com poucos arbustos, ou seja, seus requerimentos ecológicos são semelhantes e não parece haver pressão de competição nesse caso. No segundo caso, as espécies que chegam no interior de manchas com entornos mais diversos apresentam maior divergência no uso das estruturas vegetais de folhas e ramos de arbustos. Quanto mais diverso o entorno das manchas, menor parece ser a pressão de competição pelas estruturas vegetais entre aranhas.

ABSTRACT

Habitat fragmentation is one of the major causes of biodiversity loss. Fragmentation studies, in the beginnings, based on assumptions and predictions of the Island Biogeography Theory, which explains the diversity in oceanic islands by the balance between colonizations and extinctions linked to size and distance from mainland. From the beginning of the century, the metacommunity concept was developed, allied with the landscape patch mosaic. The metacommunity is a set of local communities bounded by dispersion of potential competitor species. This concepto expands the vision of community ecology from local level to other scales and considers the existence of four types of metacommunities: patch dynamics, species sorting, mass effect and neutral. These models have different assumptions regarding the responses of functional traits of species, from ecological equivalence to strong competition.

This thesis aimed to “evaluate the response of species diversity, habitat selection decisions and species composition of spider assemblages at patches of forest vegetation and experimental patches to environmental and spatial descriptors”. Specific objectives were: 1) Analyze the relative influence of environmental and spatial variables on the patterns of variation of web spider composition among remnants of Atlantic Forest in a fragmented landscape in southern Brazil. 2) Evaluate microhabitat selection convergence and divergence of web spiders in Atlantic forest patches in relation to two between-patch and one within-patch environmental gradients. 3) Examine the rates of colonization, immigration activity (abundance), richness, and composition of foliage dwelling spiders.

Mensurative experiment was done at 16 remnants of Atlantic Forest in Torres, RS. Manual collections of web spiders were done in 12 × 2 × 2 m plots. Habitat selection variables were measured for each individual spider in the field. Additionally, measures of the vegetation structure of the understorys and patch vegetation were done. The patch areas, isolations and shapes were calculated from a shape file in ArcView 3.0. Manipulative experiment was performed at an experimental landscape made of vegetation patches inserted in a grassland matrix. The experimental landscape was composed of five blocks each one containing four patches of vegetation. Two treatment levels were randomly assigned to the patches: size (big and small) and diversity (more

and less). The patches consisted of sets of seedlings of three native plants and one artificial seedling. All spiders colonizing the patches were collected along eight time periods (mean 28.2 days).

It was collected 3852 spiders in the forest remnants, distributed in the families Araneidae (N = 588), Hahniidae (9), Linyphiidae (39), Mysmenidae (4), Nephilidae (2), Tetragnathidae (1647), Theridiidae (1027) e Uloboridae (838). A total of 254 adult spiders were identified and sorted in 55 species. The rarefied richness and the abundance of web spiders did not respond to environmental variables (between-patch and within-patch). There was no species-area relationship.

Three environmental variables and two spatial variables influenced the beta diversity of web spiders in the remnants. Roughly 15% of beta diversity variation was due to a combination of environmental and spatial variables. The greater part of this variation corresponded to the environment control.

Two microhabitat selection structures maximized the assembly divergence, and one maximized the assembly convergence of the metacommunities associated to an environmental gradient. The Rao's quadratic entropy (divergence) based on bush/tree leaves and twigs microhabitat selection, increased from local communities in patches with pasture surroundings to local communities with more diverse surroundings. The selection of vine twigs by web spiders was associated to less dense understorys.

The size and diversity of experimental vegetation patches did not influence the spider colonization rates. However, the composition of spider communities varied among the time periods of the experiment, but there was no influence of size and diversity. There was a temporal effect on the variation of richness and adult abundance of spiders. On the other hand, the total abundance was higher in bigger patches, and in less diverse patches.

We may infer that the metacommunity at the regional level was not limited by dispersion (it was corroborated by the mesoscale manipulative experiment). In that sense, more irregular remnants with dense understorys passively sample the dispersers at regional level. Once a spider reach a remnant (local community), the choice it makes on to use the habitat structures determines whether it will result in convergence or divergence of microhabitat selection variables. In the first case, the species chose the same vegetal structures (similar ecological requirements): vine twigs. The competition does not seem to be important. In the second case, the species showing divergence on the use of bush/tree leaves and twigs arrive at remnant interiors of patches with more diverse surroundings. In this case, more competition for these vegetal structures seems to happen between web spiders.

ORGANIZAÇÃO GERAL DA TESE

Esta tese foi organizada em forma de capítulos, que correspondem a três artigos científicos em inglês, precedidos por uma introdução geral e sucedidos por considerações finais, ambas em português. Na capa de cada artigo estão inseridos os nomes dos co-autores que participaram ativamente em cada artigo. Os artigos serão submetidos a revistas internacionais depois de formatados adequadamente. Os dois primeiros artigos correspondem aos resultados obtidos no experimento mensurativo, enquanto o último artigo é o resultado do experimento manipulativo.

INTRODUÇÃO

Fragmentação da Mata Atlântica

A fragmentação de habitats imposta pelas atividades humanas é uma das principais causas do declínio da biodiversidade por todo o mundo. A paisagem que resulta da fragmentação se caracteriza por diferentes números de manchas espacialmente heterogêneas circundadas por uma matriz de ambientes modificados (Turner & Gardner 1991). A intensidade do efeito da fragmentação sobre a biodiversidade depende do nível de conectividade entre os habitats remanescentes, o que está ligado diretamente à qualidade da matriz (Ewers & Didham 2006).

A fragmentação da Mata Atlântica (*lato sensu*) teve início com a chegada dos primeiros colonizadores europeus. Atualmente, é o bioma brasileiro que se encontra nas áreas de maior pressão antrópica, pois sua distribuição se dá nas regiões de maior densidade populacional humana. Os remanescentes florestais da Mata Atlântica se apresentam com diversos tamanhos, formas e idades, além de apresentarem diferentes tipos de impactos nos seus entornos. Atualmente, os remanescentes florestais continuam sofrendo pressões para dar lugar à agricultura, para o uso de lenha e também para a construção de estradas, pontes, gasodutos, barragens e expansão urbana.

A área que abrange o nordeste do Rio Grande do Sul apresenta a conjunção entre a Serra Geral e a zona costeira. As características paisagísticas se alternam entre formações pioneiras junto ao mar com herbáceas em dunas permanentes, áreas de restingas e a mata paludosa em áreas alagadas, passando pela região da Floresta Ombrófila Densa, nas áreas mais altas da planície e junto aos contrafortes da Serra Geral e chegando até a Floresta Ombrófila Mista no planalto. Esse gradiente ambiental está inserido em uma região de mosaico ambiental principalmente na região mais baixa. Quando se chega até os contrafortes da Serra Geral, áreas de mata nativa ainda estão preservadas, apesar das manchas de plantações de culturas que se estendem por toda encosta. Dessa forma, a toda região da planície costeira até os sopés da serra apresenta uma alta heterogeneidade ambiental.

Comunidades em paisagens fragmentadas

No caso de uma paisagem de remanescentes florestais, como é o caso da Mata Atlântica no município de Torres, tem-se manchas de florestas secundárias, que reproduzem, até certo ponto, as condições e recursos da floresta original, os quais são importantes para a manutenção da comunidade animal. Ao mesmo tempo, a paisagem apresenta outros tipos de manchas que se conectam com os remanescentes e as características dessas manchas determinam a extensão na qual a conectividade entre os remanescentes é mantida.

De acordo com Ewers & Didham (2006) Os efeitos da fragmentação podem ser comumente agrupados em cinco categorias que descrevem os atributos espaciais dessas unidades da paisagem no mosaico: (1) área do fragmento; (2) forma do fragmento; (3) isolamento do fragmento; (4) efeito de borda; (5) estrutura da matriz.

A Teoria de Biogeografia de Ilhas (MacArthur & Wilson 1967) foi o ponto de partida que embasou as premissas e predições nas primeiras pesquisas de fragmentação de habitats. Essa teoria propõe que a área e o isolamento influenciam na dinâmica de colonização e extinção em ilhas, o que influi no número de espécies que cada ilha pode apresentar. Porém, essa teoria assume uma matriz uniforme e neutra, condições raramente encontradas em ecossistemas artificialmente fragmentados. Atualmente, muitos estudos, principalmente envolvendo comunidades de aves e mamíferos, têm utilizado a abordagem do mosaico da paisagem para inferir padrões de respostas da diversidade à fragmentação e perda de habitats. Essa abordagem leva em consideração aspectos da estrutura e funcionamento da paisagem como um todo, incluindo forma dos fragmentos, contraste com a matriz e efeito de borda. Porém, esses aspectos ainda contemplam padrões paisagísticos. Para acessar os processos que concorrem para explicar os padrões emergentes de comunidades é necessário se aprofundar nos mecanismos subjacentes ao movimento e interações das populações.

Basicamente, a teoria ecológica de formação das comunidades leva em consideração dois aspectos básicos da dinâmica das populações: a dispersão (ou migração) e as interações intra e interespecíficas. A teoria de metacomunidades, desenvolvida principalmente no início deste século, concebeu uma visão mais abrangente da dinâmica das espécies entre as comunidades locais, que, ao final, estão inseridas em uma paisagem formada por diversos tipos de manchas de hábitats. Ao colocar as comunidades locais dentro dessa rede denominada metacomunidade, essa abordagem assume que há diferentes dinâmicas que alteram a diversidade de espécies em nível local tanto diretamente, quanto indiretamente através de mudanças nos processos de comunidades locais que refletem em alterações na biota regional (Leibold *et al*. 2004). Existem quatro paradigmas básicos, dentro da teoria de metacomunidades, que procuram explicar a relação entre as comunidades locais: dinâmica de manchas, seleção de espécies, efeito de massa e neutralidade. Basicamente, essas quatro abordagens possuem premissas diferentes quanto aos mecanismos que atuam na dinâmica da metacomunidade: processos de nicho ou processos de dispersão (Cottenie 2005). A neutralidade presume que as espécies são ecologicamente equivalentes, mas com variações nas capacidades de dispersão, o que resulta em uma forte estrutura espacial, pois as espécies com maior limitação dispersiva colonizariam manchas mais próximas e o aumento da distância entre manchas locais criaria um decaimento na similaridade de espécies nas comunidades locais ligado à distância entre manchas. Uma dispersão abrangente em um ambiente heterogêneo com diferenças de nicho entre as espécies promove uma seleção de espécies ao longo de gradientes ambientais. O efeito de massa se manifesta caso a distribuição não seja determinada por gradientes ambientais, mas sim quando a comunidade é determinada quantitativamente por dispersão em relações fonte-dreno. Dessa forma, apesar do ambiente desfavorável, algumas espécies se manteriam pela dispersão entre as comunidades locais. Por fim, a dinâmica de manchas pressupõe diferenças de nicho entre as espécies, mas o gradiente ambiental não é tão importante e, sim, as compensações espaciais e temporais entre as espécies.

É importante ressaltar que esses quatro modelos assumem diferenças nos atributos funcionais das espécies. A teoria neutra pressupõe que as espécies são similares quanto aos atributos. O modelo de dinâmica de manchas presume suficiente variação na capacidade competitiva com uma covariação negativa com a capacidade de dispersão para possibilitar a convivência regional. Já os modelos de efeito de massa e de seleção de espécies presumem que há trocas nas habilidades das diferentes espécies em lidar com diferenças ambientais ao longo do gradiente.

Revisão bibliográfica sobre a resposta de artrópodes à fragmentação florestal

Uma pesquisa realizada na plataforma ISI Web of Knowledge (até junho de 2010) para avaliar a resposta de artrópodes à variação na área e isolamento de fragmentos, e à alteração de hábitat resultantes da fragmentação florestal selecionou 32 artigos (Figura 1). Os critérios de seleção foram:

1. Fragmentos jovens, com contrastes suaves com uma matriz de ambientes perturbados;
2. No mínimo três fragmentos;
3. Medida de riqueza e/ou abundância;

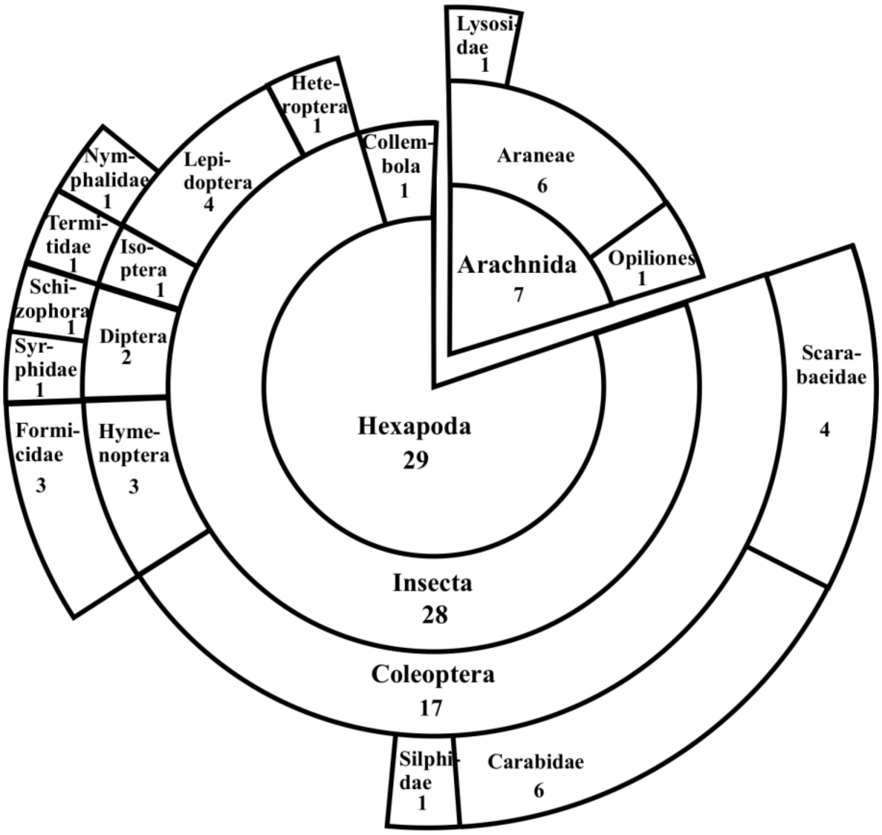

Figura 1 – Distribuição hierárquica do número de ocorrência de cada táxon de artrópodes em 32 estudos de fragmentação florestal.

Apesar de ainda insipiente, houve um aumento no número de artigos desde os anos 80. O táxon mais estudado foi Insecta, mas apenas seis ordens foram contempladas (dentre 25-30 ordens existentes, dependendo da classificação). A ordem mais estudada foi Coleoptera, mas com uma predominância de Scarabaeidae e Carabidae.

As respostas dos táxons à diminuição de área variaram de negativas (diminuição da riqueza) a neutras (sem variação na riqueza). Em áreas de Floresta Boreal, um estudo mostrou um aumento na abundância de besouros carabídeos *com a diminuição da área de fragmentos*. Porém, a maior parte das respostas foi neutra ou negativa. O efeito do isolamento sobre a riqueza e abundância de artrópodes foi muito pouco estudado. Somente cinco artigos abordaram, de alguma forma, o efeito do isolamento de fragmentos sobre a riqueza ou abundância. Quanto à alteração de hábitat, estudos mostram resultados diferentes. Alguns taxa aumentaram a riqueza e/ou a abundância em áreas perturbadas da matriz em relação aos fragmentos, provavelmente pelo aumento da diversidade de habitats ligado à conversão de florestas em outros tipos de habitats.

Resposta de comunidades de aranhas à fragmentação

Os estudos relacionados às mudanças na diversidade de aranhas em fragmentos ou remanescentes florestais são escassos, apesar desse grupo animal ser extremamente abundante em remanescentes e facilmente coletado. Dos poucos estudos que explicitamente abordam fragmentação florestal *stricto sensu*, i.e. ilhas de vegetação remanescentes de florestas contínuas inseridas em uma matriz de manchas diversas, pode-se inferir que a resposta da riqueza das comunidades de aranhas à variação na área das manchas pode ser negativa ou neutra (Pajunen *et al*. 1995; Miyashita *et al*. 1998; Kappor 2008). Esses autores não encontraram influência da área sobre a abundância. Quanto ao isolamento, Miyashita *et al*. (1998) encontraram que o isolamento de fragmentos florestais urbanos influenciou negativamente na riqueza e abundância de aranhas de teia no Japão. Vandergast & Gillespie (2004) e Pajunen *et al*. (1995) encontraram respostas diferentes das assembléias de aranhas aos efeitos de borda. Enquanto os primeiros encontraram que a riqueza e diversidade foram menores na área de matriz, os últimos reportaram maior riqueza nessa área.

Nenhum estudo foi encontrado com uma abordagem da influência da forma do fragmento e do contraste da matriz sobre comunidades de aranhas. Em dois outros estudos, as respostas também são contrastantes. Horváth *et al*. (2000) encontraram maior diversidade de aranhas arbustivas em uma borda de floresta de carvalhos e campo na Hungria, enquanto Baldissera *et al*. (2004) não encontraram diferenças na riqueza entre borda e interior em uma floresta de *Araucaria* no Rio Grande do Sul.

Essas aparentes contradições ilustram as dificuldades envolvidas na análise das respostas das comunidades à fragmentação e/ou perda de hábitat. Tanto os tipos de fragmentos/matriz (fragmentos de floresta/derrame de lava × fragmentos de floresta/floresta plantada) e a abordagem metodológica de coleta utilizada podem ter influenciado nas diferentes respostas (coleta direta na vegetação × armadilhas de solo).

Por outro lado, as diferentes técnicas de amostragem e os diferentes ambientes onde foram feitos estudos de fragmentação não podem, por si só, explicar as diferenças encontradas nas respostas dos organismos e comunidades. Em extensas revisões bibliográficas Debinski & Holt (2000) e Ewers & Didham (2006) concordam em elencar alguns fatores que podem obscurecer ou potencializar a detecção dos efeitos da fragmentação: diferenças nas características de vida das espécies, atrasos na manifestação dos efeitos da fragmentação, sinergias entre efeitos em diferentes escalas (e.g. isolamento + diminuição na polinização) e escolha de uma escala de paisagem adequada.

Por causa de características contrastantes de história de vida entre espécies e mesmo guildas, como tamanho corporal e padrão de forrageio, aranhas são organismos adequados para acessar que tipos de histórias de vida são mais sensíveis à fragmentação (Miyashita *et al*., 1998). Por serem altamente responsivas às estruturas vegetais (Uetz 1991) aranhas de teia podem ser utilizadas para se inferir padrões de seleção de hábitats nas comunidades locais dos fragmentos e suas respostas às variáveis de hábitat dentro e entre fragmentos.

OBJETIVO GERAL

O presente trabalho teve como principal objetivo “avaliar a resposta da diversidade de espécies, da composição de espécies e das taxas de colonização de aranhas, bem como avaliar diferenças na seleção de microhabitats por aranhas de teia em manchas de vegetações florestais e experimentais”. A pesquisa foi desenvolvida no município de Torres, litoral norte do RS.

OBJETIVOS ESPECÍFICOS

Os três capítulos desta tese tiveram como objetivos específicos:

1. Analisar a influência relativa de variáveis ambientais e espaciais nos padrões de variação da composição de espécies de aranhas de teia entre remanescentes florestais da Mata Atlântica no sul do Brasil.
2. Avaliar o padrão de convergência e de divergência de seleção de microhabitat de aranhas de teia em remanescentes de Mata Atlântica no sul do Brasil e sua relação com variáveis ambientais.
3. Acessar os padrões de variação nas taxas de colonização da comunidade de aranhas em relação à manipulação da área e da diversidade de habitats em manchas de vegetação em uma paisagem experimental.

MÉTODOS GERAIS

A área de estudo se localiza na região nordeste do Rio Grande do Sul, no município de Torres. O clima da região é classificado como mesotérmico brando (Cfa) (Vieira & Rangel 1988). A região se encontra em área de contato entre as formações recentes quaternárias do litoral riograndense e o planalto formado por derrames basálticos antigos. Essa última formação encontra o mar na altura de Torres. A vegetação da planície costeira, portanto, sofre diretamente a influência da proximidade com o planalto. A vegetação tem capacidade de desenvolvimento devido à presença abundante de água estagnada, ao maior índice pluviométrico, à imigração de muitas espécies serranas e à proximidade das comunidades do litoral catarinense (Rambo 1956). A paisagem é extremamente fragmentada, com áreas de mato contínuo nas encostas da serra Geral. A vegetação florestal predominante é a Floresta Ombrófila Densa Sub-Montana nas encostas da Serra Geral e Floresta Ombrófila Densa de Baixada principalmente nos topos dos pequenos morros da planície.

A forma original da paisagem no município era caracterizada pela presença de praias mais estreitas do que as atuais e com dunas mais elevadas (até 20 m); na parte posterior das dunas estendiam-se pantanais com vegetação própria (tiriricas, sedinhas, juncos, ciperáceas) e capões; a oeste dos banhados, se descortinava a Mata Atlântica, formando uma massa compacta de árvores e arbustos tropicais, que fechava a periferia de Torres e se estendia com poucas clareiras de campo até a serra (Ruschel 2006).

Atualmente, a paisagem da planície após os banhados, na área originalmente coberta pela Mata Atlântica, é composta de vários fragmentos remanescentes principalmente nas áreas mais altas circundados por diferentes usos de terra. Segundo relatos de moradores da região rural, há indivíduos de árvores com pelo menos 100 anos de idade (*Cedrela fissilis*) em um fragmento com área de 6 ha. Dobrovolski (2006) cita as áreas de florestas ombrófila de encosta como uma das classes da paisagem que teve um aumento de cobertura de 1974 para 2002 e que as áreas com domínio quaternário foram as que tiveram menor estabilidade da paisagem, cedendo lugar, principalmente, para áreas de campo, urbanas e banhado.

Em uma paisagem de aproximadamente 26 km^2 foram selecionados 16 remanescentes florestais preponderantemente na zona rural do município (Figura 2). Os tamanhos dos remanescentes variaram de 0,4 a 13,6 hectares. A seleção dos remanescentes foi baseada na acessibilidade, permissão dos proprietários, ausência de perturbação recente por pastagem e tamanho mínimo. O tamanho mínimo foi baseado em uma distância mínima de 25 m de qualquer borda para diminuir os efeitos de borda.

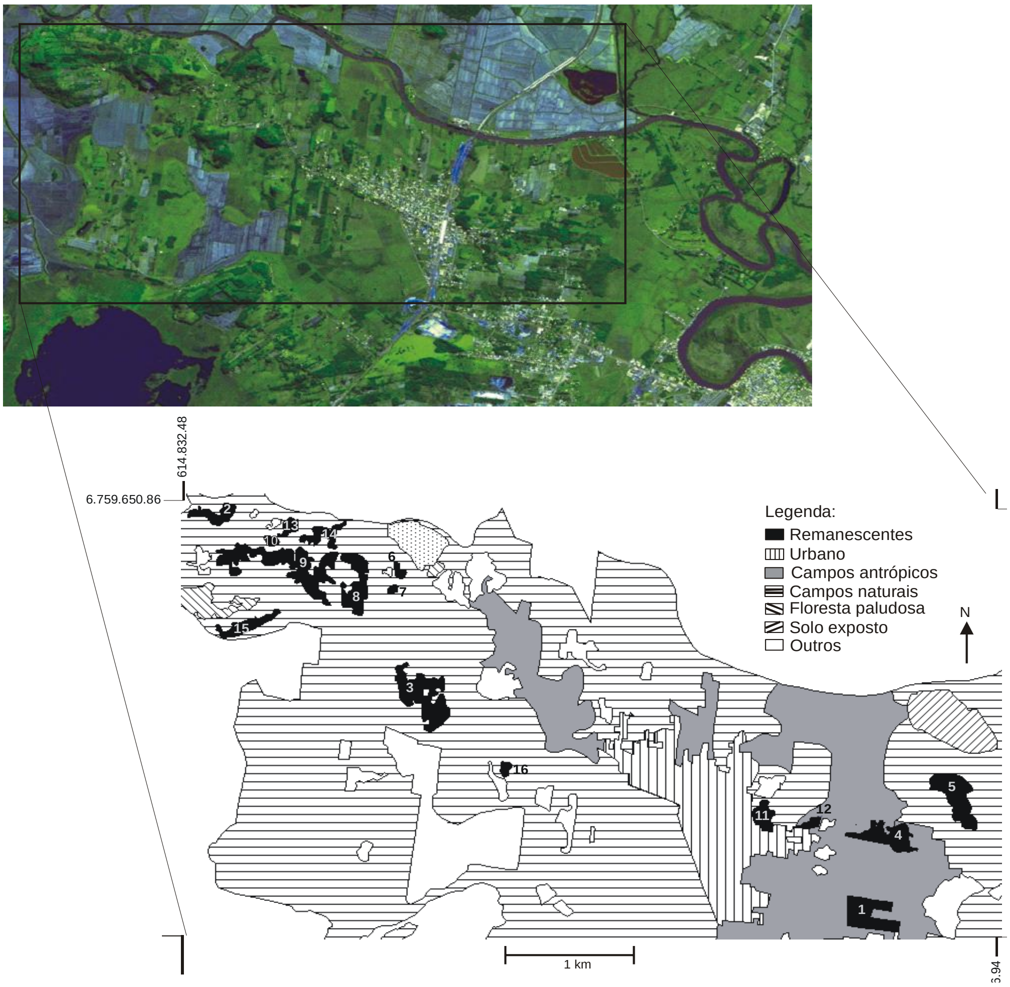

Figura 1 – Imagem spot de parte do município de Torres, RS. No detalhe, remanescentes florestais amostrados e paisagem do entorno. Classificação do uso do solo baseada em Dobrovolski (2006). Mapa montado pelo autor em software ArcView 3.0.

Foram realizadas amostragens proporcionais aos tamanhos dos remanescentes: duas unidades amostrais em pequenos, entre 0,36 e 4,9 ha; três unidades amostrais em médios entre 6,3 e 6,9 ha e quatro unidades amostrais em grandes entre 12 e 13,7 ha. Cada unidade amostral consistiu em um espaço tridimensional de 12 metros de comprimento, por dois de largura e dois de altura entre 20 cm e 220 cm do chão (total de 96 m^3). Cada conjunto de unidades amostrais foi inserido exatamente no centro geográfico de cada remanescente distante 10 m entre si.

Para o experimento, foi montada uma paisagem com tamanho de 1125 m^2 e com cinco blocos, cada um contendo quatro manchas com dois níveis dos seguintes tratamentos: tamanho (menor – 0,25 m^2/maior – 1 m^2) e diversidade (mais – quatro espécies vegetais/menos – uma espécie vegetal). Três mudas eram de árvores nativas, enquanto uma foi artificialmente manipulada. As mudas foram limpas de animais e colocadas nos blocos que ficaram equidistantes entre si. Em cada mancha grande havia 32 mudas da mesma espécie, ou oito de cada uma das quatro espécies. Coletas sucessivas foram realizadas em oito tempos (média de 28,2 dias) quando todas as aranhas eram coletadas e armazenadas.

PRIMEIRO CAPÍTULO

Metacommunity composition of web-spiders in a fragmented Neotropical forest: relative importance of environmental and spatial effects

Trabalho realizado em conjunto com Sandra Maria Hartz e Everton Nei Lopes Rodrigues

Abstract

Distribution of beta diversity is shaped by factors linked to environmental and spatial control. Relative importance of both processes in structuring spider metacommunities has not yet been investigated in Atlantic Forest. We compared variance explained by purely environmental, spatially structured environmental and purely spatial components for a metacommunity of web spiders. Study was carried out in 16 patches of Atlantic Forest in southern Brazil. Field work was done in one landscape mosaic representing a gradient of urbanization. Environmental variables encompassed plot- and patch-level measurements, and a vector of temperatures for each remnant, while principal coordinates of neighbour matrices (PCNMs) were used as spatial variables. Forward selection (RDA) procedure was carried out to select environmental and spatial variables influencing web spider beta diversity. Variation partitioning was used to estimate the contribution of pure environmental and pure spatial effects and their shared influence on beta diversity patterns and to estimate the relative importance of environmental structured variation and pure spatial variation at multiple spatial scales. Three environmental variables and two spatial variables were selected by forward selection procedures. Variation partitioning revealed that 15% of the variation of beta diversity was explained by a combination of environmental and PCNM variables. Most of this variation (12%) corresponded to the influence of pure environmental effect associated to spatilly structured environemtal effect. The influence of vegetation and patch variables was dependent on the spatial scale analysed. It was found that (1) spatial legacy was not important in explaining the web spider beta diversity; (2) environmental effect explained a significant portion of web spider composition distribution; (3) part of environmental effect was due to a spatial structure that jointly explains the diversity variation and the spatial influence is dependent on the scale; (4) much of the composition variation is due to unpredictable processes probably due to environmental dynamics linked to frequently human disturbances.

Keywords

Araneae, arthropod, beta diversity, forest fragmentation, human disturbance.

Introduction

The study of the variation in community composition among sites (beta diversity *sensu* Whittaker 1960) is crucial to understand many ecological and biogeographical issues such as the origin and distribution of diversity (Harrison et al. 1992; Lennon et al. 2001). It also provides valuable information to conservation biology questions such as the identification of intersection areas and transition zones, and helps to determine the number and arrangement of protected areas required to characterize the diversity within a region of interest (Williams 1996; Spector 2002; McKnight et al. 2007). If beta diversity is entirely the result of contemporary and historical random processes, resources can be taken anywhere in the region without adverse effects as long as we are not depleting them (Legendre et al. 2005). But if there is a spatial organization linked to species-environment relationships it must be necessary to preserve the pattern for nature to maintain beta diversity.

The historical process of Atlantic Forest fragmentation originated various forest fragments distributed in a matrix of different land-uses (Ribeiro et al. 2009) creating the possibility of a non-directional variation in metacommunity composition (Anderson et al. 2011) among the network of forest remnants. The study of factors driving the variation in species composition among forest patches is of utmost importance in order to properly manage the fragmented and highly disturbed Atlantic Forest. Recently, several studies have increased the understanding of the causes and consequences of Atlantic Forest loss and fragmentation showing that variation in arthropod species composition among fragments is dependent upon the presence of human disturbance, and that mosaics of native and managed forests can harbor significant portion of arthropod diversity (Baldissera et al. 2008; Fonseca et al. 2009; Metzger et al. 2009; Pardini et al. 2009; Uehara-Prado et al. 2009).

Two basic mechanisms have been proposed to explain the variation of beta diversity (Legendre et al. 2005). The environmental control proposes that the variation in the environmental characteristics is responsible for the variation in species composition by the differentiation of available niches, which favour the establishment of diverse assemblages of species. The second mechanism highlights the importance of neutral mechanisms (Hubbell 2001; Hubbell 2005). In that sense the beta diversity would emerge by the dispersal limitation of species, which would create aggregated patterns inducing spatial autocorrelation in species distributions.

Spiders are abundant generalist predators in most ecosystems. They are at the top of invertebrate food chain and thus act in an important way to shape terrestrial arthropod communities (Wise 1993). Spiders respond to natural and human environmental changes (Entling et al. 2007; Finch et al. 2008). At local scales richness and abundance of spiders can be strongly influenced by the vegetation structure at the local level (Baldissera et al. 2004; Baldissera et al. 2008). Therefore, spiders may be good indicators of the variation in habitat structure within forest fragments, a factor directly linked to historical human disturbances. Recent studies have shown that spider metacommunities tend to be controlled mainly by environmental or climatic effects with little influence of spatial variables indicating that these arthropods are not dispersal limitated at regional scales (Jiménez-Valverde et al. 2010; Sattler et al. 2010). However, the relative importance of environmental and spatial factors to the composition of arthropod metacommunities in Neotropical fragments is poorly known. In the context of metacommunity ecology (*sensu* Leibold et al. 2004) the partitioning of environmental and spatial factors influencing beta diversity may provide potential causal mechanisms (species interactions/dispersal) for explaining observed patterns of species distributions in the local communities' network (Cottenie 2005).

In the present study we analyzed the relative influence of environmental and spatial variables on the patterns of variation of web spider composition among remnants of Atlantic Forest in a fragmented landscape in southern Brazil. We asked the following questions: (1) What environmental variables, represented by vegetation structure and patch metrics, best explain the variation of web spider metacommunity composition? (2) Is there a joint effect of patch metrics and vegetation structure on web spider composition, i.e. is there a hierarchically structured effect of both set of variables on web spider composition? (3) What is the relative importance of purely environmental, spatially structured environmental and purely spatial variables for the variation of web spider composition? To our knowledge this last question has not yet been addressed for arthropod fragmentation studies in the Neotropics. Our hypotheses were that (1) vegetation structure exert higher influence on web spider beta diversity and there is a hierarchical effect of patch metric variables (patch-level) on vegetation structure variables (plot-level) associated to human activities (Uetz 1991; Cushman and McGarigal 2002); (2) Spatial variables are not significant descriptors of web spider beta diversity, because these animals display a passive dispersion mode (ballooning) that allows random distribution of colonizers over the landscape (Suter 1999; Bowman et al. 2002; Soininen et al. 2007).

Methods

Study area

The study area is located in the municipality of Torres, coastal plain of State of Rio Grande do Sul, southern Brazil (UTM Coordinates 22 J 65756248 N – 620219 E). The altitude in the region varies from 0 to 90 m, with a subtropical mesothermic and humid climate. The mean annual minimum and maximum temperature varied from 15.6 to 22.3 °C respectively, and total annual precipitation was 1387 mm (meteorological data for 1962-90; Brasil [1992]).

The site was originally covered with Atlantic Forest vegetation, inserted in the Tropical and Subtropical Moist Broadleaf Forest biome, Serra do Mar Coastal Forests ecoregion (Olson et al. 2001). Field work was performed in one landscape mosaic representing a slight gradient of urbanization (Figure 1). Rural matrix consisted of small farms showing cattle breeding and agriculture as the main activities. Patches of Atlantic Forest were basically second-growth forests presenting old remnant trees interspersed with different degrees of regenerating stratum. Newly disturbed patches showed less abundance of regenerating trees in the understory. Patches were surrounded by six basic patch types: agriculture (mostly bean, corn, and sugarcane), banana plantations, buildings, *capoeira* (forest succession early initial stage), *Eucalyptus* plantation, and pasture.

Sampling design

We sampled 16 forest patches ranging from 0.36 to 13.7 ha in size (Table 1) distributed in a landscape *ca*. 26 km^2 in size (Figure 1). We chose the patches based on accessibility, land owner permission, absence of recent grazing activities, and minimum size (see below). Proportional sampling procedure was used to set the number of sampling units in each patch. We divided the fragments into three classes based on their sizes: two sampling units in each of 12 small-sized-fragments (< 5 ha), three units in each of two medium-sized fragments (6 to 10 ha), and four units in each of two large-sized (11 to 14 ha) fragments, totalling 38 sampling units.

Table 1 – Description of final matrix of environmental variables (after RDA forward selection) and XY coordinates of 16 patches of Atlantic Forest in southern Brazil. PCA1 = site scores obtained by principal component analysis over a matrix of composition of forest patches land-use surroundings. Percentage of variance explained by axis 1 = 73%.

	Size (ha)	X	Y	Number of bushes	PCA1	Shape
P1	3.8	5663	1512.10	12	1.954	1.0024
P2	2.4	559.64	4764.66	15	1.564	1.1234
P3	12	2234.07	3330.70	86	1.337	1.1283
P4	6.9	5983.46	2096.93	83	1.845	1.1568
P5	4.9	6432.11	2537.56	9	1.143	1.0759
P6	0.8	2025.77	4316.11	4	0.654	1.0360
P7	0.4	1985.71	4171.91	12	0.654	0.9946
P8	6.3	1689.29	4139.87	52	1.625	1.0902
P9	13.7	1264.67	4404.24	88	1.826	1.2018
P10	0.6	1024.32	4572.49	42	1.136	0.9939
P11	2.8	4917.93	2297.22	44	1.625	1.0229
P12	1.1	5310.50	2241.13	48	1.143	1.0425
P13	1.3	1160.53	4692.66	20	2.046	1.0550
P14	2.4	1489.01	4636.59	71	1.735	1.0420
P15	1.3	816.02	3875.50	21	1.136	1.0691
P16	1.1	2866.98	2681.76	30	0.654	1.0218

Digitalized maps were inspected previously to the field trip to set the coordinates of the centres of each patch. We used the coordinates in the field to set the sampling units. The centred sampling units should fall at least 30 m distant from the patch edge to circumvent the influence of edge effects. This characteristic prevented the use of very small patches. Each sampling unit consisted of cubic plots 12 × 2 × 2 m. The plot’s height was measured from 0.20 m up to 2.20 m above the ground. We selected the sampling units in the field by sorting two, three or four out of the eight basic geographic directions. Plots’ vertices were at least 10 m apart from each other. Sampling units inside each patch were pooled in order to perform the analyses (see *Scaling beta diversity* section).

Figure 1 – Map showing the 16 forest patches of Atlantic Forest, and the landscape mosaic of the region with corresponding classification of land uses. Coordinates are in UTM system (22 J).

Spider sampling

We opted to collect only web spiders because (1) they are easy to find with the aid of a web highlighter, in our case wheat powder, and (2) the distribution of these animals are strongly linked to variations in vegetation structure (Uetz 1991). Therefore, web spiders were manually collected by visual inspection of each plot after the collector spread the powder on the vegetation. Collections were made during dry days between March and July 2009. The time spent in each plot was dependent upon its vegetation amount and complexity, so it took from four to 20 hours to sample one individual plot. Each collected web spider was stored in an individual vial with 70% alcohol. Adult web spiders' identification was done by the second author. Voucher specimens are deposited in the spider collection of Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul, in Porto Alegre, Brazil.

Environmental variables

Patch vegetation structure

We measured ten variables in each plot to characterize the general forest structure: number of trees (woody plants > 3 m), number of bushes (woody plants between 0.2 and 3 m), number of palm trees, number of woody vines, presence of multistrata (0 for two strata, 1 for multistrata), number of tree/bush leaves, number of tree/bush branches, number of tree/bush twigs, number of tree/bush dry branches, and number of vine branches. The first five variables were censued inside each plot. For the measurements of the last five variables we utilized the point-counting method described in Baldissera et al. (2008). The collector positioned a 2.2 m long pole vertically along 36 equally distant points inside each plot and the plant structures touching the pole were counted and classified. Additionally, we calculated the Shannon index of diversity (*H'*) based on the five last variables in order to achieve a measure of understory vegetation diversity.

Patch metric variables

We measured five patch metric variables: log transformed area, nearest-neighbour distance, patch shape complexity, level of urbanization, and surrounding land-use. The first four variables were measured from data on a land-use classification shape file generated in ArcView Gis 3.3 (Environmental Systems Research Institute, Inc.) (Dobrovolski 2006). Fractal dimension *Frac* = 2ln[(P/4) / ln(A)] was used to assess patch shape, where *P* is the patch perimeter and *A* is the patch area (McGarigal et al. 2002). Lower values of fractal dimension indicate squared or more structured shape (usually man made), and higher values approaching 2 indicate more complex shapes (natural). Level of urbanization was set as a binary variable: patches within urban areas (presence of land-uses urban, bare soil, and anthropogenic grasslands – Figure 1), and patches within rural areas (absence of those land-uses). In order to characterize the land-uses surrounding the patches, we checked *in situ* the types of land-uses contiguous to each patch. Six types of land-uses were found: *capoeira*, *Eucalyptus* plantation, buildings, pasture, agriculture, and banana. A presence-absence matrix of land-uses surrounding the 16 patches was then constructed and a PCA based on a product moment resamblance measure between variables was performed. The first ordination axis was then used as the surroundings land-use variable. Analysis was made in software Multiv v.2.1 (Pillar 2001).

Climatic variable

The air temperature measured for each day of collection was computed from the Torres Meteorological Station data (INMET, Brazil, http://www.inmet.gov.br/). The data for each patch was averaged by the number of days spent to sample all sampling units. Therefore, we were able to account for temporal variation in web spider composition associated to the temporal range of our sampling (March – July).

Spatial variables

We derived the spatial variables by using principal coordinates of neighbour matrices (PCNM), a well-suited method for the detection of spatial trends across a wide range of scales (Borcard and Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). Before PCNM variables calculation, it was certified that the web spider hellinger transformed matrix did not show a linear trend by performing a RDA (Redundancy Analysis) with the spatial coordinates of the centre of each remnant as explanatory variables. It is necessary because PCNMs are basically sine-waves that would be "wasted" on linear trends (Borcard et al. 2004). Afterwards, the spatial coordinates of the centre of each forest patch were used to build a Euclidean distance matrix. Then, this matrix was truncated at the smallest distance that keeps all sites connected into a single network, which corresponds to the maximum distance between two patch centres in a one-dimension (2,068.68 m in our case). The truncated portion was filled with an arbitrarily large distance value. Then, a principal coordinate analysis (PCoA) was carried out, and the eigenvectors associated with positive eigenvalues were retained as spatial variables (PCNM variables) (Borcard and Legendre, 2002; Borcard et al., 2004). PCNM eigenvectors were created using the function "pcnm" in "vegan" package for the R language (R Development Core Team 2009).

Data analysis

Scaling beta diversity

Because our main purpose was to analyze beta diversity *among forest patches,* we assumed higher beta diversity among patches, and lower beta diversity within patches. In order to check this assumption, software Partition 3.0 (Veech and Crist 2009) was used to hierarchically decompose total amount of diversity (*gamma*) into the components of mean diversity within patches ($alpha_2$) and plots ($alpha_1$) and diversity among patches ($beta_2$) and plots ($beta_1$). Results corroborated the assumptions: observed beta diversity within patches ($\beta = 6.38$) was significantly lower than expected by chance ($P < 0.01$), while observed beta diversity among patches ($\beta = 42.94$) was significantly higher ($P < 0.01$). Therefore, pooled composition was used for each patch, i.e. our working sampling units were the patches.

In the following analyses we used the “vegan” and “packfor” packages of R language v. 2.13.1 (R Development Core Team 2011) to perform all analyses. We applied the Hellinger transformation (Legendre and Gallagher 2001) on community abundance data prior to analyses. Hellinger transformation make the community composition data containing many zeros suitable for analysis by linear methods such as RDA (Legendre 2008). Our general null hypothesis is that web spider beta diversity was not related to environmental or spatial variables.

Beta diversity explained by environmental variables

In order to address our first and second questions we performed two sets of analyses. First, a forward selection analysis (RDA) was run separately for each one of the three environmental matrices: vegetation structure, patch metrics and climate. We used the double-stop criterion proposed by Blanchet et al. (2008) in the analyses. The procedure initiated by performing a global test (RDA) with all variables of each environmental data matrix. Afterwards, α-values ($P < 0.1$ after 9999 random permutations) and adjusted coefficient of multiple determinations (R^2_{adj}) of global tests were used as stopping criteria in the forward selection of variables. The variables that fulfilled both stopping criteria for each matrix were identified as the significant environmental variables shaping the variation in metacommunity composition. Second, we used the selected variables in a variation partitioning procedure (Borcard et al. 1992) to address the proportions of variation of web spider composition explained by each variable alone and also by their joint effects. Negatives values of R^2_{adj} were treated as zero values (Daniel Borcard, personal communication). Finally, we analysed the influence of sample size on environmental variables by performing a variance partitioning with the forward selected environmental variables and the number of plots of each fragment as an extra explanatory variable. Results showed that variance added to the environmental model was negligible ($R^2_{\text{adj}} < 0.0001$). Analysis of the independent fraction of variance of the Hellinger-transformed web spider abundance matrix explained by the sample size (RDA) was not significant (*pseudo-F* = 0.97, $P = 0.5$).

Beta diversity explained by environment and space

We used the environmental variables and the spatial variables in another variation partitioning to assess our third question. The environmental data variables were the ones previously forward selected. The spatial variables were chosen by a similar forward selection procedure, i.e. the same significant α-value and the adjusted coefficient of multiple determinations were used as stopping criteria in the variables selection.

We built scale-specific additive spatial models (Laliberté et al. 2008; Carvalho et al.2011) in order to access the relative importance of spatially structured environmental variation and spatial effects alone on community composition (decomposition of fraction [b]). Using RDA, the Hellinger-transformed matrix of species abundances was fitted against each forward selected PCNM variables. Afterwards, we used the fitted values in a variation partitioning procedure with the environmental variables previously forward selected.

Results

General patterns

We collected a total of 3854 web spiders from 16 Atlantic Forest patches. From that total, 55 species from 255 adults were determined and utilized in the analyses. Chao 1 estimator (Magurran 2004) showed the number of species collected reached 68% of the absolute number of species in the metacommunity (see Appendix 1 for species list and values of alpha diversity).

Land-use surroundings

The first PCA axis explained 73% of the variation in the composition of land-use surrounding of forest patches. The values of the correlation coefficients of each variable with PCA axis 1 were buildings (R = 0.77), agriculture (R = 0.70), *capoeira* (R = 0.60), banana plantations (R = 0.40), *Eucalyptus* (R = 0.39), and pasture (R = 0.00). Lack of correlation between axis 1 and pasture came from the fact that all patches showed the presence of pasture in their surroundings. Therefore, we may interpret the PCA axis 1 as a surrounding compositional gradient from solely-pasture (more likely to be disturbed by cattle) to more diversified forest patches surroundings.

Influence of environmental variables

Forward selection procedures identified number of bushes, land-use surroundings and patch shape as significant predictors of web spider metacommunity variation among forest patches (Table 2). Climatic matrix did not influence web spider beta diversity (*pseudo-F* = 1.41; *P* = 0.13). RDA analysis showed that the three selected environmental variables significantly explained 12% of the variation in the web spider metacommunity variation (Table 2). From that variation the composition of patch surroundings (49%) was the variable with the higher individual contribution to the variation (Figure 2). The joint fractions of variation explained by the environmental variables at the plot- and patch-levels were negligible. Biplot illustration for web spiders showing the first two canonical axes of the RDA analysis with the selected environmental variables and species is found in Figure 3.

Table 2 – Results of variation partitioning of environmental and spatial effects on web spider metacommunity composition in 16 patches of Atlantic Forest in southern Brazil. It is showed the decomposed total explained variation [a+b+c] into an environmental component [a+b] and a component [c] which estimates the spatially-structured variation of web spider metacommunity composition not explained by the environmental variables (Legendre & Legendre 1998). Environmental variables: number of bushes, composition of patch surroundings, shape of patches. Spatial variables: two PCNM variables.

Fractions of variation	R^2	R^2_{adj}	*F*	*P*
[a+b] Environmental + shared	0.30	0.12	1.68	0.005
[b+c] Spatial + shared	0.19	0.07	1.56	0.01
[a+b+c]	0.43	0.15	1.52	0.005
[a] Only environmental		0.08	1.40	0.025
[b] Environment spatially structured		0.05		
[c] Only spatial		0.02	1.19	0.23
[d] Residual		0.85		

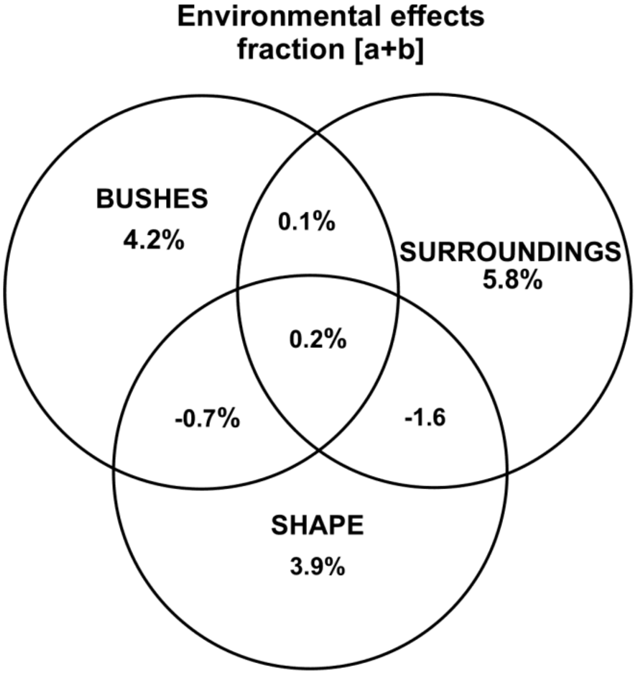

Figure 2 - Venn diagram showing the results of the variation partitioning procedure carried out on the forward selected environmental variables coupled with a common variation explained by spatial variables (fraction [a+b]).

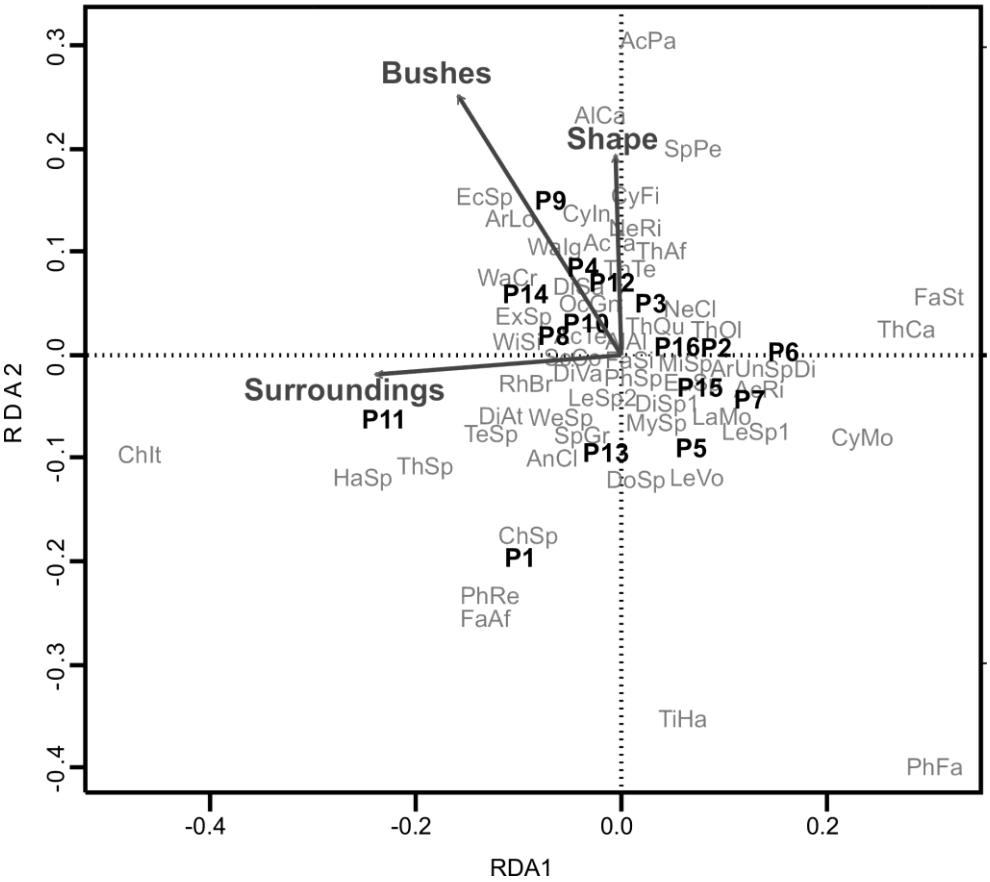

Figure 3 – Biplot of species metacommunity analysis of web spiders (Araneae) for 16 patches of Atlantic Forest in southern Brazil. Names abbreviated may be found in Appendix 1.

Partition of environmental and spatial effects

Forward selection selected two PCNMs (PCNM4 and PCNM7; $R^2_{\text{adj}} = 0.07$; *pseudo-F*= 1.56; $P = 0.03$). Because the eigenvectors are ordered by decreasing spatial scales (Borcard & Legendre 2002) we may interpret the PCNM7 variable as representing the patch scale (grain) and the PCNM4 an intermediary scale between the patch and the spatial extent of the study.

The partitioning of environmental and spatial effects showed that the variation attributable to pure environmental effects had significant influence on web spider composition and that the spatial effect fraction was negligible (Table 2), suggesting that pure neutral processes exert little effect on web spider composition. The spatial variation shared with the environment explained 7% of variation. On the other hand, 33% of the variation explained by environmental variables was spatially structured (Table 2). The scale-specific additive spatial analysis showed that the amount of variation explained by spatially structured environmental effects was similar at the two spatial scales (Figure 4).

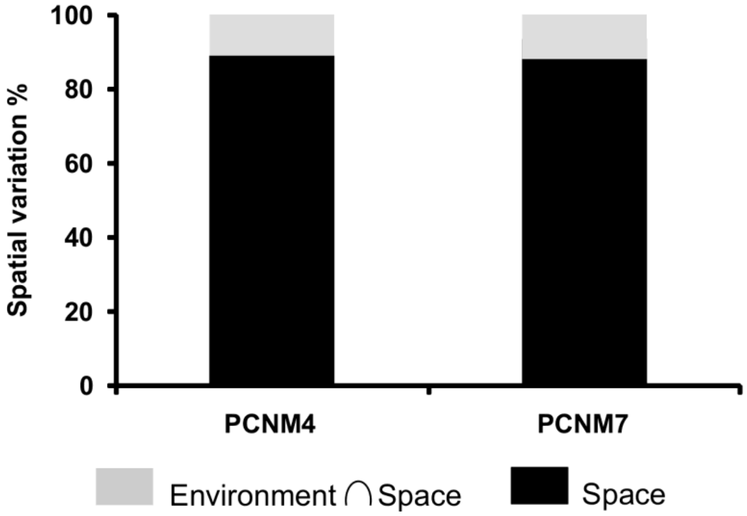

Figure 4 – Relative influences of spatially structured environmental variation (environment ∩ space) and space on the web spider metacommunity composition at two scales: intermediate (PCNM4) and fine (PCNM7).

The scale-specific models also showed that at the intermediate scale patch shape explained most of the variation (16%; *F* = 3.27, *P* = 0.086) and the positive joint effects of number of bushes and surrounding composition also contributed to explain a significant part of variation at intermediate scale (fraction not testable) (Figure 5). At the fine scale the surrounding composition became more important (22.7%; *F* = 4.26, *P* = 0.06) and there was an expressive jointly influence of number of bushes and patch shape (fraction not testable).

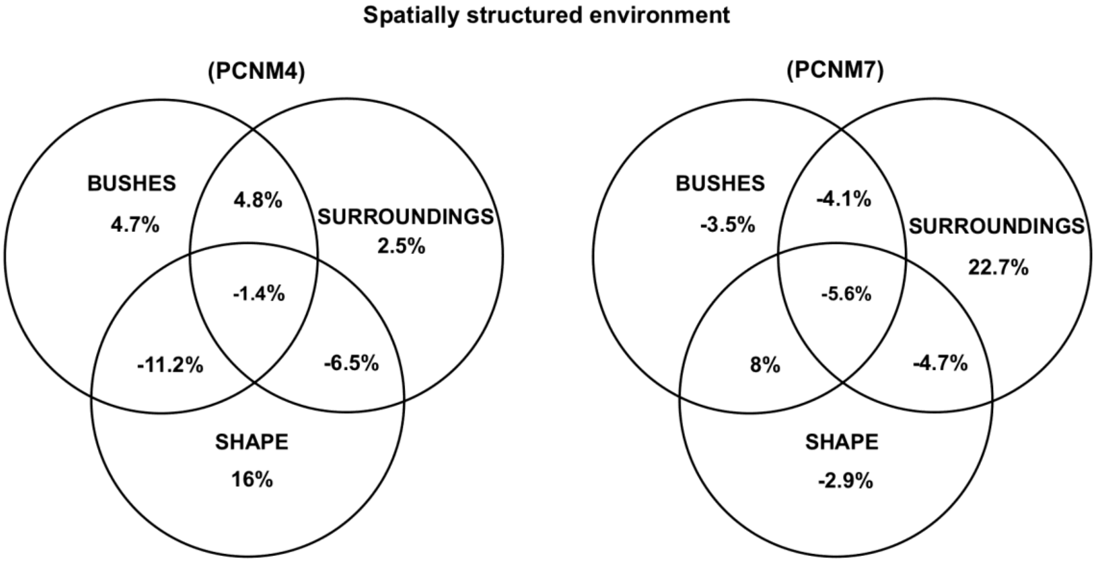

Figure 5 – Relative influences of number of bushes, composition of patch surroundings, and patch shapes on the web spider metacommunity at the scales defined by the two forward selected PCNMs.

Discussion

We detected important features of the variation in web spider composition among Atlantic Forest patches. First, spatial legacy (Peres-Neto and Legendre 2010) was not important in explaining the variation of web spider composition among Atlantic Forest patches. Second, environmental predictors explained more of web spider composition variation compared to spatial predictors. Third, there was a common spatial structure in species distributions and environmental processes (spatial nuisance, Peres-Neto and Legendre [2010]) that jointly explains variation in species distributions, and this influence is dependent on the scale.

Absence of spatial legacy

The lack of a strictly spatially structured variation in web spider composition among Atlantic Forest patches showed that the relative contribution of spatial autocorrelation to the overall pattern was negligible, a result already suggested for the same Atlantic Forest ecoregion (Bonaldo et al., 2007). The absence of purely spatial influence may be due to the lack of dispersal limitation (Peres-Neto and Legendre 2010). Most neutral models predict that species composition changes across space because species have limited dispersal distances (Hubbell 2001; McGill et al. 2006). We found evidence that the web spider metacommunity dispersal is not limited because there was a significant inverse relationship between local community dominance and local species richness ($R^2 = 0.73$; $P < 0.0001$) (as predicted by Hubbell [2001], pp. 215-216). In that sense, high rates of dispersal bring more regional diversity to the local community since under high rates of dispersal, species occur at lower abundance in local communities having higher species richness (Hubbell 2001). Therefore spatial effects to the web spider species turnover in human-disturbed landscapes seem to be of minor importance when compared to the effects of the reduction of suitable habitat in combination with habitat fragmentation (Bonte et al. 2006; Sattler et al. 2010).

The study extent may also play an important role in determining the initial similarity between plots, with the extent and the initial similarity exhibiting a significant negative relationship (Soininen et al. 2007). In that sense, small scale extents tend to show lower species turnover, therefore relaxing the dispersal limitation effect on web spider metacommunity variation. Nevertheless, this pattern was not general when considering other studies of spider communities. For example, Muff et al. (2009) found a high relative importance of spatial variables (24.5%) in structuring a spider community while Jimenez-Valverde et al. (2009) reported a lack of significant correlation between spider assemblage composition and geographic distance in a geographic extent similar to the present study.

Presence of environmental control

Environmental variables accounted for most part of the variation in web spider metacommunity composition among Atlantic Forest patches. The amount of vegetation was the only variable linked to forest structure that influenced the composition of web spiders. None of the measured microhabitat variables was selected as significant environmental effects to the web spider composition, a result also found in another Atlantic Forest study (Pinto-Leite 2008). We found a gradient of change in web spider local communities linked to the change of understory vegetation quantity. This finding highlights the importance of variables linked to vegetation structure to the responses of spider composition in fragmented landscapes (Pajunen et al.1995). An extensive study in Central Europe, showed that shading by vegetation was one of the main factors driving spider composition variation between habitats (Entling et al. 2007). In the

Brazilian Cerrado plant density also was related to the variation in spider composition among patches of vegetation (Rinaldi and Trinca 2008). In the present study, the presence of more closed understory suggests that less disturbed patches show particular web spider compositions. In that sense, it is expected that the web spider composition time since disturbance influence the similarity of patches (Yanoviak et al. 2003; Floren and Deeleman-Reinhold 2005). At the patch-level shape of patches and land-use surroundings influenced the variation in web spider composition. It suggests that the kind and the composition of matrix management may be an important factor affecting web spider metacommunity composition. Clearly, there was a web spider community linked to patches more likely to be disturbed by cattle and patches with more structured shapes. Sampling in heavy grazed patches was avoided, but two patches inside a farmland showed clear signs of previous grazing. Therefore, there must be a web spider community linked to the initial development of the understory vegetation after cattle disturbance. It is unlikely that this community comes from the intervening matrix (pasture) since a study performed in one of the patches presently studied showed that the composition of arbustive patch dwelling spiders was completely different from the contiguous early stage area indicating that spider forest species avoid matrix habitats (Baldissera and Silva 2010). This characteristic coupled with the absence of dispersal limitation suggests that the web spider local communities in the early disturbed patches are composed by dispersing individuals from other patches of Atlantic Forest. These species would be able to colonize recovering habitats with low understory vegetation density. The interaction betwen shape and land-use surroundings further suggests that as the surroundings of less disturbed patches became more diversified a different set of web spider species would colonize them. Indeed, patches showing more complex shapes may offer more chances to colonization by dispersing individuals (Ewers and Didham 2006). Other studies also highlighted that species with different habitat affinity respond differently to the human-generated disturbance (Alaruikka et al. 2002; Chen and Tso 2004). On the other hand, Schmidt et al. (2005) did not find effects of surrounding structure of the matrix on the composition of spiders dwelling farmlands in Germany.

Part of the variation in web spider composition was spatially structured (fraction [b]). We believe that most part of this fraction of variation represents missing predictors that are themselves spatially structured (Peres-Neto and Legendre 2010) since only 20% of the variation explained by that fraction was attributable to the spatialized component of the environment. It is surprising when we consider the fine scale approach we used, where we expected to find more environmental influence considering the various microhabitat variables sampled (not selected to the final model). On the other hand, the analysis of the variation attributable to the environmental spatially structure showed that environmental factors act in a scale-dependent way. At the intermediate scale shape was the predominant influence on web spider composition. At this scale the joint effect of bushes and land-use surroundings demonstrated a hierarchical effect of the kind of contiguous patches and the vegetation cover on web spiders. At the patch scale land-use surroundings composition became more important and a shared component of bushes and shape again suggested the effect of hierarchical effects. Therefore, the influence of spatially structured environmental variables on web spider composition in Atlantic Forest patches is driven by factors acting across two spatial levels: plot and patch (Cushman and McGarigal 2002). This result is very important because it demonstrates that different factors act at different scales on web spider metacommunities (Carvalho et al. 2011) and that the influence of patch-level variables linked to human activities may be shared by plot-level variables. In that sense studies dealing with one or another set of variables can find significant influences difficult to explain at a single scale approach (Cushman and McGarigal 2002).

Unpredictable variation

Large amounts of variation in web spider metacommunity composition remained unexplained. Nevertheless, the proportion of total variance accounted for environmental variables in our study is similar to the ones found in three urban areas of Switzerland (Sattler et al. 2010). These authors suggested that there is a gradient of influence of stochasticity from natural (less stochastic) to urban areas (more stochastic). On the other hand, other variables that were not measured may in fact be important to web spider composition variation. In this highly disturbed landscape human activities such as cattle, extractivism, leisure, and crop diversification can play an important role in web spider distribution and occurrence. However, we were able to detect important factors related to matrix management influencing the web spider beta diversity patterns, which are probably linked to historical events of forest deforestation.

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Appendix 1 – List of the web spider species found in 16 patches of Atlantic Forest in southern Brazil. Data are ordered by decreasing abundance.

Species	Abbreviation	Family	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	Total
Achaearanea passiva	AcPa	Theridiidae	0	1	6	1	1	3	0	1	2	1	0	5	1	4	0	1	27
Chrysometa itaimba	ChIt	Tetragnathidae	2	1	2	2	1	0	0	6	3	2	3	0	2	1	0	1	26
Philoponella fasciata	PhFa	Uloboridae	1	1	1	0	7	1	0	0	0	0	0	0	2	0	6	0	19
Tidarrem haemorrhoidale	TiHa	Theridiidae	1	0	0	0	1	1	3	1	0	1	0	0	3	1	0	6	18
Sphecozone personata	SpPe	Linyphiidae	0	0	1	2	0	1	0	0	1	0	0	10	1	0	1	0	17
Theridion quadripartitum	ThQu	Theridiidae	0	0	1	0	1	0	0	9	0	0	0	0	1	0	0	4	16
Alpaida canoa	AlCa	Araneidae	0	0	0	2	0	0	0	2	2	2	0	0	0	0	3	0	11
Faiditus striatus	FaSt	Theridiidae	0	3	2	2	1	1	1	0	0	0	0	0	0	0	0	1	11
Alpaida alticeps	AlAl	Araneidae	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	3	9
Theridion calcynatum	ThCa	Theridiidae	0	0	1	0	0	1	5	0	0	0	0	0	0	0	0	2	9
Hahnia sp.	HaSp	Hahniidae	1	0	1	2	1	0	0	1	0	0	2	0	0	0	0	0	8
Thymoites sp.	ThSp	Theridiidae	0	0	0	0	0	0	0	0	0	0	1	3	1	1	1	0	7
Cyclosa fililineata	CyFi	Araneidae	0	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	5
Leucauge sp.3	LeSp3	Tetragnathidae	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	5
Achaearanea tesselata	AcTe	Theridiidae	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	3
Cyclosa morretes	CyMo	Araneidae	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	3
Echinotheridion sp.	EcSp	Theridiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	3
Leucauge sp.1	LeSp1	Tetragnathidae	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3
Neospintharus rioensis	NeRi	Theridiidae	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	3
Phoroncidia reimoseri	PhRe	Theridiidae	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3
Theridion olaup	ThOl	Theridiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
Wagneriana iguape	WaIg	Araneidae	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Araneus unanimus	ArUn	Araneidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2
Ariamnes longíssimus	ArLo	Theridiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2
Dolichognatha sp.	DoSp	Tetragnathidae	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2

Exalbidion sp.	ExSp	Theridiidae	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2
Faiditus affinis	FaAf	Theridiidae	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Nephila clavipes	NeCl	Nephilidae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Philoponella sp.	PhSp	Uloboridae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2
Tekellina sp.	TeSp	Theridiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2
Wamba crispulus	WaCr	Theridiidae	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	2
Wendilgarda sp.	WeSp	Theridiosomatidae	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2
Achaearanea rioensis	AcRi	Theridiidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Achaearanea taim	AcTa	Theridiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Anodoration claviferum	AnCl	Linyphiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Chrysso sp.	ChSp	Theridiidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cyclosa inca	CyIn	Araneidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Dipoena atlantica	DiAt	Theridiidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Dipoena santacatarinae	DiSa	Theridiidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Dipoena sp.	DiSp	Theridiidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Dipoena variabilis	DiVa	Theridiidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Eustala sp.	EuSp	Araneidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Faiditus sicki	FaSi	Theridiidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Larinia montecarlo	LaMo	Araneidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Leucauge sp.2	LeSp2	Tetragnathidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Miagrammopes sp.	MiSp	Uloboridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Mysmenidae sp.	MySp	Mysmenidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ocrepeira gnomo	OcGn	Araneidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Rhomphaea brasiliensis	RhBr	Theridiidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Scoloderus cordatus	ScCo	Araneidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Sphecozone diversicolor	SpDi	Linyphiidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Spintharus gracilis	SpGr	Theridiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Theridion teresae	ThTe	Theridiidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Thwaitesia affinis	ThAf	Theridiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Wirada sigillata	WiSi	Theridiidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Total abundance (N)			10	13	20	20	15	12	16	22	14	16	7	23	17	14	13	23	255
Total richness (S)			8	11	12	11	9	10	9	8	10	9	4	8	13	10	6	10	

SEGUNDO CAPÍTULO

Patterns of microhabitat selection by web-spiders (Araneae) in fragments of a Neotropical forest in southern Brazil

Trabalho realizado em conjunto com Sandra Maria Hartz

Abstract

The selection of habitat structures by spiders to attach their webs can have major consequences for animal’s biology and may shed some light on the mechanisms behind the community assembly patterns. In the present study we measured web site microhabitat selection by web spiders in fragments of Atlantic forest in relation to environmental variables. Study was carried out in 16 fragments of Atlantic Forest in southern Brazil. Field work was done in one landscape mosaic representing a slightly gradient of urbanization. Environmental variables encompassed mean bush density, land-use surroundings and fragment shape. We measured 12 microhabitat selection variables of 43 web spider species. Two microhabitat selection variables maximized the divergence and one maximized the convergence of behavioral characteristics along the environmental gradients. Functional diversity (divergence) of bush/tree leaves and twigs increased along the local communities associated to increased land-use surroundings patch composition. Convergence of vine twigs using was correlated to decreasing mean bush density. Our results highlight the concomitant presence of convergence and divergence assembly patterns of web spiders linked to environmental variables. Depending on the web spider microhabitat selection decisions, local communities may be limited in their similarity leading to species assortment or, on the other hand, habitat filtering may enhance the coexistence of web spider species with the same environmental requirements.

Key-words: fragmentation, assembly rules, habitat selection, environmental filtering, species assortment, limiting similarity.

Introduction

The selection of habitat structures by spiders to attach their webs can have major consequences for animal's biology. It may influence the extent of interactions with the environment and other species, and may also determine lifetime fitness (Henschel and Lubin 1997; Goldsbrough et al. 2004). The fixed webs do not act as simple filters, but perform different functions in prey capture (Eberhard 1990), so they are of utmost importance to colonization of new habitat and survival. Once a spider has selected a site, it moves only when prey capture is below some threshold and, because it cannot easily move great distances, it tends to remain in the same subhabitat (Mcnett and Rypstra 2000). Thus, the habitat structure of local patches affects the patterns of web spider colonization and establishment influencing the assembly of local communities.

It is understood that species have evolved biological and behavioral characteristics allowing them to exploit the given combination of resources represented in their niche (Legendre et al. 1997). Animal species distribution reflects the ecological heterogeneity of a region, the adaptations of individuals to physical conditions, and vegetation structure (Rickleffs 2008). Spatial distribution of web spiders in local vegetation patches within a regional landscape can provide information about their relative success in different habitats and suggest which features of the habitat contribute to their success. One way to describe habitat selection is to compare variation in specific habitat features at particular local habitats with the distribution of individuals of the species. Alternatively, one can relate biological (e.g. abundance) and behavioral characteristics (e.g. microhabitat selection) of animal populations to a set of environmental variables (Legendre et al. 1997). Species in a community tend to be similar in their ecological requirements (Weiher et al. 1998), which may lead to the convergence of web's attachment structures. On the other hand, the coexistence of species may be restricted by their similarity in microhabitat structures to construct the webs (Pillar et al. 2009).

The Atlantic Forest fragmentation originated various forest fragments distributed in a matrix of different land uses. The structural conditions of fragments within the landscape are mainly influenced by human use and management (Ribeiro et al. 2009). Web spiders may respond strongly to the pattern of local habitat structure (Uetz 1991) within fragments creating a non-directional variation in web spider metacommunity composition among the patches network (Anderson et al. 2011).

The study of the environmental factors driving the variation in arthropod biodiversity among forest fragments and the patterns of local community assembly is important in order to properly manage these fragmented and highly disturbed landscapes. Although spiders are ubiquitous generalist predators in most ecosystems and especially sensitive to environmental change (Cardoso et al. 2011), fewer studies have been performed on the responses of spider behavioral characteristics to predictors linked to forest fragmentation.

In the present study we used a method for discriminating convergence and divergence of behavioral characteristics in a metacommunity framework (Pillar et al. 2009) to evaluate the selection of attachment points by web spiders in forest fragments in relation to three environmental variables. From the results we were able to infer niche mechanisms partly responsible for the assembly of the local communities in the metacommunity (Leibold et al. 2004; Cottenie 2005; Carlucci et al. 2011). Based on 1) the assumption of weak interspecific competition among spiders (Wise 1993, Marshall and Rypstra 1999), 2) that web spiders in the studied system are not limited by dispersion (Baldissera et al. submitted), and 4) the uniformity in dispersal potential of web spiders (ballooning), we hypothesized that web spider selection of web attachment points shows only convergence of behavioral characteristics influencing the structure of web spider metacommunity.

Material and Methods

Study area

The study area is located in the Municipality of Torres, coastal plain of the State of Rio Grande do Sul, southern Brazil (UTM Coordinates 22 J 65756248 N – 620219 E). The altitude in the region ranges from 0 to 90 m, with a subtropical mesothermic and humid climate. The mean annual minimum and maximum temperatures varied from 15.6 to 22.3 °C respectively, and total annual precipitation was 1387 mm (meteorological data for 1962-90; Brasil [1992]).

The site was originally covered with Atlantic Forest vegetation, part of the Tropical and Subtropical Moist Broadleaf Forest biome, Serra do Mar Coastal Forests ecoregion [29]. This is the southern limit of the Atlantic Forest (*stricto sensu*) classified as Dense Ombrophilous Forest [30]. Field work was performed in one landscape mosaic representing a slight gradient of urbanization (Figure 1). The rural matrix consisted of small farms, with cattle breeding and farming as the main activities. Forest fragments were basically second-growth forests with old remnant trees interspersed with different degrees of regenerating stratum. Recently disturbed patches had fewer regenerating trees in the understory. The surrounding patches are of six types: agriculture (mostly beans, corn, and sugarcane), banana plantations, buildings, *capoeira* (forest succession early initial stage), *Eucalyptus* plantations, and pasture.

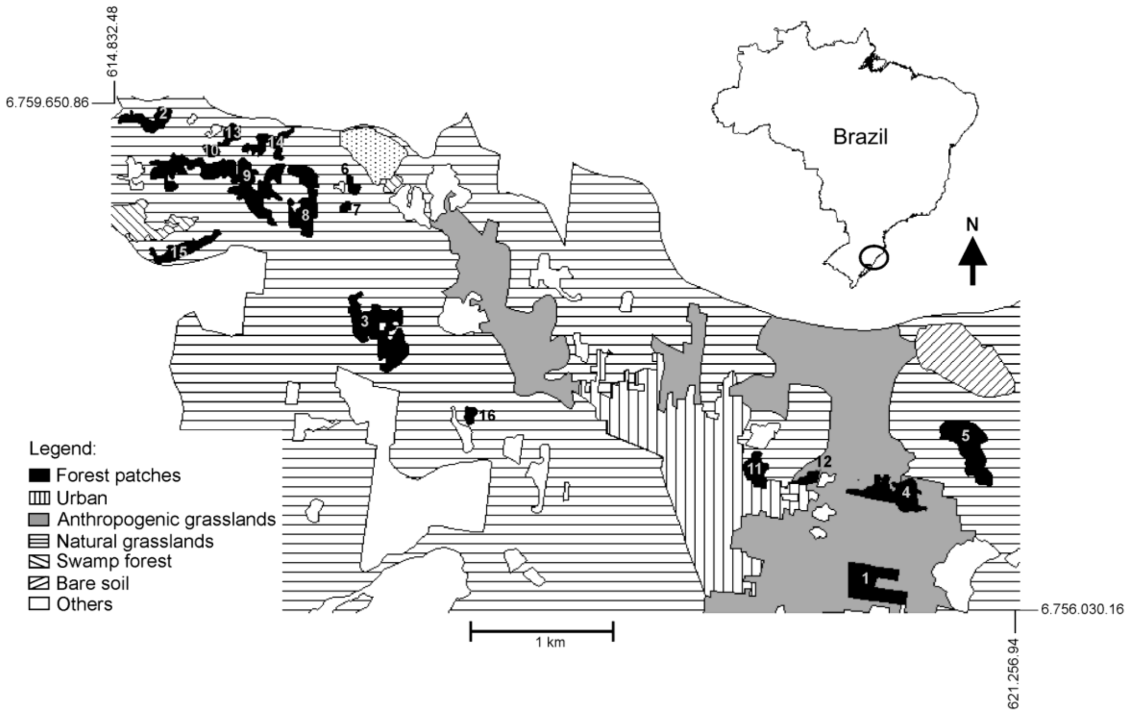

Figure 1 - Map showing the 16 forest patches of Atlantic Forest and the patch surroundings. Coordinates are in UTM system (22 J).

Sampling design

We sampled 16 forest fragments ranging from 0.4 to 13.7 ha in size, distributed in a landscape *ca*. 26 km^2 in area. Proportional sampling procedure was used to set the number of sampling units in each patch. We divided the fragments into three classes based on their sizes: two sampling units in each of 12 small-sized-fragments (< 5 ha), three units in each of two medium-sized fragments (6 to 10 ha), and four units in each of two large-sized (11 to 14 ha) fragments, totalling 38 sampling units.

Geographical coordinates of remnant centres were used in the field to set the sampling units. The centred sampling units should fall at least 30 m distant from the patch edge to circumvent the influence of edge effects. Each sampling unit consisted of cubic plots 12 × 2 × 2 m. The plots' height was measured from 0.20 m up to 2.20 m above the ground. Selection of sampling units in the field was done by sorting two, three or four out of the eight basic geographic directions. Sampling units inside each patch were pooled in order to perform the analyses.

Spider sampling

We collected only web spiders because (1) they are easily to find with the aid of a web highlighter, in our case wheat flour, (2) the distribution of these animals are strongly linked to variations in vegetation structure (Uetz 1991), and (3) microhabitat variables are easily measured in the field. Therefore, all web spiders found inside each plot between 0.2 – 2.2 m in height were manually collected by visual inspection after the collector spread the powder on the vegetation. Collections were made during dry days between March and July 2009. The time spent in each plot was dependent upon its vegetation amount and complexity, so it took from four to 20 hours to sample one individual plot. Each web spider collected was stored in an individual vial in 70% ethanol. Voucher specimens are deposited in the spider collection of Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul, in Porto Alegre, Brazil.

Microhabitat selection variables

We used 43 web spider species from which it was possible to measure 12 microhabitat selection variables *in situ* (Table 1). We measured the vertical distance between the spider and the ground, and the vegetation life forms utilized by the animal to fix the web prior to each web spider specimen collection in the field. Four basic types of plants were classified in the field: trees, bushes, palm trees, and vines. Trees were woody trees higher than 3 m in height, while bushes were between 0.5 and 2.95 m in height. Any part of a tree or bush that was an elongated shoot that arises directly from the stem was classified as *branch*, while any part of a tree or bush that was an elongated shoot that arises from the branches was classified as *twig* (i.e. a secondary branch). We separated leaves of palm trees from the others because of their particular configuration and size. However, palm tree stem was classified as *tree or bush stem* (depending on the palm tree height; see Table 1 for further details). Typically, *tree or bush twigs* were thinner than the *tree or bush branches*, which would influence the choice of a substrate by the web spiders. For each web spider population the microhabitat selection vector encompassed the presence or absence of each type of vegetation life form used by the species individuals, which reflects individual animal choice during web placement.

Table 1 - List of microhabitat variables measured for 43 web-spider species in 16 fragments of Atlantic Forest. All variables are binary.

Variable	Definition
Bush stems	Any stem part of a bush
Bush/tree branchs	Any branch part of a tree or a bush (see definitions on text)
Bush/tree leaves	Any leave part of a tree or a bush (see definitions on text)
Bush/tree twigs	Any twig part of a tree or a bush (see definitions on text)
Dry branchs	Any dry branch separated from the original plant
Dry leaves	Any dry leave separated from the original plant
Dry twigs	Any dry twig separated from the original plant
Height	Vertical distance between an individual spider on the web and the ground
Palm leaves	Any leave part of a palm tree
Tree stems	Any stem part of a tree
Vine leaves	Any leave part of a vine
Vine twigs	Any twig part of a vine

Enrivonmental variables

We utilized three predictors proved to influence the beta diversity distribution of web spiders in the forest fragments to construct the environmental matrix (**E**) (Baldissera et al. submitted): mean number of bushes, land-use surrounding, and remnant shape. We averaged the total number of bushes in each fragment in order to standardize the sample sizes. Fractal dimension *Frac* = 2ln[(P/4) / ln(A)] was used to assess patch shape, where *P* is the fragment perimeter and *A* is the patch area (McGarigal et al. 2002). Six types of land uses were found *in situ* surrounding the fragments: *capoeira*, *Eucalyptus* plantation, buildings, pasture, agriculture, and banana plantation. A presence-absence matrix of the land uses was constructed, and a PCA based on a product moment resemblance measure between variables was performed. The first ordination axis explained 76% of the variation in the composition of land uses surroundings the fragments. We interpreted the PCA first axis as a surrounding compositional gradient from solely pasture to more diversified surroundings (Baldissera et al. submitted).

Data analyses

The performance of each species in each forest patch comprised the matrix of species abundances $n \times p$ (matrix **W**). The microhabitat selection pattern of each web spider population was organized in a matrix $p \times s$ describing the s microhabitat variables for the p species (matrix **B**). A third matrix $n \times m$ characterized the forest fragments in relation to the three environmental variables.

Convergence and divergence of microhabitat variables

In order to relate the performance matrix (W) and the behavioral matrix (B) of web spider microhabitat selection to the environmental variables (E) we used the method proposed by Pillar et al. (2009). Briefly in each step of the analysis, the matrix **B** and the matrix **W** (after standardization by plot total) were used with the environmental matrix (**E**). From matrix **B** a matrix of Gower similarities (matrix $\mathbf{S_B}$) was obtained. The row totals in $\mathbf{S_B}$ were standardized and the resulting matrix (matrix **U**) defined degrees of belonging of each species i in the fuzzy sets defined for each species j = 1 to s species. Therefore **U** is a matrix of fuzzy sets defined by the microhabitat selection similarities between species. Afterwards, matrix **T** was calculated from the multiplication of **B’W**, which was composed by the mean microhabitat selection variables by community, and other **X** matrix were calculated from the multiplication of **U’W**, resulting in a description of metacommunity by the species taken as fuzzy sets. From the three matrices (**T**, **X** and **E**) it was computed pairwise resemblance matrices between local communities: $\mathbf{D_T}$, $\mathbf{D_X}$ and $\mathbf{D_E}$, respectively based on chord distances for $\mathbf{D_X}$, and Euclidean distances for $\mathbf{D_T}$ and $\mathbf{D_E}$ (after proper standardization of microhabitat selection variables by unit length in matrix **T**). Microhabitat selection convergence related to variation in **E** emerged from the correlation between matrices $\mathbf{D_T}$ and $\mathbf{D_E}$ (ρ[**TE**]). The correlation ρ(**XE**) between matrices $\mathbf{D_X}$ and $\mathbf{D_E}$ indicates both convergence and divergence of microhabitat selection variables related to the variation in **E**. Finally, microhabitat selection divergence patterns is found by a partial Mantel correlation [ρ[**XE.T**]) that remove the convergence component involved in the correlation ρ(**XE**). Therefore, we were able to verify (1) whether similarities in the environment are correlated with similarities in the microhabitat selection variables, i.e. microhabitat selection convergence along the environmental gradient; and (2) microhabitat selection divergence patterns, which reflects biological interactions that force organism to diverge along the environmental gradient.

Before abovementioned analysis we iteratively searched for microhabitat selection variables maximizing convergence assembly patterns and divergence assembly patterns (Pillar and Sosinski 2003). Afterwards, we used only the microhabitat selection set that maximized the concerned pattern (convergence/divergence). The statistical significances of microhabitat selection convergence and divergence were tested against null models (Pillar et al 2009).

We used stepwise multiple linear regressions of the metacommunity mean microhabitat variable maximizing TCAP on the environmental variables. The Rao's quadratic entropy index (Rao 1982) was used to measure the expected dissimilarity between two randomly chosen individuals from the sampled communities. In that sense, the index measures the diversity of microhabitat selection variables maximizing TDAP among populations. Rao's index was used as response variable in a stepwise multiple regression analysis with the three environmental predictors.

Results

We found convergence and divergence of microhabitat selection variables based on the environmental variables. Two microhabitat selection variables maximized the divergence pattern of web spider metacommunity: bush/tree leaves and bush/tree twigs (ρ[**XE.T**] = 0.340; P = 0.005). Backward stepwise multiple regression analysis showed a significant influence of land-use surrounding on Rao's quadratic entropy ($R^2 = 0.342$; $F_{1.13} = 6.768$; $P = 0.022$; Figure 2). Thirty two species used the bush/tree leaves as microhabitat selection, while bush/tree twigs were used 20 times.

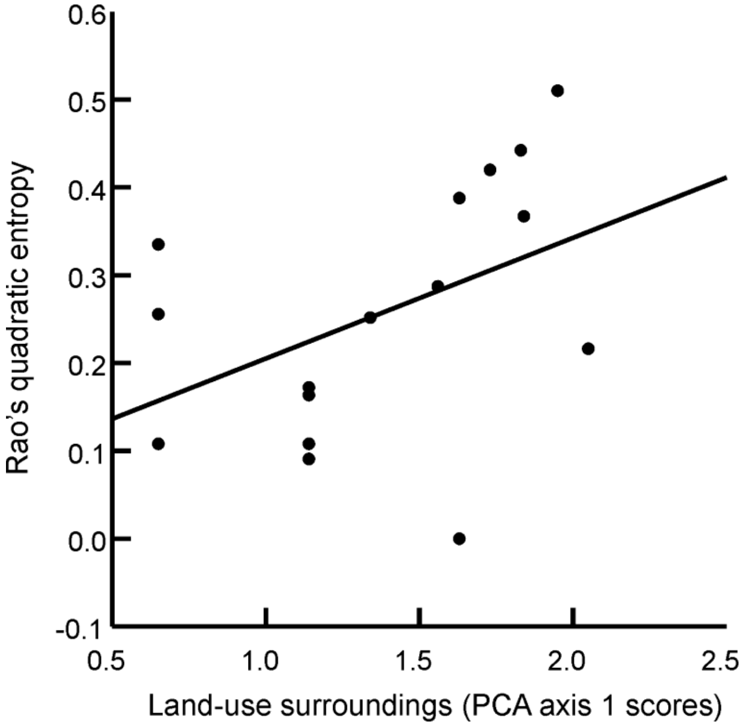

Figure 2 – Relationship of Rao's quadratic entropy based on bush/tree leaves and twigs microhabitat selection divergence patterns among web spider populations within local communities and land-use surrounding based on the scores of first axis of PCA ordination of land uses surrounding the fragments.

One microhabitat selection variable was important in maximizing the convergence assembly patterns of web spiders: vine twigs (ρ[**TE**] = 0.2; P = 0.042). Backward stepwise multiple regression analysis showed a significant influence of mean bush density on microhabitat selection variable ($R^2 = 0.430$; $F_{1.12} = 9.040$; $P = 0.011$; Figure 2).

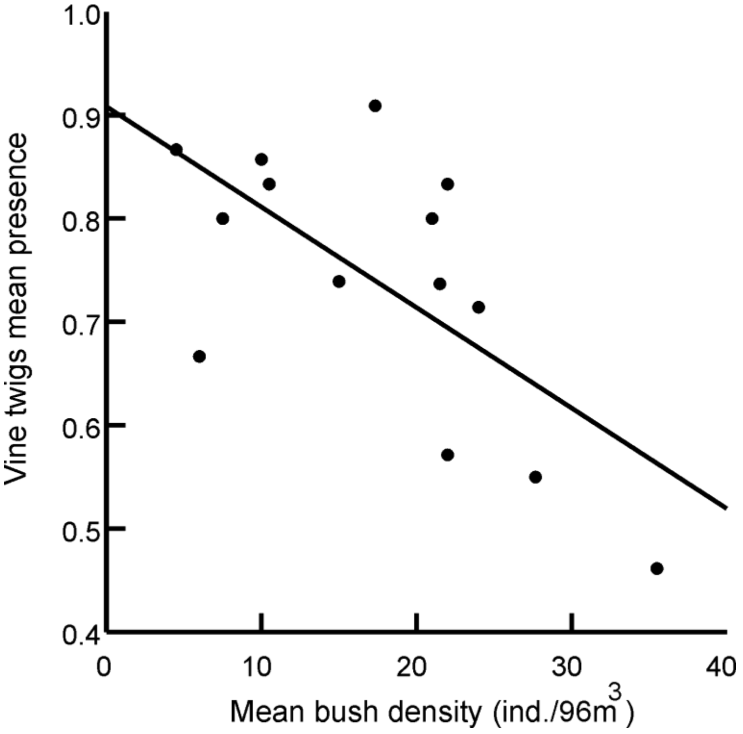

Figure 3 – Relationship between vine twigs microhabitat selection (averaged at community level - matrix T) and mean bush density of fragments.

Discussion

Habitat selection in sit-and-wait predators such as web building spiders may determine lifetime fitness, because movements to new web sites occur only once or at most a few times in their lifetime (Riechert 1976; Ward & Lubin 1993). The method used in the present study permitted assessment of patterns of microhabitat selection between populations scaled up to local communities. Therefore, we were able to assess similarities (underdispersion) and dissimilarities (overdispersion) in the ecological requirements of web spider species that colonized forest fragments and its relationship with environmental gradients (Pillar et al. 2009).

There is a tendency for increasing divergence of web attachment points in fragments with more diversified surroundings. These surroundings characterized fragments not influenced by cattle foraging, which may increase the amount of vegetation structures to web construction in the forest understory. The web spider populations in these fragments do not share the resources. Instead, decisions of which resource to use diverge among populations leading to overdispersion of microhabitat selection variables. In that sense, we can suppose there was an increase of exploitative competition for optimal web sites leading to limiting similarity in fragments showing more available microhabitats. However, it may be that the individuals colonizing these fragments show different resource utilization patterns because they came from the different patches in the vicinity of the fragments. Therefore, divergence in microhabitat selection may be simply a result of the inherent habitat-related traits of each population colonizing the fragments, which permit co-existence.

The convergence pattern of local web spider communities was linked to the presence of more closed understorys. Web spiders in fragments with fewer bushes tended to converge in the selection of vine twigs as web sites. In that sense, the decrease in the amount of vegetation structures to the establishment of spider webs leads the individuals of the populations to converge in the use of other available resources. The use of alternative resources may affect population growths, but spiders may in fact select diverse microhabitats more in response to physical factors and vegetation structure than in response to competitive interactions (Horton and Wise 1983; Mcnett and Rypstra 2000).

The populations scale decisions about the type of resource to construct the webs drive the local communities either to limiting similarity (divergence) or to habitat filtering (convergence). Other studies pointed that communities can be simultaneously constrained by both types of filters, so that microhabitat selection associated with environmental filtering may be clustered, while microhabitat selection associated with interactions may be overdispersed (Weiher et al. 1998; Weiher et al. 2011).

Microhabitat selection decisions seemed important in structuring the web spider metacommunity in this fragmented forest. We were able to show that convergence or divergence in the web attachment structures used by web spiders can be dependent on the environment conditions. Therefore, local habitat structures resulting from the use and management of forest fragments may be determinant to the assembly patterns of top-predators in the local communities with potentially effects on arthropod food chain.

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TERCEIRO CAPÍTULO

Experimental colonization of spiders (Araneae) in patches of vegetation with different sizes and habitat diversities

Trabalho realizado em conjunto com Sandra Maria Hartz e Everton Nei Lopes Rodrigues

Abstract

Establishment of communities is a dynamic process initiated with immigration. Therefore, movements of individuals within a metacommunity is important to species maintains and increases its distribution. We present a mesoscale landscape-level experiment that manipulates habitat size and diversity. We examine rates of colonization, immigration activity, richness, and composition of foliage dwelling spiders. Estimation of colonization rates was based on maximum likelihood estimation. Landscape was manipulated such that confounding explanatory factors were controlled. It was composed of five blocks with four patches (two big – 1 m^2 and two small – 0.25 m^2). Less diverse patches had seedlings of one plant species, whereas more diverse patches had four species. Periodic census of spiders arriving to the patches was done during eight times (28.2 mean days). Initial composition of colonizers was significantly different from final composition, but rates of colonization did not differ between sizes and diversities, and there was no factor interaction. Total abundances of spiders were positively influenced by patch size and negatively by diversity, whereas adult abundances responded positively to patch size. Pooled richness of spiders was determined mainly by spider abundance. Compositions in each temporal sample are determined by differences in the species pool migrating and arriving at experimental landscape irrespective of habitat size or diversity. Larger patches are more likely to receive more colonists representing a wider array of species than small patches. Probability of colonization is independent of patch size and diversity, which contradicts theoretical predictions. Immigration seems to be unimportant to determined diversity patterns of spider communities.

Keywords: Immigration, Passive sampling, Community composition, Temporal variation.

Introduction

The establishment of ecological communities is a dynamic process. It is initiated with immigration, the movement of organisms from the regional pool of species to a target habitat. What comes next is the phenological development of organisms in that habitat, which must culminate in reproduction in order to establish the species. The population growth in the local community is determined by the set of available resources and the interactions with other species. Therefore, there is a limit to the population growth and individuals exceeding the limit must either die or disperse to other habitats. In that sense, immigration within the local communities is of utmost importance in order to a species maintains and increases its distribution in the suitable habitats within a landscape. Populations within a community exhibit different dispersal potential based on their traits and this limits the dispersal activity of individuals.

The process of colonization includes survival and establishment as well as immigration (Lomolino 1990). Colonization is a key process in the Theory of Island Biogeography (TIB), which proposed that the number of species arriving on a given island would depend on the size of the island in question, as well as on its distance from a mainland that serves as a species pool (Clark & Rosenzweig 1994). This is the definition of the *area per se* hypothesis. But the *habitat diversity* hypothesis postulates that larger areas may have more habitat diversity, and hence more species, than small areas (Nilsson et al. 1988). The TIB was appropriated in early years of fragmentation research to fit the patterns of diversity observed in habitat islands, but ecological process in remnants are in various ways critically influenced by direct interactions with surroundings, whereas such interactions are negligible in oceanic islands (Haila 2002).

Cause and effect between habitat fragmentation and ecological processes can only be inferred reliably from study designs with replicated treatment allocation randomized among an adequate sample of experimental units (McGarigal & Cushman 2002). Experimental examination of the dynamics of species colonization in local communities and the associated changes to species richness and abundances at regional scales is extremely difficult to perform. However, small-scale experimental landscapes may provide some idea of the factors involved in setting the rate and extent of colonization in fragmented landscapes.

While several papers assessed the responses of spider community richness and abundance to patch area and diversity (e.g. Pajunen et al. 1995; Miyashita et al. 1998; Baldissera et al. 2008; Bolger et al. 2008; Kapoor 2008; Johnson et al. 2010), studies of colonization rates of spiders using data from periodic surveys are rare. Typically, researchers did comparative studies of colonization between different habitats by considering the initial arrival and establishment of spiders on patch habitats as colonization (e.g. Sackett et al. 2009). While this approach is valid to compare spatially different habitats, it tells nothing about the likelihood of colonization and its relationship with environmental factors like patch size and diversity. This information is crucial to understand the importance of temporal variation in the structure of populations to the emergent community structure.

In this paper, considering that the effect of the pattern of landscape on spider community responses is more effective in a fine scale (De Mas et al. 2009), we present a small-scale landscape experiment that manipulates habitat size and diversity in a complete randomized block design. Specifically, we examine the rates of colonization, immigration activity (abundance), richness, and composition of foliage dwelling spiders. This study employs a method based on maximum likelihood estimation to assess colonization rates from periodic surveys (Clark & Rosenzweig 1994). The landscape was manipulated in such a manner that confounding factors supposed to influence the spider responses were controlled. Therefore, shape of patches, distance among patches, and matrix surroundings were all held constant.

The experimental landscape was composed of five blocks with two levels of patch area: large and small-sized, and two levels of patch diversity: more and less diverse. Comparison among these different patch treatments provides insight into the relative importance of size and diversity to spider colonization. When patch size is important, independently of patch diversity, we may infer that the area per se hypothesis (Connor & McCoy 2001) is the main mechanism shaping the colonization. If patch diversity is important, independently of size, the probable important mechanism is the habitat heterogeneity hypothesis (Cramer & Willig 2005). If size and diversity both influence the colonization rates in the same direction, the increase in patch diversity is linked to increasing patch size. Based on the predictions of island biogeography theory and on the assumption that spider distribution and occurrence are strongly influenced by habitat structure (Uetz 1991) we expect an increase in colonization rates of spiders in bigger and more diverse patches.

Methods

Experimental design

We conducted the study in five replicated experimental blocks within a matrix of grassland in the coastal plain southern Brazil. The experiment was isolated from early successional vegetation, mainly sparse bushes, and a *Pinus* hedgerow by at least 10 m (Figure 1). Each block consisted of four vegetation patches with two treatments (factors): size and diversity. The patches were composed of plant seedlings of three native woody species and one artificial species. Native seedlings showed markedly morphological differences (Table 1): *Citharexyllum montevidense* (Verbenaceae), *Eugenia uniflora* (Myrtaceae), and *Tabebuia chrysotricha* (Bignoniaceae). Each natural seedling was rooted in plastic pots with a hole on the bottom to allow root growing. The artificial seedlings were constructed with three 20 cm long wood rods mimicking vegetation twigs with five artificial leaves made of nonwoven tissue in each rod. The rods were partly buried in sand within plastic pots. We inserted an artificial seedling with simple architecture to ensure a broad range of variation in diversity in the more diverse patches. Factor *size* was divided in big squared patches (1 m^2) composed of 32 seedlings, and small squared patches (0.25 m^2) composed of eight seedlings. Factor *diversity* was divided in more diverse patches composed of seedlings of the four species, and less diverse patches composed of just one randomly selected species (*Eugenia uniflora*). Distance between two consecutive seedlings was 10 cm. We randomly assigned the position of each seedling group in each experimental unit as well as the position of each experimental unit within each block.

Sampling procedure

Prior to spider sampling we removed all insects and spiders from seedlings. We censused all spiders that colonized the experimental units by manual collection eight times. The first sample was carried out in December 2010, thirty days after the experiment was set. The mean days between two consecutive samples varied from 27.3 to 30.4 depending on the block. The spider collections were carried out in dry days and the variation in the intervals of days between samples reflect rainy days that postponed the sample in that particular period. All collected spiders were put in vials with alcohol and the adult individuals were identified at species level whenever possible. We assumed species showing at least one adult individual as a colonizer irrespective of sex status. Although it is a simplistic assumption, we reasoned that any solitary male or female that arrives or matures in a patch found suitable habitat to establish there. Therefore they are potential breeding individuals. Voucher species are deposited in the spider collection of Museu de Ciências Naturais of Fundação Zoobotânica do Rio Grande do Sul, in Porto Alegre, Brazil.

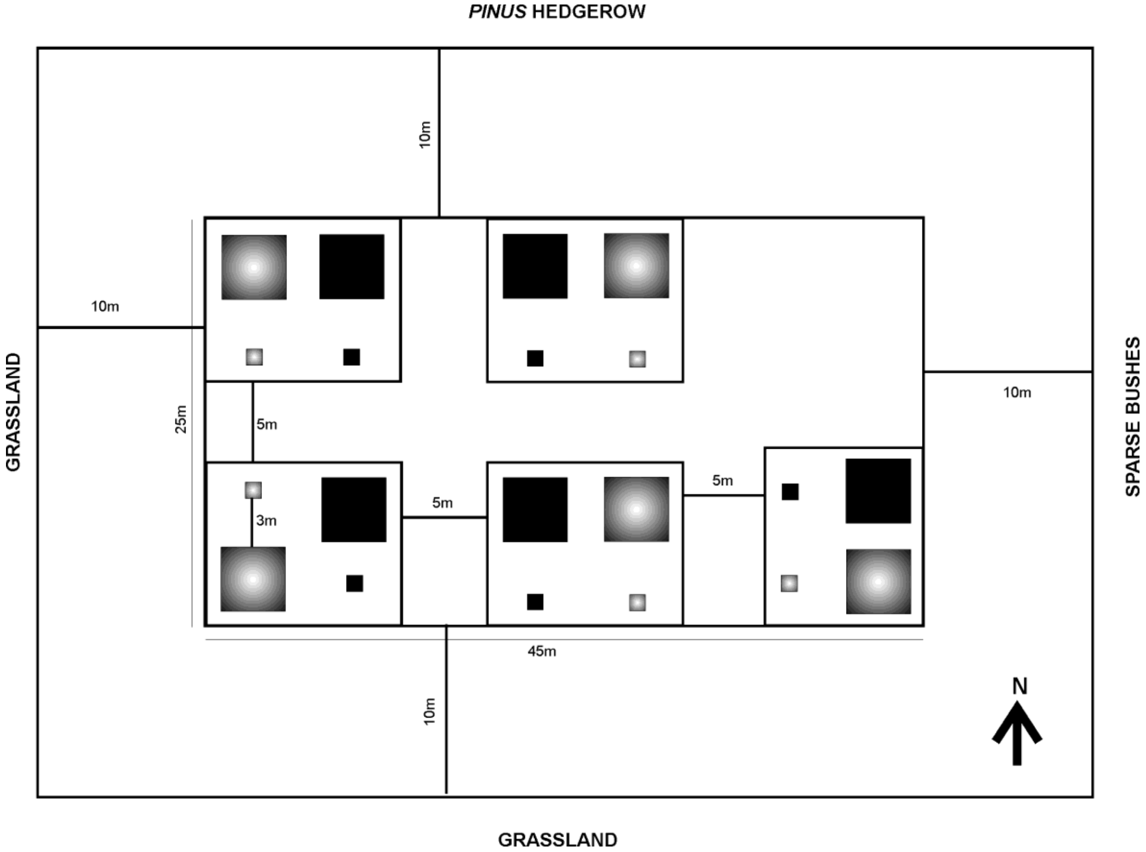

Figure 1 - Experimental landscape showing the five blocks with the two levels of factors. Black squares = less diverse patches; shaded squares = more diverse patches. Matrix was composed of managed grassland. Factor levels were assigned randomly to each patch within blocks.

Data analyses

We utilized the method for estimating colonization rates from sporadic census data developed by Clark and Rosenzweig (1994). The method estimates the colonization rate for one species by first calculating parameter *k* = number of transitions from absence in time *T* to presence in time *T + 1*... *T + 8* and parameter *l* = number of transitions from absence to absence in the same time frame. The colonization rate λ = *k / k + l* is the probability that a species not present in the community will enter it in a given time interval. In our case the time interval is 28.2 mean days. We assumed that the probability of colonization is the same for all species in the experimental units and grouped the data for all species on each experimental unit (Clark and Rosenzweig 1994). We assessed the variation in mean colonization rates of spiders between factors size and diversity by a permutational two-factor anova based on a Euclidean distance dissimilarity matrix between sampling units restricting random allocations within the defined blocks. We performed 1000 permutations to assess significance of factor effects on colonization rates.

We assessed temporal changes in the richness, total abundance, adult abundance, and composition of spiders among the eight time periods. Richness and abundances variations were assessed by performing repeated measures two-factor anovas based on Euclidean distance dissimilarity matrices between sampling units. Variation in the composition of spider species was analyzed by performing a repeated measures two-factor permanova based on a chord distance dissimilarity matrix between sampling units. Abundance matrix was subjected to log (x + 1) transformation. The repeated measure analyses were performed by restricting random allocations within the eight time periods. The approach allowed us to evaluate the variation in the spider richness, abundances, and composition between the eight time periods, between the two factors, and the interaction terms (1000 permutations). A PCoA ordination was carried out to visualize the distribution pattern of sampling units according to species composition (Pillar 1999a).

We utilized Multiv v. 2.63b to perform permutational anovas and manova, and ordination. Multiv utilizes randomization tests to compare groups of sampling units based on a sum of squares between groups as test criterion (Pillar and Orlóci 1996). The results are interpreted similarly to the ones in an analysis of variance table.

Results

A total of 2183 spiders were collected during the experiment distributed in 19 families. Fifty spider species were identified from 575 adults. Web spiders were the most speciose and abundant spider group with 33 species (66% of total richness) and 394 individuals (69% of total abundance). The most speciose and abundant family was the web spider Theridiidae with 22 species and 345 individuals. The cursorial Salticidae was the second most speciose family with seven species. Three of most web spider abundant species was theridiids *Cryptachea hirta* (n = 129), *Theridula gonygaster* (109), and *Anelosimus ethicus* (25). *Cheiracanthium inclusum*, the only Miturgidae (cursorial) species was the second most abundant species with 102 individuals. Predictably the same abundant species showed higher occurrences in the 160 temporal samples showing a dispersal limitation among the species.

The rates of colonization did not differ between sizes (SS = 0.0006; P = 0.399) and diversities (SS = 0.0014; P = 0.222), and there was no significant factor interaction (SS = 0.00004; P = 0.849). However, the composition of spider species was significantly different among time periods (SS = 9.223; P = 0.001), but there was no interaction between time and size (SS = 5.04; P = 0.218) or diversity (SS = 4.723; P = 0.368). Ordination scatterplot showed three distinct spider compositions along the time corresponding to initial, intermediate and final stages of the experiment (Figure 2).

Mean total abundances of spiders (migration activity) did not differ among times (SS = 458.49; P = 0.65) and there were not interactions between time and size or diversity (SS = 295.99; P = 0.863 and SS = 506.94; P = 0.58, respectively). Therefore, we pooled total abundances and performed a two-factor permutational anova. Pooled abundance of spiders was influenced by patch size and diversity. Mean abundances was higher in larger patches (SS = 86461; P = 0.004) (Figure 3) and in less diverse patches (SS = 7644; P = 0.02) (Figure 4). There was no interaction between the two factors (SS = 120.05; P = 0.654).

Adult mean abundances were significantly different among time periods (SS = 478.94; P = 0.001), but there was no interactions between time and size (SS = 84.144; P = 0.236) or diversity (SS = 36.494; P = 0.789). Mean richness followed the pattern of adult abundances; there was a significant time effect on mean richness (SS = 187.17; P = 0.001), but no interaction of time and size (SS = 24.3; P = 0.405) or diversity (SS = 18.575; P = 0.574). Mean richness of spiders at the eight times were highly correlated to spider abundances ($R^2 = 0.961$; $F_{1.6} = 147.83$; $P < 0.0001$).

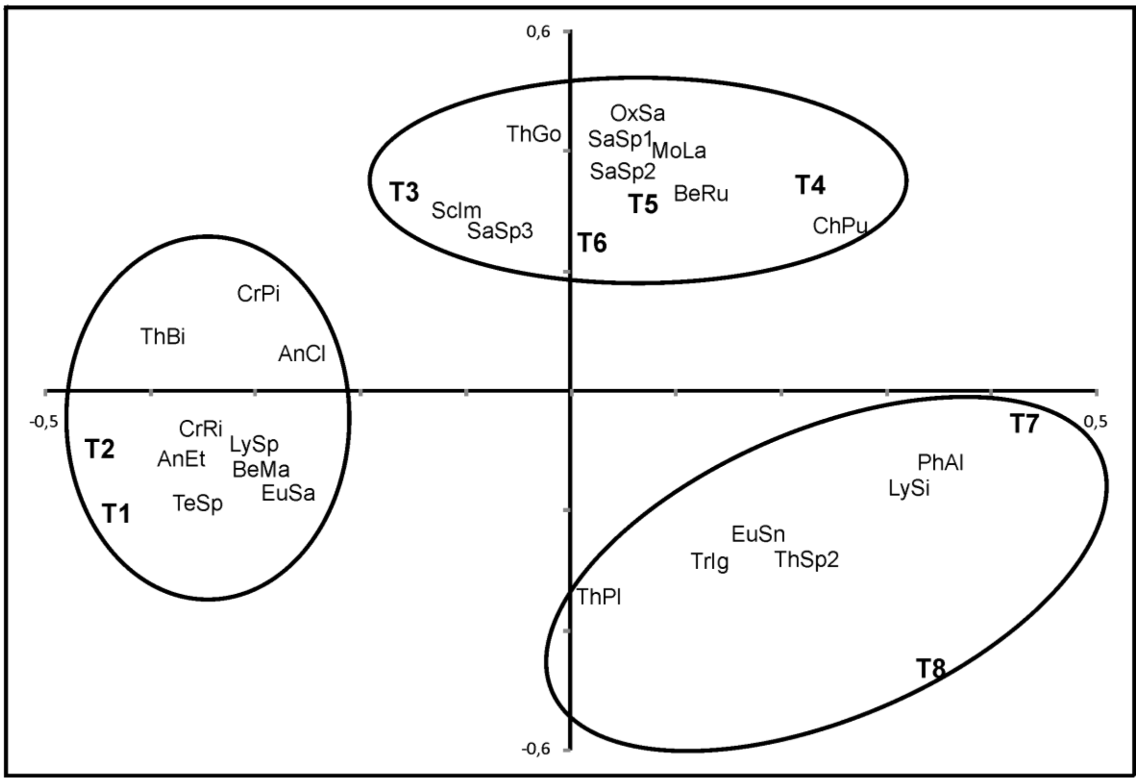

Figure 2 - Resulting axis 1 and 2 of the PCoA ordination based on chord distance dissimilarity between the eight time periods. T1… T8 = time periods. Species showing the highest correlation coefficients with the axes: AnCl: *Anodoration claviferum*, AnEt: *Anelosimus ethicus*, BeMa: *Berlandiela magma*, BeRu: *Bertrana rufostriata*, ChPu: *Chrysso pulcherrima*, CrPi: *Cryptachea pinguis*, CrRi: *Cryptachea rioensis*, EuSa: *Eustala saga*, EuSn: *Eustala sanguinosa*, LySi: *Lygarina silvicola*, LySp: *Lygarina* sp., MoLa: *Mopiopia labyrinthea*, OxSa: *Oxyopes salticus*, PhAl: *Phycosoma alta*, SaSp1: Salticidade sp.1, SaSp2: Salticidae sp.2, SaSp3: Salticidae sp.3, ScLm: *Scytodes imbituba*, TeSp: *Teudis* sp., ThBi: *Theridion bisignatus*, ThGo: *Theridula gonygaster*, ThPl: *Theridion plaumanni*, ThSp2: *Thymoites* sp.2, TrIg: *Triplogyna ignitula*.

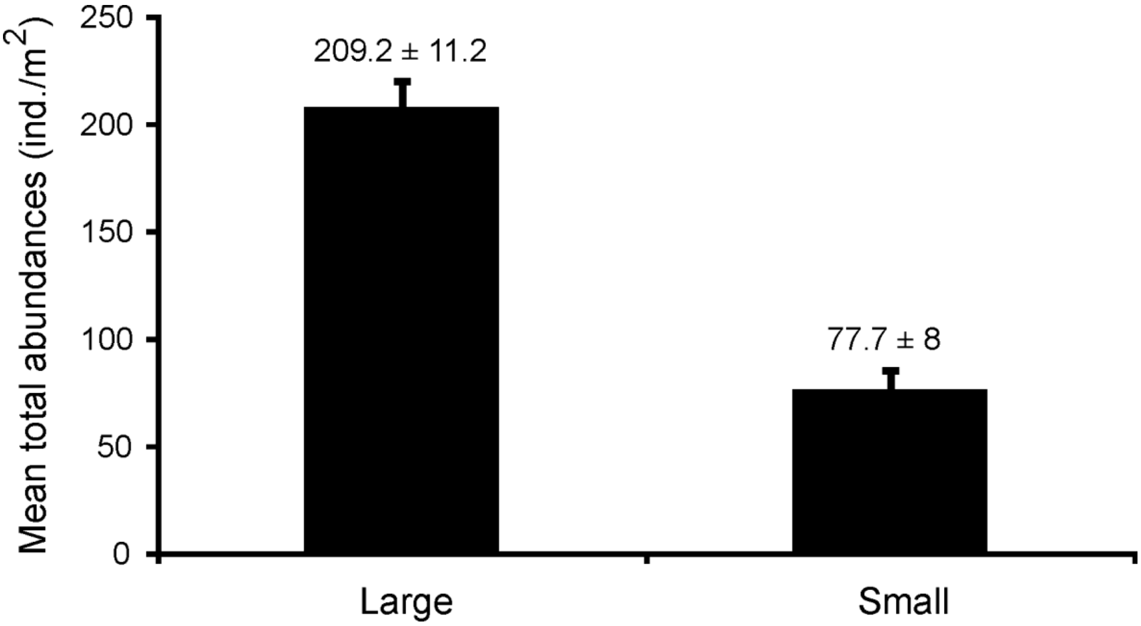

Figure 3 – Mean ± standard errors of spiders collected in large and small experimental patches of vegetation. Data pooled for the eight time periods.

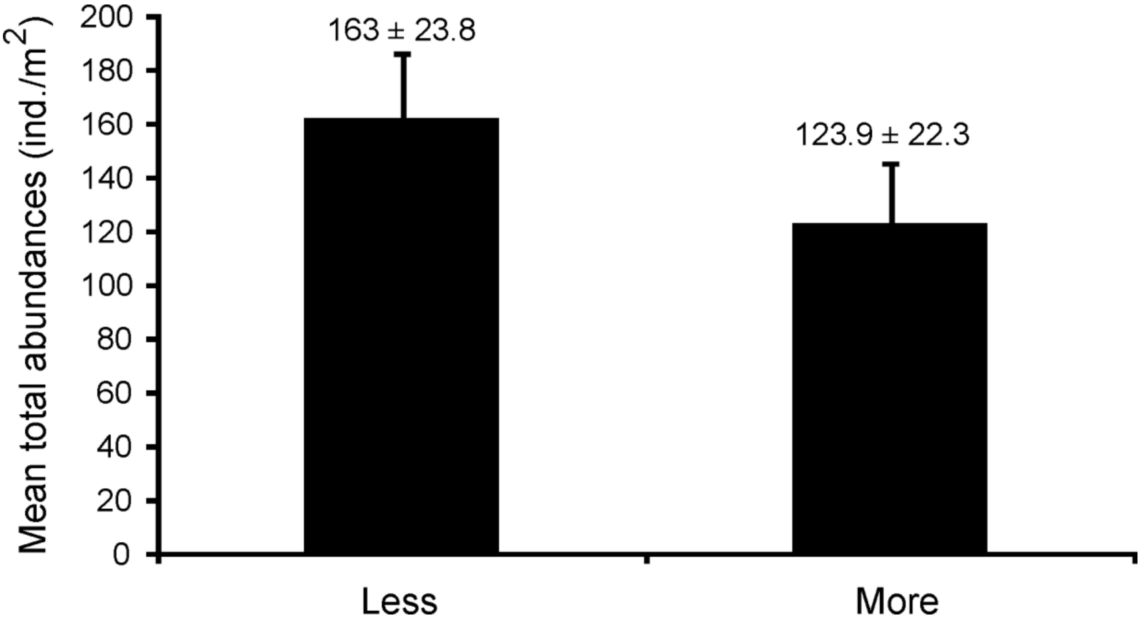

Figure 4 – Mean ± standard errors of spiders collected in less diverse and more diverse experimental patches of vegetation. Data pooled for the eight time periods.

Discussion

In this study, we observed that rates of colonization of spider community in an experimental landscape were not affected by size and diversity of habitat patches, in spite of temporal changes in spider composition of colonizers. This finding contradicts theoretical predictions of increased colonization rates in large areas. Under the regime of continuous change imposed to the spider community, its structure undergoes continuous adjustment and has a dynamic form (Loreau et al. 2001). Defaunation of patches occurred at very short time periods, which emphasizes the capacity of spider community to initiate rapid succession after disturbances (Stefano et al. 2007; Fattorini & Borges 2011). On the other hand, we found significant variation in migratory activity of spiders associated to patch size and diversity.

Measurements of colonization rates take in account the probability that a species absent in previous time will be present in the next consecutive time. The method proposed by Clark and Rosenzweig (1994) also calculates extinction rates, which, in the present study, were artificially manipulated once we performed periodic census of spiders, which means that the community was periodically extinct. We can infer there is a continuous flux of immigrants able to continuously arrive at the vegetation patches, a pattern also found for spider community in a Brazilian cerrado experiment, where spiders were the only taxon that continuously colonizes litter plots (Vasconcelos et al. 2009). In spite of this steady state in colonization rates, there is a series of compositional changes during the time, which alter the previously composition of species. These changes were pronounced at the end of time, suggesting that frequently intense disturbances may lead the spider community away from its initial state. This indicates that initial spider community composition is largely determined by temporal differences in the pool of species that migrate and arrive at the experimental landscape irrespective of habitat size or diversity. Ballooning is presumed to be an efficient mechanism for distant dispersal and hence for colonization of suitable but unoccupied habitats (Duffey 1998; Bonte et al. 2004), but due to the short time frame between samples in the present study it can be that adult spiders undergo short-distance dispersal even by ballooning or via ground in the case of cursorial species (Samu et al. 2003).

Migration activity in our study was positively related to patch area. The result indicates that positive relationship between abundance and area may be established already at early colonization of patches matching the passive sampling hypothesis (Connor & McCoy 2001). The short time frame between consecutive samples in our study allows us to discard strong interspecfic interaction effects in structuring the spider community and hypothesis linked to resource concentration (Root 1973) may be disregarded as explanation to the pattern. Therefore, we must consider mechanisms linked to community dispersal to explain area effects. Hambäck & Göran (2005) emphasized the importance of search mode of animals in the observed relationships between insect density and patch size. In that sense, the spider behavior may be equivalent to some contact searchers (Bukovinszky et al. 2005), which are essentially unable to identify suitable habitat before alighting on the substrate. Spiders disperse mainly by short or long distance ballooning in a chaotic atmosphere (Suter 1999). Consequently, dispersers have little control over their ultimate destination and the decision to stay or leave a substrate is based on tactile clues after landing. Therefore, larger patches may passively receive more colonists. Hambäck & Göran (2005) set two parameters that define the model for the relation between animal density and patch size, one scaling emigration and other scaling immigration to patch area. Their model predicts that animals with a behavior such that the latter parameter is greater than the former show a decreasing density with patch size in small patches and increase density with patch size in large patches. The influence of emigration in our study is minimal, because we lead the local communities to periodic extinction. Therefore, we were not able to unequivocal confirm the validity of their model to explain our data, but the importance of the model to explain abundance-area relationships in spider communities should be further analyzed.

We did not find temporal variation in migration activity of spiders following the defaunations. A different pattern was found for spider abundance in a study in Brazilian cerrado following a fire disturbance (Vasconcelos et al. 2009). However, their study did not manipulate spider numbers, indicating the high capacity of spider community to increase abundance through time. We infer that the negative relationship between total spider abundance and patch diversity in our study characterizes a major feature of spider community immigration pattern in this experimental landscape. Other studies also failed to encounter significant relationship between plant diversity and arthropod abundances, but there was evidence of increased predator abundance in areas of high plant productivity and small diversity (Siemann 1998; Koricheva et al. 2000; Perner et al. 2005. Possible effects linked to prey abundance seems to be unimportant in shaping spider abundance in this study because there was not enough time between consecutive samples to allow important interactions between spider community and other arthropods. Therefore, the smaller abundance of immigrants in more diverse patches can be a response of spider community to other aspects of habitat structure. Because web spiders comprised 70% of immigrants, it may be that the plant habitat in less diverse patches provides particular structures to support web construction.

In the manipulative experiment employed in this study, we were able to physically manipulate attributes of the landscape in a controlled manner, while holding patch size and diversity constant. Therefore, the control over variation and confounding factors like patch isolation, shape, edge effect and matrix surrounding allows us to attribute many of observed patterns to the imposed factors. Additionally, the short time frame between two consecutives samples maintained the spider communities at initial succession stage. In that sense, immigration from the pool of species in the surrounding landscape can be viewed as the principal mechanism that affected the local spider communities in the study. The results suggest that rates of colonization of spider community are uniform irrespective of spider composition turnover along the time.

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Appendix 1 – List of species collected during the entire experiment.

Species	Family	N	PRESENCE
Anelosimus ethicus	Theridiidae	25	20
Anodoration claviferum	Linyphiidae	3	2
Aphirape aff. uncifera	Salticidae	6	5
Araneus unanimus	Araneidae	1	1
Argiope argentata	Araneidae	1	1
Berlandiela magma	Philodromidae	5	3
Bertrana rufostriata	Araneidae	4	4
Cheiracanthium inclusum	Miturgidae	102	56
Chrysso pulcherrima	Theridiidae	5	5
Cryptachaea hirta	Theridiidae	129	78
Cryptachaea passiva	Theridiidae	2	2
Cryptachaea pinguis	Theridiidae	10	9
Cryptachaea rioensis	Theridiidae	8	7
Cryptachaea sicki	Theridiidae	3	3
Deinopis aff. amica	Deinopidae	1	1
Dipoena sp.	Theridiidae	2	2
Eustala saga	Araneidae	9	9
Eustala sanguinosa	Araneidae	1	1
Exalbidion sp.	Theridiidae	1	1
Lygarina silvicola	Linyphiidae	15	14
Lygarina sp.	Linyphiidae	5	4
Meriola cutiformis	Corinnidae	1	1
Misumenops maculissparsus	Thomisidae	1	1
Misumenops sp.	Thomisidae	1	1
Mopiopia labyrinthea	Salticidae	10	8
Neospintharus rioensis	Theridiidae	3	3
Oxyopes salticus	Oxyopidae	20	16
Parasteatoda tesselata	Theridiidae	1	1
Phycosoma alta	Theridiidae	13	10
Salticidae sp.1	Salticidae	6	6
Salticidae sp.2	Salticidae	3	3
Salticidae sp.3	Salticidae	4	4
Salticidae sp.4	Salticidae	2	2
Scytodes aff. imbituba	Scytodiidae	4	4
Sphecozone rubescens	Linyphiidae	8	5
Steatoda iheringi	Theridiidae	2	2
Tariona sp.	Salticidae	1	1
Tasata sp.	Anyphaenidae	2	2
Teudis sp.	Anyphaenidae	12	7
Theridion bisignatus	Theridiidae	15	13
Theridion pernambucum	Theridiidae	1	1
Theridion plaumanni	Theridiidae	9	7
Theridion sp.	Theridiidae	2	2
Theridula gonygaster	Theridiidae	109	59

Thomisidae sp.1	Thomisidae	1	1
Thwaithesia affinis	Theridiidae	2	2
Thymoites sp.1	Theridiidae	1	1
Thymoites sp.2	Theridiidae	1	1
Tidarren haemorroidale	Theridiidae	1	1
Triplogyna ignitula	Linyphiidae	1	1
TOTAL		575	

CONSIDERAÇÕES FINAIS

A pesquisa ecológica de comunidades de aranhas

A literatura de pesquisas de fragmentação florestal *stricto sensu* envolvendo comunidades de aranhas é ainda insipiente. Apesar de ser um grupo de predadores abundante e fortemente influenciado pela estrutura de hábitats, a pesquisa de comunidades de aranhas ligada à fragmentação ainda precisa progredir muito para fazer frente aos desafios constantes da ação humana sobre as florestas, principalmente nos trópicos. Por que essa limitação? Parece que, historicamente, a pesquisa de ecologia de aranhas ficou relegada ao segundo plano. Citando Bell (2005) "parece que muitos pesquisadores trabalhando durante a fase embrionária da ecologia de aranhas ficaram isolados sem quase nenhuma troca de informações". Além disso, esse autor afirma que "é evidente que a maioria dos estudos realizados nos inícios da pesquisa em ecologia aracnológica teve somente um interesse periférico no teste de teorias ecológicas. Isso explica por que a ecologia de aranhas estava estagnada e se mantinha ensimesmada durante um período em que outras disciplinas abraçaram a interação entre teoria, experimentos e estes empíricos." Claramente, pesquisas abordando a ecologia de insetos, por exemplo, deram várias contribuições ao desenvolvimento da ecologia de invertebrados. A teoria de concentração de recursos (Root 1973) é um exemplo. Isso é tão aparente, que revistas entomológicas publicam pesquisas aracnológicas. Adicionalmente, o viés zoológico, de uma ciência mais descritiva e baseada em processos em nível de indivíduos e populações parece ter mais adeptos entre os pesquisadores.

Apesar disso, vê-se que a pesquisa em ecologia de comunidades de aranhas tem crescido nos últimos anos. Muitas perguntas básicas ainda precisam ser respondidas: por que a contradição na resposta de aranhas aos efeitos da fragmentação? Será um efeito amostral ou um padrão intrínseco? Qual a influência de fatores ambientais e espaciais nos padrões encontrados? O balonismo é um processo puramente *estocástico*? Como atributos funcionais respondem às variações no ambiente? Essas são apenas algumas, dentre várias, perguntas que podem dar origem a pesquisas no campo da ecologia de comunidades de aranhas, as quais trariam luz sobre pontos importantes da própria teoria ecológica.

Limitações nos métodos

Alguns pontos em relação a limitações dos experimentos realizados devem ser ressaltados nessas considerações finais. Em primeiro lugar, o pequeno tempo de amostragem do experimento mensurativo nos remanescentes. Porém, essa constatação ficou clara para mim somente após a identificação das aranhas. Por experiência, supus que em torno de 15% dos indivíduos coletados poderiam ser identificados em nível específico; porém, esse número mal passou de 5%, o que diminuiu muito o tamanho amostral (dos mais de 3800 indivíduos, o previsto era que 600 pudessem ser identificados). Alie-se a isto o fato de que jovens aranhas, geralmente, não são consideradas nas análises estatísticas. Originalmente, as coletas deveriam ter sido iniciadas em dezembro de 2008. Porém, nas primeiras coletas, já percebi que seria inviável continuar com o mesmo esforço amostral, ou seja, quatro parcelas em remanescentes menores, seis parcelas em médios e oito parcelas em maiores. Como vários atributos de cada indivíduo e muitas outras variáveis ambientais eram medidas, o tempo de coleta de dados ficou muito grande. É claro que se poderia ter pensado em um desenho não proporcional... Mas, pensando-se em relações espécies-área, esse tipo de desenho fica mais plausível em manchas homogêneas. E, *a priori*, remanescentes de florestas tropicais apresentam heterogeneidade interna de habitats, principalmente considerando-se a presença de impactos constantes por ação humana.

De qualquer forma, essa é uma crítica legítima. E penso que poderia ter feito uma mega-coleta e direcionado o esforço até mesmo para fazer coletas sazonais (dois anos seguidos, ou mais), o que também daria condições para realizar testes metapopulacionais. Porém, o projeto de doutorado original (apresentado quando do processo de seleção ao doutorado) previa outros experimentos. De qualquer forma, julgo importante ressaltar que, até mesmo para efeito de publicação posterior, o ideal é fazer coletas extensivas no maior tempo possível. Acredito, agora, ser mais produtivo diminuir o número de testes (experimentos) para focalizar na qualidade dos dados.

Outro ponto importante diz respeito à amostragem proporcional nos remanescentes. Houve uma confusão quanto ao que quer dizer "proporcionalidade" nesse caso. A confusão gerou a igualdade no número de parcelas em remanescentes com 0,4 ha e 4,9 ha, e, depois, pula-se para três parcelas em remanescentes com +/- 6,5 ha. Obviamente, isso causou um certo ruído nos dados. Porém, todas análises de diversidade alfa, considerando apenas uma parcela mais rica em remanescentes muito pequenos, duas parcelas nos dois fragmentos com mais de 4 ha e assim por diante; e também com o desenho original, não mostraram influência do tamanho dos remanescentes sobre a riqueza e abundância. Mais ainda, o número de parcelas, utilizado como uma variável descritiva na análise de beta diversidade (expediente advogado por Schoereder *et al*. [2004] para diversidade alfa em estudos de relação espécies-área), teve pouquíssima influência sobre a variação de composição entre os remanescentes. Dessa forma, o desenho proporcional utilizado não interferiu de maneira decisiva nos resultados. Parece que o que determinou mesmo a falta de relações espécies-área e abundâncias-área foi mesmo a pequena amplitude nos tamanhos dos remanescentes, o que, posso especular, coloca essa variação nos tamanhos na fase inicial da função descritora da relação espécies-área, a qual mostra um incremento suave antes do aumento mais exponencial.

Quanto ao experimento de manipulação, julgo que se poderia ter previsto um certo tempo extra para que as manchas de vegetação "descansassem" (por exemplo, 6 meses). Isso proporcionaria com que as comunidades locais se estabelecessem e se poderia ter uma ideia do que poderia ocorrer com as comunidades sujeitas aos dois processos básicos de formação e estabelecimento das comunidades: dispersão e nicho. Isso traria um enriquecimento importante até para se ter uma ideia se as comunidades locais seriam controladas por interações ou neutralidade, além de servir como um controle. Porém, as mudas das espécies, que foram emprestadas pela Prefeitura de Torres, precisaram ser devolvidas, o que inviabilizou a extensão do tempo do experimento.

Distribuição de espécies e fatores descritivos

Enquanto aracnólogos tem se preocupado em elaborar protocolos de coleta extensivos e abrangentes, poucos esforços têm sido feitos, nos trópicos, em acessar quais os fatores ecológicos, históricos e evolutivos que afetam a distribuição das espécies. Nossas pesquisas mostraram que coletas extensivas de dados em campo não seriam necessárias (variáveis ambientais redundantes) e que um direcionamento deve ser feito em criar modelos descritivos da distribuição de espécies de aranhas que facilitem e direcionem futuras pesquisas.

Um importante achado de nossas pesquisas foi a aparente pouca limitação espacial na dispersão de aranhas de teia entre remanescentes florestais (e manchas experimentais) em uma matriz altamente antropizada, baseada na falta de autocorrelação espacial na similaridade de espécies nos remanescentes. A dispersão aleatória (pressupondo-se uma dispersão passiva sem objetivo) de espécies na paisagem parece desencadear um processo de estabelecimento nos remanescentes ligado principalmente aos filtros ambientais em nível dentro-de-manchas, que estão ligados diretamente aos efeitos das perturbações humanas no entorno (entre-manchas). Dessa forma, a dispersão passiva, apesar de não ser direcionada ativamente no sentido de uma aranha “procurar” seu alvo, é direcionada passivamente pela forma dos remanescentes, o que coaduna com a hipótese de amostragem passiva, ou seja, manchas de hábitat mais irregulares criam maiores chances de serem alcançadas pelos dispersores. Essa observação foi duplicada no nosso experimento, no qual vimos que o que determinou a riqueza local das manchas de vegetação foi o número de imigrantes. Obviamente, a escala em que os remanescentes estavam inseridos é importante nessa discussão, pois, uma vez que aumentássemos ainda mais a escala, presume-se que a similaridade entre manchas próximas aumente, enquanto a similaridade entre manchas mais distantes diminua. Porém, o mais cham a atenção é que a escala analisada no estudo de beta diversidade na paisagem, para aranhas, já é considerado grande. De Mas et al. (2009) ressaltam que aranhas, geralmente, já respondem aos processos de paisagem em pequenas escalas (220 × 220 m). Qual a importância de um estudo multiescalar para a ecologia da conservação, por exemplo? Em que escala a fragmentação de hábitats inicia a limitação de dispersão? Um futuro direcionamento nas pesquisas, portanto, pode ser a análise dos padrões de respostas na similaridade entre manchas de hábitat em diferentes escalas.

Pode-se notar, nos resultados, que há diferenças na composição de aranhas de teia ligadas a três variáveis ambientais e que padrões de seleção de microhábitats podem convergir ou divergir em resposta a essas mesmas variáveis. Isso mostra que diferentes processos podem estar atuando em diferentes escalas e, mais ainda, em diferentes descritores das comunidades (beta diversidade / características comportamentais). A beta diversidade mede variações na similaridade da composição das comunidades locais baseada na ocorrência das espécies, sem considerar que as espécies que compartilham o mesmo hábitat podem ter requerimentos ecológicos semelhantes ou diferentes e essa informação, por si só, enseja uma abordagem teórica importante, ligada diretamente à história de formação e manutenção das comunidades. Weiher et al. (2011) ressalta que processos que influenciam na montagem de comunidades ligados à teoria de nicho não precisam que a composição de espécies seja previsível ou determinística. Comunidades podem convergir nas suas caracterísiticas morfológicas ou comportamentais, enquanto divergem com relação à composição de espécies. Os autores citam que isso se dá porque diferentes subconjuntos de espécies do conjunto regional podem ser selecionados por seus atributos, enquanto processos históricos de dispersão e deriva determinam a composição real de espécies. Nossa pesquisa mostrou que os processos tanto de convergência, quanto de divergência de características comportamentais são influenciados por variáveis diretamente ligadas ao manejo dos fragmentos. Dessa forma, e considerando que diferentes variáveis de seleção de microhabitat convergiram e divergiram, podemos especular que a comunidade de aranhas de teia, apesar de ser um grupo “relativamente” homogêneo quanto às exigências ecológicas, possui uma estratificação nos processos de interação dentro dos remanescentes que é influenciada por variáveis ambientais em um nível maior, e que se reflete na estrutura de hábitat no nível menor, levando ou à competição, ou à convivência. Esse nível menor é, realmente, onde acontecem as interações. É importante ressaltar que a análise das características comportamentais, apesar de ser realizada em nível de metacomunidades, é determinada pelas populações das espécies nas comunidades locais. Até que ponto a escolha de microhabitat é direcionada dentro das comunidades locais? E quais processos intra e inter-populacionais influenciam na seleção? Parece que a colonização dentro das manchas é um processo ligado diretamente à distribuição espacial dos indivíduos, a qual está correlacionada à estrutura da vegetação que os indivíduos de cada espécie encontram durante o processo de montagem das comunidades locais.

Os resultados que encontramos no nosso experimento corroboram esse aspecto dos processos de imigração já inferido em nível regional, qual seja, aranhas não possuem limitações que influenciem na probabilidade de colonização de manchas de vegetação em uma paisagem ao longo do tempo. As espécies, individualmente, podem apresentar limitações dispersivas, mas o resultado do agrupamento de espécies, apesar de levar a diferentes composições, mantém o padrão de imigração intacto.

De qualquer forma, parece ficar claro que uma abordagem comportamental *in loco* em nível de medição de características morfológicas, fisiológicas e comportamentais intrínsecas aos indivíduos pode trazer informações contundentes a respeito da resposta funcional das comunidades às influências ambientais e espaciais. Isso mostra que é necessário se levar em consideração aspectos específicos e individuais para se ter uma ideia mais clara do papel das espécies no ecossistema e de como ocorre a distribuição da diversidade em um nível regional.

Inferências sobre o funcionamento das comunidades

Originalmente, o projeto apresentado para ser aprovado no Doutorado do PPG-Ecologia possuia o seguinte objetivo geral:

“Este projeto tem como objetivo geral avaliar como os componentes da fragmentação da paisagem da Mata Atlântica e as características ambientais dentro dos fragmentos influenciam nos padrões de diversidade de espécies, na resposta de espécies com diferentes características de vida e na dinâmica de populações de aranhas de teia no nordeste do Rio Grande do Sul”.

Pelo menos dois objetivos foram alcançados. Porém, as duas espécies mais abundantes nos dois experimentos: *Achaearanea passiva* e *Cryptachea hirta*, podem ser utilizadas para, de um lado, analisar a influência das variáveis ambientais e espaciais na ocorrência nos remanescentes e a dinâmica entre eles e, por outro lado, analisar a influência do tamanho e da diversidade de manchas vegetais na dinâmica populacional, já que foram coletadas informações a respeito do sexo e da presença de ootecas da segunda espécie.

Portanto, apesar de questões metodológicas inerentes aos trabalhos de campo, pode-se inferir que a metacomunidade em nível de paisagem não é limitada pela dispersão (isso foi corroborado no experimento manipulativo). Dessa forma, as espécies transitam pela paisagem e o que influencia a chegada em uma mancha é a amostragem passiva, que determina um filtro para manchas irregulares (menos impactadas) com sub-bosque denso. Uma vez em uma mancha (comunidade local), a escolha que as espécies fazem das estruturas de habitat para fixação das teias, ligada à variação ambiental, determina se haverá convergência ou divergência no processo de montagem das comunidades. No primeiro caso, as espécies escolhem a mesma estrutura vegetal: ramos de trepadeiras, sendo, assim, seus requerimentos ecológicos são semelhantes e não parece haver pressão de competição. No segundo caso, as espécies que chegam no interior de manchas com entornos com vários tipos de manchas apresentam maior divergência no uso das estruturas vegetais de folhas e ramos de arbustos. Quanto mais manchas diferentes no entorno, maior parece ser a pressão de competição por essas estruturas vegetais entre as aranhas de teia. Ou, por outro lado, as espécies presentes nos diferentes tipos de entornos podem já possuir características comportamentais distintas, o que proporciona a diversidade de estruturas de seleção de microhábitat nesses fragmentos.

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