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INTERAÇÃO ENTRE ÁRVORES E TREPADEIRAS: PADRÕES, PROCESSOS E IMPLICAÇÕES

Este exemplar corresponde à redação final da tese defendida pelo(a) candidato (a) TULA CARAM SFAIR

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Resumo

A interação entre lianas (trepadeiras lenhosas) e forófitos (árvore-suporte) é caracterizada como antagonística, uma vez que as lianas diminuem a produção e a taxa de crescimento de árvores, aumentando a sua taxa de mortalidade. Esses estudos focam na interação entre pares de espécies, não dando ênfase na estrutura de interação sob uma perspectiva da comunidade. Essa tese teve como objetivo a compreensão dos padrões de interação entre lianas e forófitos utilizando a análise de redes, bem como a compreensão dos processos e implicações que surgem desse padrão. Mostramos que, para três áreas no sudeste brasileiro (cerradão, floresta estacional semidecídua e floresta ombrófila densa) o padrão foi o mesmo: aninhado. O aninhamento implica em um gradiente no número de interações, que pode ser explicado por caracteres e sua combinação (tamanho de lianas e de forófitos, mecanismos e morfologias de árvores que evitam lianas e modos de ascensão de lianas) e neutros (abundância). Apresentamos uma nova métrica (contribuição da espécie para o aninhamento) e mostramos que variáveis relacionadas aos caracteres e neutras explicam o aninhamento. A partir das análises de redes foi possível propor um novo método de manejo de lianas, que privilegia o corte de espécies com mais interações. Dessa maneira, espera-se que haja a manutenção da riqueza de lianas na comunidade.

Abstract

The interaction between lianas (woody climbers) and phorophytes (host-tree) is characterized as antagonistic, since lianas decrease the fruit production and the rate of tree growth, which increases their mortality rate. These studies focus on the interaction of liana and phorophyte pairs, not emphasizing the community perspective as a whole. This thesis aimed at the understanding of interaction patterns between lianas and phorophytes using complex network analysis, as well the understanding of process and implications that arise from this pattern. We showed that three vegetation formations in southeastern Brazil (savanna woodland, seasonal dry tropical forest and tropical wet forest) have the same pattern: nestedness. Nestedness presupposes a gradient of number of interactions (from least to most linked species), that are explained by traits (liana and tree size, mechanisms and morphologies to avoid lianas, and liana climbing mode) and neutral (abundance) factors. We developed a new metric (species contribution to nestedness), which also varied according to traits and neutral factors. Using this knowledge, we proposed a new liana management method, which focuses on the most linked species. This method was designed to maintain the liana richness in a forest.

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Introdução Geral

Trepadeiras são plantas autotróficas, vasculares, que germinam no solo, mantêm contato com ele durante todo o seu ciclo de vida e perdem a capacidade de auto-sustentação à medida que crescem, necessitando de uma sustentação mecânica para o seu desenvolvimento. Lianas são plantas trepadeiras lenhosas, já as vinhas não apresentam crescimento secundário e, portanto, não formam lenho (Weiser *et al. in prep.*). A árvore utilizada como suporte às trepadeiras é denominada forófito (Moffett 2000).

Por muito tempo pouco estudadas, as trepadeiras vêm recebendo um número cada vez maior de publicações, principalmente a partir dos anos 2000. Alguns estudos demonstram a importância desse hábito de vida com relação aos processos de fragmentação florestal (Laurance *et al.* 2001), de perturbação, como o surgimento de clareiras (Schnitzer *et al.* 2000) e de aumento de CO₂ na atmosfera (Phillips *et al.* 2002). Poucos trabalhos sobre trepadeiras foram realizados no Sudeste brasileiro quando comparamos com o número de estudos com árvores. Por exemplo, Oliveira (2006) analisou a composição florística de árvores em 57 áreas apenas no estado de São Paulo. Os trabalhos com lianas focam principalmente a florística e a fitossociologia (Kim 1996, Morellato & Leitão-Filho 1998, Hora & Soares 2002, Udulutsch *et al.* 2004, Rezende & Ranga 2005, Tibiriçá *et al.* 2006, Rezende *et al.* 2007, Santos *et al.* 2009) e alguns aspectos ecológicos de trepadeiras lenhosas e herbáceas (Morellato & Leitão-Filho 1996, Lombardi *et al.* 1999, Weiser 2002, 2007, Appolinário 2008, van Melis 2008, Dias 2009).

As trepadeiras podem reduzir a produção de frutos dos forófitos (Kainer *et al.* 2006, Fonseca *et al.* 2009). Por exemplo, Fonseca *et al.* (2009) encontraram que *Chrysophyllum lucentifolium* subsp. *pachycarpumé* Pires e T.D. Penn. (Sapotaceae) sem trepadeiras produz até 25,5% mais frutos do que árvores com trepadeiras ocupando mais do que 50% da copa. Árvores com trepadeiras também sofrem uma redução na taxa de crescimento (Campanello *et al.* 2007), que varia de acordo com a espécie de trepadeira envolvida (Toledo-Aceves & Swaine 2007). Dessa maneira, algumas espécies de forófitos possuem maior taxa de mortalidade do que árvores sem trepadeiras (Grogan & Landis 2009).

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Devido a esses efeitos negativos, muitos autores classificam a interação entre árvores e trepadeiras como sendo do tipo competição, que pode ocorrer principalmente nos estádios de plântula (Chen et al. 2008, Toledo-Aceves & Swaine 2008) e de jovem (Dillenburg et al. 1993a, b, 1995, Schnitzer et al. 2005). A competição entre árvores e lianas ocorreria principalmente abaixo do solo (Dillenburg et al. 1993a, Schnitzer et al. 2005, Toledo-Aceves & Swaine 2008) e essa relação depende da intensidade luminosa: em intensidades altas, a competição abaixo do solo é maior e em altas intensidades, acima do solo (Chen et al. 2008). Competição é uma interação em que um organismo consome o recurso que estaria disponível e poderia ser consumido por outro. Um organismo depriva outro e, consequentemente, o organismo cresce mais lentamente, gera menos descendentes e possui maior risco de morrer (Begon et al. 1996). Por outro lado, Stevens (1987) afirmou que lianas, ao invés de competirem, seriam parasitas estruturais de árvores. Tanto lianas quanto vinhas utilizam apenas a estrutura do suporte, sem necessitar de um órgão especial para adquirir nutrientes da planta hospedeira. Tal afirmação faz sentido, pois assim como trepadeiras necessitam de uma árvore hospedeira para atingir o dossel da floresta, plantas parasitas obrigatoriamente necessitam de um hospedeiro para retirar nutrientes e sobreviver (Press & Phoenix 2005). Dessa maneira, o tipo de interação entre trepadeiras e forófitos pode ser considerado inconclusivo, uma vez que tanto competição quanto parasitismo fazem sentido. Com base nos trabalhos realizados até o presente, podemos apenas concluir que as árvores são afetadas de forma negativa quando possuem trepadeiras, caracterizando a interação entre esses hábitos de vida como sendo antagonística.

Análise de redes complexas

Nos últimos anos, muitas áreas da ciência vêm aplicando a teoria de redes complexas, como sistemas metabólicos, genéticos e de redes tróficas (Albert & Barabási 2002). Redes são definidas como pontos (espécies, por exemplo) que se conectam por linhas (predação, por exemplo) (Bascompte 2007). Uma das áreas que mais tem recebido atenção são os estudos de interações mutualísticas, como a interação entre polinizadores/dispersores e plantas (Bascompte *et al.* 2003, Bascompte & Jordano 2007).

Redes de interações mutualísticas geralmente apresentam basicamente dois padrões estruturais: aninhado e compartimentalizado (Figura 1). Apesar de o primeiro padrão ser o mais comumente encontrado (Bascompte *et al.* 2003), a compartimentalização também é encontrada para algumas redes mutualísticas (Fonseca & Ganade 1996, Dicks *et al.* 2002, Olesen *et al.* 2007). Esses padrões de interação podem ser originados por diferentes processos, como artefatos de amostragem, restrições filognéticas, abundância e combinação de caracteres (Vázquez *et al.* 2009). Um determinado padrão de rede pode ter implicações ecológicas. Por exemplo, apenas extinções de polinizadores com muitas interações em redes aninhadas ocasionam em perda rápida de espécies de plantas (Memmott *et al.* 2004).



Figura 1. As redes mutualísticas podem ser (a) aninhadas e (b) compartimentalizadas. No caso hipotético em (b) há dois compartimentos. Cada ponto representa uma espécie e, cada linha, uma interação.

Apesar da grande ênfase em redes mutualísticas, há trabalhos com redes antagonísticas, como redes de parasitismo (Timi & Poulin 2007, Graham *et al.* 2009) e de herbivorismo (Prado & Lewinsohn 2004, Thébault & Fontaine 2010). Nessas redes, assim como ocorre em redes mutualísticas, tanto o padrão aninhado (Timi & Poulin 2007, Graham *et al.* 2009) quanto o padrão compartimentalizado (Prado & Lewinsohn 2004, Thébault & Fontaine 2010) e a estrutura composta (aninhamento em cada compartimento, Lewinsohn et al. 2006) podem surgir. Entretanto não há trabalhos que focam nos processos que podem levar a esses padrões em redes antagonísticas entre plantas, tampouco trabalhos que focam nas implicações dos padrões encontrados.

Os estudos de interação entre plantas com abordagem de redes demonstram os mesmos padrões encontrados em redes animal-planta e animal-animal. O aninhamento, por exemplo, é encontrado em rede de facilitação entre plantas (Verdú & Valiente-Banuet 2008) e entre epífitas e forófitos (Burns 2007, Silva *et al.* 2010). O aninhamento pode reduzir a competição e aumenta a riqueza de espécies que coexistem em redes mutualísticas (Bastolla *et al.* 2009). É possível que as implicações de uma rede aninhada possam ser semelhantes para interações de diferentes naturezas. Por exemplo, o aninhamento em redes de facilitação previne a perda e mantém a diversidade de espécies (Verdú & Valiente-Banuet 2008). Dessa maneira, é possível que a interação entre plantas explique padrões de diversidade em diferentes ambientes. Por outro lado, conforme mostrado por Blick & Burns (2008), redes de interação entre trepadeiras e forófitos e de hemiparasitismo não apresentam aninhamento, mas sim padrões de co-ocorrência negativa, indicando preferência mutuamente exclusiva de trepadeiras e hemiparasitas por forófitos. Vale ressaltar que a organização de uma matriz de co-ocorrência negativa é similar a de uma matriz com dois compartimentos (Almeida-Neto et al. 2007), mostrando que redes de interação entre lianas e forófitos e de hemiparasitismo é do tipo compartimentalizada (Figura 1b).

Objetivo geral da tese

Esta tese tem como objetivo geral a investigação dos padrões de interação entre trepadeiras e forófitos sob a perspectiva de teoria de redes, bem como a busca dos processos e implicações que surgem desse padrão. Para isso, é necessário entender como as trepadeiras e os forófitos interagem e como essa interação está relacionada com padrões de diversidade no sudeste brasileiro.

Organização da tese

O **Capítulo 1** dessa tese foca no padrão de interação entre lianas e forófitos. Mostramos que, para três áreas no sudeste brasileiro (cerradão, floresta estacional semidecídua e floresta ombrófila densa) o padrão é o mesmo: aninhado. Mostramos também, por meio da técnica de arrefecimento simulado, que não há compartimentos em nenhuma das redes. Nesse capítulo confrontamos nossos dados (três redes de interação) com os resultados de Blick & Burns (2008), em que os autores demonstram que a estrutura de interação entre trepadeiras e forófitos não é aninhada, mas sim apresenta co-ocorrência negativa. Mostramos que a rede antagonística de interação entre lianas e forófitos é similar a redes mutualísticas e algumas redes antagonísticas aninhadas.

Antes de entender os processos que levam ao aninhamento, no **Capítulo 2** fazemos uma revisão das variáveis que podem influenciar a ocupação de árvores por lianas. Mostramos que as variáveis: tamanho (diâmetro, altura), morfologias (presença de espinhos, casca do caule decídua) e mecanismos (arquitetura de palmeiras, crescimento rápido) agem conjuntamente na ocupação de lianas. Além disso, a importância dessas variáveis depende da estrutura da floresta.

No **Capítulo 3** investigamos quais processos levam ao gradiente do número de ligações da espécie (grau) em uma rede aninhada. Nesse caso, mostramos que quanto maior a abundância da espécie, maior o número de ligações que ela possui.

No **Capítulo 4** elaboramos um novo índice: a contribuição da espécie para o aninhamento (ni). Ao aplicar esse índice, mostramos que, assim como redes mutualísticas, em redes antagonísticas variáveis neutras e os caracteres influenciam o aninhamento.

A implicação de redes aninhadas é exemplificada no **Capítulo 5**, em que damos uma abordagem aplicada ao manejo de lianas. Se quisermos aperfeiçoar o manejo de lianas, devemos focar nas espécies com maior número de interações, que são também as espécies mais abundantes. Esse enfoque matemático pode ajudar a dar embasamento a novos programas de manejo frente aos programas de manejo tradicionais de lianas, que focam no corte aleatório de lianas. Essa abordagem também mantém a riqueza de lianas, permitindo que essa forma de vida continue fornecendo alimento à fauna.

Essa tese possui também dois anexos. No primeiro (**Anexo 1**) relacionamos os descritores de diversidade de lianas com os mesmos descritores de árvores em seis sítios no sudeste brasileiro. Mostramos que a riqueza de trepadeiras está relacionada à diversidade de árvores, indicando que a heterogeneidade ambiental (refletida no nicho potencial de trepadeiras: as árvores e sua combinação de caracteres) influencia a sua especiação. Esse trabalho foi inserido como anexo, pois foi um estudo paralelo feito durante o trabalho de tese. No segundo anexo (**Anexo 2**) há tabelas em que são caracterizadas as redes complexas para as três localidades estudadas. Mostramos o número de ligações, número de espécies, número de espécies sem ligações, entre outros descritores.

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Capítulo 1 - Nested liana-tree network in three distinct neotropical vegetation formations

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Research article

Nested liana-tree network in three distinct neotropical vegetation formations

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ABSTRACT

Despite the increasing number of studies on lianas, few of them have focused on liana and host-tree (phorophyte) interactions from a network perspective. Most studies found some network structure in other systems, such as plant facilitation and host-epiphyte. However, a recent study found no structure in a small network of liana-phorophyte interactions. Our aim was to investigate the hypothesis that rich, highly diverse systems yield large interaction networks with some structure. If so, networks of liana-phorophyte interactions in highly diverse systems will have one or more of the following structures: compartmentalized, nested or compound. We sampled three highly diverse vegetation formations: a tropical rainforest, a tropical seasonally dry forest, and a woodland savanna, all in southeastern Brazil. We used simulated annealing to test compartmentalization and found no compartment in any of the three networks analyzed. By means of a modified classical temperature index, we found a nested structure in all three sites sampled. We inferred that these nested structures might result from phorophyte characteristics and sequential colonization by different liana species and might promote increased diversity in tropical tree formations. We propose that, according to the system complexity and the different variables associated with site and liana-phorophyte characteristics, a network may have a structure, which arises in more complex systems. Since we have investigated highly diverse systems with large networks, nestedness could be clearly detected in our study.

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Introduction

Woody climbing plants (lianas) and their host-plants (phorophytes) are considered to engage in antagonistic interactions. Lianas compete with trees above ground for light and below ground for nutrients, both in the stages of seedling (Toledo-Aceves and Swaine, 2008) and sapling (Dillenburg et al., 1993a,b, 1995; Schnitzer et al., 2005). Consequently, lianas decrease phorophyte fecundity (Kainer et al., 2006) and growth rate (Campanello et al., 2007).

The studies cited above focused on pairs of particular species, but recently Blick and Burns (2009) analyzed the interaction between all species of lianas and phorophytes in a community and found no structure in the liana-phorophyte network. The absence of structure may be due to their small network, since

larger mutualistic networks are more prone to have some structure (Bascompte et al., 2003; Guimarães et al., 2006; Rodríguez-Gironés and Santamaría, 2006; Olesen et al., 2007; Almeida-Neto et al., 2008; Bastolla et al., 2009). However, networks of different interaction types, such as parasitism and mutualism, have some structure, which may assume three basic forms: compartmentalized (or modular), nested, and compound (Lewinsohn et al., 2006). A compartmentalized structure is characterized by recognizable subsets of interacting species that are more linked within subsets than across them (Lewinsohn et al., 2006). Ant-plant mutualism (Fonseca and Ganade, 1996) and pollination (Dicks et al., 2002; Olesen et al., 2007) display a compartmentalized network structure. In a nested structure, species with fewer interactions are subsets of species with more interactions (Bascompte et al., 2003). In our investigation, if a network were nested, liana species with fewer interactions would link to phorophyte species with more interactions, and phorophytes would display the same pattern. In addition, liana and phorophyte species with more interactions tend to link to each other, establishing a dense core of interactions.

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Although most nested bipartite graphs had been found for mutualistic interactions (Bascompte et al., 2003; Guimarães et al., 2006, 2007), nestedness was also reported in parasitism networks (Rohde et al., 1998; Timi and Poulin, 2007; Graham et al., 2009). Hence, we assume that the implications of nestedness can be generalized to antagonistic interactions (Graham et al., 2009), such as those between lianas and phorophytes. We must highlight that both compartmentalization and nestedness may be detected in the same network, and one structure may be complementary to the other (Olesen et al., 2007). According to Fortuna et al. (2010), the presence of both structures in the same network may be due to connectance (matrix fill): if connectance is low, nested networks tend to be also modular, but if connectance is high the relationship between these two structures is negative, implying in the existence of trade-offs in the community organization. A bipartite graph can also have a compound structure, i.e., each compartment has its own nested structure, as found for a community of herbivores and Asteraceae inflorescences in Brazil (Lewinsohn et al., 2006) and for bats and their roosting sites (Fortuna et al., 2009). The analysis of a compound network structure is only applicable when compartments are detected.

The same kind of ecological interaction can be represented by networks with different structures, e.g., mutualistic networks may be either nested (Bascompte et al., 2003) or compartmentalized (Dicks et al., 2002), depending on the importance of the characters, the seasonality, and the behavior of the species and site sampled (Dicks et al., 2002). However, the size of a network may also influence the detection of a structure. On the one hand, pollination networks with more than 50 species are significantly nested and some are modular, whereas networks with more than 150 species are always modular (Olesen et al., 2007). On the other hand, smaller networks can have a haphazardly arisen structure. For example, significant nestedness can be detected in small networks (Rodríguez-Gironés and Santamaria, 2006), because they may be nested by chance, irrespective of the metric used (Almeida-Neto et al., 2008). Guimarães et al. (2006) suggested that only rich systems show nestedness, since the nestedness value increases as the network size increases (Bascompte et al., 2003; Guimarães et al., 2006; Rodríguez-Gironés and Santamaría, 2006; Almeida-Neto et al., 2008; Bastolla et al., 2009). Therefore, structures such as compartmentalization and nestedness tend to arise as a system becomes more complex.

Our aim is to investigate the hypothesis that rich, highly diverse systems yield large interaction networks with some structure. If this hypothesis holds, the network of interactions between lianas and phorophytes will show some structure in the most important types of tropical vegetation, namely, rainforest, seasonal forest, and savanna.

Methods

Site characteristics and sampling

We sampled lianas and trees rooted within plots in three different sites, all in the state of São Paulo, southeastern Brazil (Fig. 1). These sites have different plant formations, to which different sampling designs were applied, considering the peculiarities of each community, such as average height, diameter, and density of lianas and trees. For example, the savanna woodland has thinner and smaller trees than those in the tropical rainforest, so the minimum 15 cm of trunk perimeter at breast height (PBH) used to sample the tropical rainforest would include few individuals if adopted in the savanna plots. In all three sites, the sampled area corresponded to 1 ha divided into 100 plots of 10 m × 10 m each (contiguous in



Fig. 1. The three areas sampled in the state of São Paulo, Brazil, have distinct vegetation types; tropical rainforest (Ubatuba), tropical seasonally dry forest (Paulo de Faria), and savanna woodland (Bauru).

the rain and seasonal forests, and random in the savanna woodland).

The first site (23°21'54"-59"S and 45°05'02"-04"W, 348-394 m above sea level) is a tropical rainforest in the municipality of Ubatuba, in the Parque Estadual da Serra do Mar, a conservation unit of 47,500 ha. The climate is Af (after Koeppen, 1948), i.e., humid tropical with no dry season. The mean annual temperature is 20.6 °C, and mean annual rainfall is 2320 mm (van Melis and Martins, unpublished). We surveyed all dead and living plants with PBH \geq 15 cm (Rochelle et al., unpublished) and all lianas with DBH (stem diameter at breast height) \geq 1 cm (van Melis and Martins, unpublished).

The second site (19°55′-58′S and 49°31′-32′W, 400-495 m above sea level) is a fragment of 435.73 ha of tropical seasonally dry forest (Rezende et al., 2007) in the municipality of Paulo de Faria. The climate is Koeppen's Aw, i.e., hot humid tropical with summer rain and dry season in winter, with mean annual temperature of 24 °C and mean annual rainfall of 1245 mm. We excluded plots with densely tangled lianas, and sampled living trees with DBH \geq 3 cm and lianas with DBH \geq 1 cm.

The third site (22°19'41"-21'06"S and 48°59'49"-49°01'12"W, 519-603 m above sea level) is a fragment of 321.71 ha of savanna woodland in the municipality of Bauru. The climate is Koeppen's Cwa, i.e., hot temperate with a wet season from September to June and a short dry season in July and August (Weiser, 2007). Mean annual rainfall is 1331 mm, and mean annual temperature is 22.6°C. We sampled all living trees with DBH \geq 0.1 cm and all lianas with DSH (stem diameter at soil height) \geq 0.1 cm (Weiser, 2007).

Compartmentalization

To estimate the number of modules, we used the algorithm developed by Guimerà and Amaral (2005), based on simulated annealing. First, the method identifies modules in the network and, then, maximizes the modularity. The index of modularity *M* is:

$$M \equiv \sum_{s=1}^{N_M} \left[\frac{ls}{L} - \left(\frac{ds}{2L} \right)^2 \right]$$

where $N_{\rm M}$ is the number of modules, $l_{\rm s}$ is the number of links between nodes in modules, L is the number of links in the network, and $d_{\rm s}$ is the sum of degrees (number of links) of the nodes in module s (Guimerà and Amaral, 2005). M=0 indicates that all nodes are placed at random into modules or all nodes are in the same cluster (Guimerà and Amaral, 2005). We generated 100 random networks with the same matrix fill as the original matrix and examined whether the original network was more or less modular than the random networks.

Although an algorithm for bipartite network was available (Guimerà et al., 2007), we used the algorithm for one-mode network (Guimerà and Amaral, 2005). We considered this was the best approach in our case, because: (1) the one-mode network algorithm looks for modules in the entire network; (2) in the two-mode network algorithm, the group of lianas does not necessarily correspond to the group of trees; (3) null models are not available for the two-mode network algorithm. This approach was the same adopted by Olesen et al. (2007).

Nestedness

We adopted the same modified nestedness (NTm) index that Blick and Burns (2009) used to analyze their matrix of interactions between lianas and phorophytes. The classical temperature index (for calculation details, see Atmar and Patterson, 1993) has received some criticism, especially due to issues related to the algorithm used in the software, the isocline of perfect order employed to calculate nestedness temperature, the underestimation of type I error in the null model (Fischer and Lindenmayer, 2002; Rodriguez-Gironés and Santamaría, 2006), and to the fact that this method is more sensitive to matrix fill, shape and size than similar metrics (Almeida-Neto et al., 2008). Moreover, according to Rodríguez-Gironés and Santamaría (2006) and Almeida-Neto et al. (2007, 2008), classical temperature (T) should not be considered a disorder measure, since a random distribution of presences in the matrix would not return T=100. The nestedness index we used alleviates some of the problems mentioned above and furnishes a more conservative value (Ulrich, 2006). Following Blick and Burns's (2009) procedure, we calculated NTm and compared the observed values with those obtained from 1000 random matrices generated by default in the NESTEDNESS software, using fixed row and column totals with sequential swap method of matrix fill (Ulrich, 2006). The nestedness value (NTm) is obtained from the formula $N_{\text{Tm}} = (100 - T)/100$. Values range from 0 to 1, where 1 represents maximum nestedness (Bascompte et al., 2003). We used the nestedness value $(N_{\rm Tm})$ in relation to the temperature value itself (T), since we intended to emphasize nestedness and not matrix disorder (Bascompte et al., 2003).

Results

Sampling

Ubatuba was the richest site in lianas and trees (66 liana and 210 tree species), followed by Bauru (39 liana and 140 tree species) and Paulo de Faria (45 liana and 87 tree species). However, only 125, 119, and 64 tree species, respectively, had associated lianas in those sites (Fig. 2). These species were the ones we considered in our network analyses. The proportion of tree species that were free from lianas varied in each community: 40.47% in Ubatuba, 26.43% in Paulo de Faria, and 15% in Bauru. The number of links between lianas and phorophytes also varied among sites: 459 in Ubatuba, 1704 in Paulo de Faria, and 955 in Bauru (Fig. 2). Matrix fill was affected by species number and link density: the highest matrix fill

(a) Ubatuba









Lianas





Fig. 2. Network representation of liana-phorophyte (host-plants) associations in the three sites under study. Species of lianas and phorophytes are represented by squares and the associations between them are represented by lines. The figures were rearranged to maximize nested structures.

occurred in Paulo de Faria (0.2291), followed by Bauru (0.2057) and Ubatuba (0.0556).

Compartmentalization

(c) Bauru

We did not detect compartments in any liana-phorophyte interaction matrix. In Ubatuba, the modularity index (M=0.396467) was lower than the null models, with a mean of 0.403178 (SD = ±0.005851). The modularity in Paulo de Faria was lower (M=0.177980) than the null models (mean=0.204906; SD = ±0.005294). In Bauru, the modularity index was also lower (M=0.188853) than the null models, with a mean of 0.196114 (SD = ±0.003995).

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Nestedness

Interaction matrices showed high nestedness values when we used the temperature value modified by Ulrich (2006) in Ubatuba ($N_{\rm Tm}$ = 0.95), Paulo de Faria ($N_{\rm Tm}$ = 0.87), and Bauru ($N_{\rm Tm}$ = 0.93). All these values indicate significantly nested networks (p < 0.05).

Discussion

We found a nested pattern in the liana-phorophyte networks. for all three samples. Our result is different from Blick and Burns's (2009), in which a network of 9 liana and 16 phorophyte species had no pattern. Our result confirmed the hypothesis that some structure arises in large networks, whereas small networks have haphazardly arisen structures. Blick and Burns's (2009) results may be related to their matrix fill (or connectance) which was of 47%. For a small network with a matrix fill close to 40%, the chance of a random matrix to be significantly nested is small (Nielsen and Bascompte, 2007). The matrix fill must be very high to yield a significant nestedness value for a small matrix (Nielsen and Bascompte. 2007). Our networks were large and had a low matrix fill (less than 25%), According to Nielsen and Bascompte (2007), increased sampling efforts yield large networks, which also have a low matrix fill, as is the case of our matrices. Therefore, because our networks were large with a low matrix fill, we could easily detect significant nestedness.

Given that we found a nested structure in the liana-phorophyte network of each of these formations, which are very different from one another, though highly diverse, we confirmed our hypothesis that interaction structures are more easily recognizable in richer systems. However, our matrices were not large enough to split into compartments. This result corroborated the statement by Olesen et al. (2007) that compartments arise only in very large networks. A compartmentalized structure can derive from restrictions to species ranges (Lewinsohn et al., 2006), pollination syndrome and phenology (Dicks et al., 2007). A compartmentalized structure also arises in networks of systems in which parasite or pathogen spread is slowing down (Guimerà et al., 2007). We speculate that we would probably detect compartments in our networks if our samples were larger.

However, we also believe that the interaction structure may be influenced by the characteristics of the sites sampled. For example, pollination networks can be either nested (Bascompte et al., 2003) or compartmentalized (Dicks et al., 2002). In this case, compartmentalization may be explained by pollination syndromes, animal and plant seasonality, and pollinator behavior (Dicks et al., 2002), as well as by network size (Olesen et al., 2007). Similarly, we suppose that a liana-phorophyte network might have no structure (as in Blick and Burns, 2009) or might be nested (as in our results), depending on the characteristics of the sampled sites, trees, and lianas. For example, all sites we sampled are in tropical climates with high yearly average temperatures, whereas Blick and Burns (2009) analyzed samples collected in the colder climate of New Zealand.

The process of nestedness build-up is related to species abundance and to temporal and spatial distribution processes (Vázquez et al., 2009). The nested structure is less sensitive to species loss, keeping a strong cohesion in the network (Memmott et al., 2004). The significant nestedness values we found for the three areas sampled are similar to the ones observed in most studies using the bipartite graph approach (Bascompte et al., 2003; Guimarães et al., 2006, 2007; Selva and Fortuna, 2007; Graham et al., 2009), including those emphasizing plant-plant interaction (Burns, 2007; Verdú and Valiente-Banuet, 2008; Blick and Burns, 2009: Silva et al., 2010). Nestedness has considerable implications for plant-plant interactions. In epiphyte-phorophyte interactions, nestedness would derive from sequential colonization by epiphytes. Once an epiphyte establishes on a tree, it creates favorable conditions for the establishment of other epiphytes in a facilitation process (Burns, 2007; Blick and Burns, 2009). According to Pinard and Putz (1994), lianas that have already reached tree canopy would facilitate climbing for other lianas. Nestedness was also found in networks of facilitation among desert plants (Verdú and Valiente-Banuet, 2008). The facilitation process preserves plant diversity, because generalist nurse-species promote the growth of several specialist facilitated-species (Verdú and Valiente-Banuet, 2008). Likewise, several studies suggested that some phorophytes, generally the largest (Nesheim and Økland, 2007; Carrasco-Urra and Gianoli, 2009; Ding and Zang, 2009; Jiménez-Castillo and Lusk, 2009; Homeier et al., 2010), have more lianas. Smaller or juvenile trees, which do not reach the forest canopy, would be used as a shortcut by lianas, especially those with tendrils, when trying to reach taller trees (Carsten et al., 2002). Therefore, liana richness increases as phorophyte diameter increases (Burns and Dawson, 2005).

In general, nestedness denotes the presence of specialist and generalist species, i.e., species displaying numerous links and species with fewer links. Besides, 40.47% of tree species in Ubatuba, 26.43% in Paulo de Faria, and 15% in Bauru did not have associated lianas. Therefore, in all communities we analyzed, there was a gradient in the liana-phorophyte association, which ranged from species without interaction, through species with few interactions, to those with many links. Other studies using different statistical and mathematical tools obtained similar results. Carsten et al. (2002), Muñoz et al. (2003), and Nesheim and Økland (2007) also found specificity between lianas and phorophytes, i.e., certain trees never had lianas, whereas others had many of them. According to Nesheim and Økland (2007), some phorophyte species would have more lianas than others, whereas some trees would have fewer lianas than expected. Some factors, such as size, stem roughness, flexibility of trees (Carsten et al., 2002; Chittibabu and Parthasarathy, 2001; Nesheim and Økland, 2007), and the climbing mode of lianas (Carsten et al., 2002) would contribute to the specificity of liana-phorophyte associations. Yet Padaki and Parthasarathy (2000) and Pérez-Salicrup et al. (2001) found that the relationship between liana and phorophyte species is not species-specific. Other variables for trees, such as canopy illumination (Malizia and Grau, 2006), size (Nesheim and Økland, 2007; Carrasco-Urra and Gianoli, 2009; Ding and Zang, 2009; Jiménez-Castillo and Lusk, 2009; Homeier et al., 2010), fruit type (Carsten et al., 2002), compound leaves (Carse et al., 2000), spiny trunk (Maier, 1982), and palms (Carse et al., 2000; Pérez-Salicrup et al., 2001; Campanello et al., 2007) would be more important than phorophyte identity. Therefore, phorophytes with few lianas or without them would probably have some characteristics that would decrease or hinder their occupation by lianas. Additionally, generalist phorophyte and liana species would have other features that would promote their association. These particular differences among species would result in the nested structure of liana-phorophyte associations we found.

Our study showed that lianas and phorophytes have a nested interaction structure in the three sites analyzed. We did not find compartmentalized or compound structures nor, as Blick and Burns (2009) described, networks with no structure. We assume that phorophyte characteristics and their sequential colonization by lianas are plausible explanations for nestedness, which is also related to increased tree and liana diversity in tropical forests. Future works may determine the causes of nestedness in liana-phorophyte associations.

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Capítulo 2 - Liana Avoidance in Trees: New Insights from Three Distinct Vegetation Types LRH: Sfair et al.

RRH: Liana Avoidance in Trees

Liana Avoidance in Trees: New Insights from Three Distinct Vegetation Types²

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Abstract

Trees have structures and mechanisms, such as spiny or shedding bark and fast growth that prevent liana infestation. We have aimed to investigate the importance of three aspects of liana avoidance in trees – size, morphology, and mechanism – by answering two questions: (1) Is one aspect most important? (2) Is there an optimal combination of these aspects that most efficiently avoids lianas? We sampled a dense rainforest, a seasonally dry tropical forest, and a woodland savanna, and performed multiple logistic regression models, in which liana presence was the response variable and tree size, avoidance morphologies, and avoidance mechanisms were the explanatory variables. We did not found a trait that avoided lianas when occurring alone, with the exception of size: small trees bear fewer lianas. This result contradicts almost all previous studies, which suggest that tree traits are important in avoiding lianas. However, we found that a combination of traits, particularly of size and mechanism or morphology, proved to be more effective against liana infestation than a single aspect alone. We suggest that forest features, particularly light availability, are major determinants of liana climbing on a tree, because in dense and shady rainforest, lianas often occupied well-lit trees, whereas in the lighter forest lianas climbed small trees without mechanisms or morphologies to avoid them.

Keywords: cerrado; climber; host-tree; phorophyte; savanna; tropical forest; vine.

Resumo

As árvores possuem mecanismos e morfologias, como crescimento rápido e caule com espinhos, que previnem da infestação por lianas. Nosso objetivo foi investigar a importância de três variáveis de inibição de lianas por árvores - tamanho, morfologia e mecanismo - por meio de duas perguntas: (1) há uma variável mais importante? (2) Há alguma combinação dessas variáveis que pode evitar lianas mais eficientemente? Nós amostramos uma floresta ombrófila densa, uma floresta estacional semidecídua e um cerradão e utilizamos modelos de regressão logística múltipla, nos quais a presenca de liana era a variável resposta e o tamanho da árvore, morfologias e mecanismos de inibição, variáveis explanatórias. Encontramos que os caracteres das árvores que as protegem contra lianas não são suficientes para evitá-las quando ocorrem isoladamente, com exceção do tamanho: árvores maiores possuem mais lianas. Esse resultado contradiz a maioria dos estudos anteriores, que confirmou a importância dos caracteres contra lianas. Entretanto, encontramos que a combinação de caracteres, particularmente o tamanho e os mecanismos ou morfologias, provaram ser efetivos contra a infestação por lianas. Nós supomos que atributos da floresta, particularmente a disponibilidade de luz, são fatores determinantes na ocupação de árvores por lianas, uma vez que em florestas densas as lianas buscariam árvores bem iluminadas, enquanto que em florestas sazonais e mais abertas, lianas escalariam árvores pequenas sem mecanismos ou morfologias que as evitariam.

Lianas (woody climbers) are a very abundant growth habit in tropical forests, particularly in seasonally dry tropical forests (Schnitzer 2005, DeWalt *et al.* 2009). Lianas can reduce tree fruit production (Kainer *et al.* 2006, Fonseca *et al.* 2009), inhibit tree growth (Clark & Clark 1990, Ladwig & Meiners 2009), and increase tree mortality (Grogan & Landis 2009). Therefore, trees have supposedly developed traits to avoid lianas. Hegarty (1991) divided these traits in two classes: canopy and stem.

Canopy traits include large, long compound leaves (such as in palms), retention of dead leaves, and large crown depth (Hegarty 1991). For example, palms are generally less susceptible to liana infestation when compared to non-palms (Maier 1982, Putz 1980, 1984; Rich et al. 1987, Carse et al. 2000, Pérez-Salicrup et al. 2001, Campanello et al. 2007), because new leaves emerge from the terminal bud, grow vertically, and then spread out and lean over (Putz 1980). Other examples that repel liana infestation are trees with large compound leaves (Putz 1980, 1984) and tree-ferns that retain dead leaves (Page & Brownsey 1987). Exposed canopies and well-lit trees tend to carry more lianas (Malizia & Grau 2006), probably because of their size, *i.e.*, larger trees (in diameter or height) reaching the forest canopy are well-lit and have a wide canopy area (Malizia & Grau 2006). Other studies also demonstrateded that larger trees have more lianas (Clark & Clark 1990, Carse et al. 2000, Pérez-Salicrup et al. 2001, Pérez-Salicrup & De Meijere 2005, Malizia & Grau 2006, Reddy & Parthasarathy 2006, Nesheim & Økland 2007, Carrasco-Urra & Gianoli 2009, Ding & Zang 2009, Jimenez-Castillo & Lusk 2009, Homeier *et al.* 2010). Once a liana reaches the forest canopy, newly arriving lianas can be favored by the narrower stem facilitating a shortcut to reach the canopy (Pinard & Putz 1994). Another explanation is that larger trees would be older and, therefore, provide more opportunities and time for liana colonization (Pérez-Salicrup et al. 2001, Malizia & Grau 2006, Campanello et al. 2007). However, smaller trees may be as old as larger ones and also very prone to liana infestation (Balfour & Bonds 1993, Chittibabu & Parthasarathy 2001, Carsten et al. 2002). Lianas could use smaller trees as

shortcuts to reach canopy trees and their climbing mode might be an important variable: tendrillar lianas tend to occur on smaller trees (Carsten *et al.* 2002).

The stem traits suggested by Hegarty (1991) include: rapidly thickening and spiny stems as fragile barriers, flexible main stems, and harboring of protective insects. Rapid stem thickening and flexible main stems have never been demonstrated as traits against lianas (after Putz et al. 1984, Putz 1984). Insect harboring occurs on particular trees, such as ant harboring on some *Cecropia* species, for example. The ants remove invaders such as lianas from the stems (Janzen 1973). The genus *Cecropia* is also characterized by rapid height increase. Clark & Clark (1990), Carse et al. (2000) and Campanello et al. (2007) demonstrated that these trees also have fewer lianas. Consequently, lianas may delay forest regeneration, reducing the abundance of non-pioneer trees and stalling gaps (Schnitzer et al. 2000). Some trees also have long branch-free boles that are associated with few lianas (Campbell & Newbery 1993, Muthuramkumar & Parthasarathy 2001, Reddy & Parthasarathy 2006). According to Campbell & Newbery (1993), as a tree grows, its bole height increases due to the shedding of lower branches and some of the lianas they support. On the other hand, some trees are multi-stemmed and carry many lianas (Reddy & Parthasarathy 2006). Tree bark characteristics can also play an important role in liana avoidance: many species have spiny stems (Putz 1984) that would fall under the weight of lianas (Maier 1982). Trees with smooth, exfoliating (Talley 1996, Campanello et al. 2007) or allelopathic (Talley et al. 1996) barks have fewer lianas. On the other hand, bark roughness and flakiness increase liana infestation (Talley et al. 1996, Carse et al. 2000, Carsten et al. 2002, Reddy & Parthasarathy 2006). Regular renewal of the outer bark provides an ideal mechanism for shedding lianas, whereas a relatively stable and rough bark provides a suitable surface for liana attachment (Talley et al. 1996).

Single feature may repel or facilitates liana occupation. However, probably a combination of tree features influences liana load more effitiently (Carse 2000). For example, as a tree grows, its trunk

height increases and shed the lower branches (Campbell & Newbery 1993). Taller palms have fewer climbers growing into their crowns than shorter palms, because their crowns grow above the microsites that would be suitable for some climbers and because climbers would be shed together with leaves (Rich *et al.* 1987). This combination of features and tree age makes improbable that liana infestation be species-specific, *i.e.*, that some particular lianas species interacts with some particular tree species (Sfair *et al.* 2010). Therefore, there is probably a spectrum of habits, from trees totally protected from lianas to trees without any trait that may avoid lianas (Sfair *et al.* 2010).

In this paper, we divide tree traits against liana infestation into three classes: (a) size, including diameter, and height; (b) avoidance morphology or structure (hereafter morphology or structure), such as spines or thorns, smooth or exfoliating bark, bark roughness, etc.; and (c) avoidance mechanism (hereafter mechanism), such as fast growth, vertical bud orientation and subsequent inclination of mature leaf (palm leaf emergence), leaf and branch shedding, and protective insects. These classes cover the major traits described in the literature and provide a more synthetic classification than Hegarthy's (1991). Our aim was to investigate the effectiveness of tree size, morphology, and mechanisms, as well as the combination of all three, as traits against lianas. We posed the following questions as guidelines: (1) Is one aspect most important? (2) Is there an optimal combination of these aspects that most efficiently avoids lianas?

Methods

Sites - We sampled lianas and trees rooted within plots in three different sites, all in the state of São Paulo, southeastern Brazil. These sites have different vegetation types, to which different sampling designs were applied, considering the peculiarities of each community, such as average height and diameter and density of lianas and trees. For example, the savanna woodland has shorter, thinner trees than the tropical rainforest; in addition, the minimum 5 cm of trunk diameter at breast height (DBH) we used to sample the rainforest would comprise few individuals in the savanna plots.

Ubatuba (23°21'54"- 59"S and 45°05'02"- 04"W, 348-394 m asl) is a tropical rainforest in the municipality of Ubatuba, in the Parque Estadual da Serra do Mar. Ubatuba has a humid tropical climate with no dry season (Koeppen 1948). We surveyed all dead and living plants with DBH \geq 5 cm (Rochelle 2008) and all lianas with stem diameter at breast height (DBH) \geq 1 cm (van Melis 2008). The second site (19°55'-58'S and 49°31'-32'W; 400-495 m asl) is a seasonally dry tropical forest (Rezende *et al.* 2007) in the municipality of Paulo de Faria, where we excluded plots with densely tangled lianas and sampled living trees with DBH \geq 3 cm and lianas with DBH \geq 1 cm. The third site (22°19'41"-21'06"S and 48°59'49"-49°01'12"W, 519-603 m asl) is a woodland savanna in the municipality of Bauru, where we sampled all living trees with DBH \geq 0.1 cm and all lianas with stem diameter at soil height (DSH) \geq 0.1 cm (Weiser 2007). For further sampling details, see Sfair *et al.* (2010).

Statistical analysis - For all sites, we recorded some tree traits previously reported in the literature as predictive of liana climbing. We recorded three groups of variables of host plants: (a) size: height and diameter; (b) morphology: peeling and spiny bark; and (c) mechanism: successional status (pioneer and non-pioneer; *sensu* Swaine and Whitmore 1988), growth habit (palm, tree-fern, versus non palm, and non tree-fern), and protective insects. Other morphological characters and mechanisms were not included, since data for one or more sites were missing. Mechanism variables were not used to analyze the Bauru site also due to lacking data. Grouping variables can be a solution for many independent variables in a statistical model. An analysis with many independent variables may not be practical (Crawley 2007) and its results may be hard to understand. Identities of the species of tree and liana were not recorded.

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We did not consider the number of lianas on a tree individual, but took their presence or absence into account. Therefore, we used the multiple logistic regression, a type of generalized linear model (GLM), to predict the probability of liana infestation of trees as a function of the tree features described above. Logistic regression is advocated when a response variable is binary, such as for the presence or absence of lianas (Crawley 2007). The presence of any liana on a host was considered a response variable and the variables diameter, height, mechanism, and morphology were taken as explanatory variables. To avoid multicollinearity, we applied separate tests for tree height and diameter. The best regression model was chosen by backward procedure, which selects the most favorable explanatory variables. We used the Akaike's Information Criterion (AIC) to choose the best model. AIC penalizes any superfluous parameter in the model, thus, when comparing two models, a lower AIC indicates the best fit (Crawley 2007). We performed the GLM in R statistical programming (R Development Core Team 2009). The mechanism status of some trees species in Ubatuba was unavailable and we did not consider these individuals in the analysis. Those with missing variables summed to 6.58 percent of all individuals.

We also tested whether tree size was related to morphologies or mechanisms to avoid lianas. For example, taller trees may have mechanisms to avoid lianas, which may explain the multiple regression results. We used the Wilcoxon test (W), since tree size did not have a normal distribution, even after transformations. The Wilcoxon test was performed for all three sites sampled.

Results

In the Rainforest (Ubatuba), we sampled 1747 trees, of which 19.8 percent had at least one liana. The best logistic models included diameter and mechanism (AIC = 1615.5) or height and mechanism (AIC = 1661.6). These models are more adequate than the full models, *i.e.*, those including diameter,

morphology, and mechanism (AIC = 1620.2) or height, morphology, and mechanism (AIC = 1667.2). The presence or absence of morphological characters was not relevant in our model, probably because the Rainforest is a well-structured forest, with 81.22 percent of trees without morphology to avoid lianas. Larger trees (P < 0.05; Tables 1 and 2) and trees with mechanisms had fewer lianas (P < 0.05; Tables 1 and 2) and trees with mechanisms had fewer lianas (P < 0.05; Tables 1 and 2). The combination of taller trees with mechanisms had no significant effect on the presence of lianas (P > 0.05; Table 2). However, trees with larger diameter and mechanisms carried more lianas (P < 0.05; Table 1). The Wilcoxon test showed that trees without mechanisms had larger diameters (W = 280,306; P < 0.05; Fig. 1).

The best model for the Seasonal Forest (Paulo de Faria) included all variables: mechanism, morphology, and diameter (AIC = 1731.9) and mechanism, morphology, and height (AIC = 1752.7). The complete model has a lower AIC than other models, for example the model in which all interactions among the variables was removed (diameter, mechanisms, and morphologies, AIC =1737.8; or height, mechanisms, and morphologies, AIC = 1754.9). Taken individually, these characters promoted liana infestation. When analyzed separately, size, morphology, and mechanism implied more lianas on the trees (all P < 0.05; Tables 1 and 2). However, the combination size-morphology or sizemechanism produced the opposite result: larger trees with structures or with mechanisms had fewer lianas (P < 0.05; Tables 1 and 2). The Wilcoxon test confirmed that morphology (W = 113,903.5; P <0.05; Fig. 2a) and mechanism (W = 168,116.5; $P = \langle 0.05;$ Fig. 2b) were positively related to trees with larger diameters. We found the same result for taller trees with morphology (W = 141,825.5; P < 0.05; Fig. 2c) and mechanism (W = 142,776; P < 0.05; Fig. 2d). However, trees with a combination of morphologies and mechanisms, like spiny trunk palms, were not able to avoid lianas (P > 0.05; Tables 1 and 2). The combination of all traits, on the other hand, was able to avoid lianas (P < 0.05; Tables 1 and 2). We consider the Seasonal Forest to be a liana forest, because most trees hosted at least one liana (61.52%).
In Woodland Savanna (Bauru), lianas occupied 30.7 percent of all stems surveyed. The best models included morphology and diameter (AIC = 12,913.8) or morphology and height (AIC = 12,508.5). Simpler models have higher AIC values, such as the one that excludes the interaction between diameter and morphologies (AIC = 12,9) and that that excludes the interaction between height and morphologies (AIC = 12,5). Larger trees or trees with morphologies were positively related to liana presence, *i.e.*, had more lianas (P < 0.05; Tables 1 and 2). However, trees that were both larger and had structures hosted fewer lianas (P < 0.05, Tables 1 and 2). The Wilcoxon test confirmed the positrive association between structures and larger diameters (W = 4,973,921; P < 0.05; Fig. 3a) and greater height (W = 5,736,408; P < 0.05; Fig. 3b), *i.e.*, larger trees had morphologies to avoid lianas. Therefore, in the Savanna, lianas occupied smaller trees without morphologies to avoid them.

Discussion

Tree size was the only trait negatively correlated with liana presence when analyzed alone in all three sites. Larger diameter trees had more lianas, confirming many previous studies (Clark & Clark 1990, Carse *et al.* 2000, Pérez-Salicrup *et al.* 2001, Pérez-Salicrup & de Meijere 2005, Malizia & Grau 2006, Reddy & Parthasarathy 2006, Nesheim & Økland 2007, Carrasco-Urra & Gianoli 2009, Ding & Zang 2009, Jimenez-Castillo & Lusk 2009, Homeier *et al.* 2010). This result may be a consequence of facilitation processes (Pinard & Putz 1994) or of the fact that larger trees are older (Pérez-Salicrup *et al.* 2001, Malizia & Grau 2006, Campanello *et al.* 2007). Therefore, smaller trees would not play an important role on liana presence, as some studies have shown (Balfour & Bons 1993, Chittibabu & Parthasarathy 2001, Carsten *et al.* 2002).

In all three sampled forests, morphology proved to be important. However, we observed that this variable produced a different effect from that reported in the literature. For example, palms (Putz 1980) and spiny trunks (Maier 1982) are reported as morphologies associated with liana avoidance, but we found that trees with morphologies had more lianas. Our results suggest that trees with morphological traits alone are not able to repel lianas, a result that is opposite to that found in the literature (for example, Putz 1984, Malizia & Grau 2006). The exception is Ubatuba, where the presence of mechanisms such as fast growth, palms, and tree-ferns was related to fewer lianas. Results from Ubatuba confirmed data from the literature that pioneers (Clark & Clark 1990, Carse *et al.* 2000, Campanello *et al.* 2007) and palms (Putz 1980, Maier 1982, Putz 1984, Rich *et al.* 1987, Carse *et al.* 2000, Pérez-Salicrup *et al.*, Campanello *et al.* 2007) have fewer lianas.

The combination of different tree traits to avoid lianas produced different results. In spite of the fact that larger trees usually do not have mechanisms to avoid lianas, the logistic model showed that, in the Rainforest, lianas climb trees with both larger diameter and mechanisms. Ubatuba is a dense rainforest, where light is a limiting factor. Consequently, lianas occupied well-lit trees, although these trees generally have some mechanism (like palm architecture). In this case, the forest structure played an important role in liana presence and could be considered more important than tree mechanisms. Moreover, in this forest, the backward procedure demonstrated that morphologies (such as shedding and spiny barks) were not relevant, but some mechanisms were important, due to the abundance of the palm *Euterpe edulis* Mart. This species is a very abundant host-tree, with 10.30 percent of all individuals sampled. In addition, trees with lianas in the Rainforest represented only 20 percent of all trees, the smallest proportion in all three forests we studied, indicating that probably lianas are not significantly harmful to trees in Ubatuba.

Conversely, in the Seasonal Forest and the Woodland Savanna, the combination of size and mechanism or morphology was negatively related to the presence of lianas. In these forests light is not a limiting factor as it is in the Rainforest. Paulo de Faria is a seasonally dry tropical forest in which the canopy is lower than in the rainforest, such as that in Ubatuba (Lopes *et al.* 2008). Bauru is a woodland

savanna, with a low canopy too. The woodland savanna is characterized by trees less than 15 m covering 50-90 percent of ground surface (Ribeiro & Walter 1998). Both are forests with more open canopies, where light reaches the forest floor with more intensity than in the Rainforest. Consequently, lianas avoid larger trees with mechanisms or morphologies to avoid them, indicating the importance of the mechanisms and morphologies. Therefore, lianas climber smaller trees, because larger trees usually have mechanisms or morphologies to avoid them. These results may also indicate that lianas in Paulo de Faria and Bauru are still young, probably as a result of recent perturbations (this thesis, chapter 5) and have not occupied larger trees yet. However, in Paulo de Faria, trees with a combination of larger size, morphology, and mechanisms carried more lianas. This result suggests that the combination of the three variables was not sufficient to avoid lianas. A reasonable explanation is that lianas reached the canopy trees when they were young, and, after the tree reachs the canopy trees (Balfour & Bond 1993), since larger trees generally have more structures or mechanisms to avoid lianas.

We propose that, in addition to tree traits, forest structure is another set of variables capable of influencing the presence or absence of lianas on trees from the time they start to climb. Tree traits should not be seen as the only factors influencing liana attachment to a tree, since forest structures, especially light, also plays an important role on liana climbing.

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1 Tables

2 Table 1. *Multiple logistic regression results for all three areas sampled. These models include tree diameter. Estimates = the*

| 3 | estimation o | f the regre | ession line ar | igle; SE = sta | ndard deviation; | z = z-value; * | <i>p</i> < 0.05. |
|---|--------------|-------------|----------------|----------------|------------------|----------------|------------------|
| | | / () | | () / | , | ~ ~ / | |

| | Rainforest | | | Seasonal 7 | Ггоріса | l Forest | Woodland Savanna | | | |
|-----------------------------------|------------|------|---------|------------|---------|----------|------------------|------|---------|--|
| - | Estimates | SE | Z | Estimates | SE | Z | Estimates | SE | Z | |
| Diameter | 0.04 | 0.01 | 7.68 * | 0.15 | 0.02 | 6.84 * | 0.01 | 0.00 | 28.29 * | |
| Morphology | - | - | - | 1.16 | 0.28 | 4.06 * | 0.62 | 0.10 | 6.33 * | |
| Mechanism | -1.71 | 0.35 | -4.96 * | 0.72 | 0.25 | 2.90 * | - | - | - | |
| Diameter + Morphology | - | - | - | -0.09 | 0.03 | -3.13 * | -0.005 | 0.00 | -6.04 * | |
| Diameter + Mechanism | 0.05 | 0.02 | 2.64 * | -0.12 | 0.03 | -4.40 * | - | - | - | |
| Morphology + Mechanism | - | - | - | -0.68 | 0.62 | -1.10 | - | - | - | |
| Diameter + Morphology + Mechanism | - | - | - | 0.12 | 0.04 | 2.65 * | - | - | - | |

- 1 Table 2. Multiple logistic regression results for all three areas sampled. These models include tree height. Estimates = the
- *estimation of the regression line angle;* SE = standard deviation; z = z-valu; ; * p < 0.05.

| | Rai | infores | st | Seasonal T | ropica | ll Forest | Woodland Savanna | | | |
|------------------------|-----------|---------|---------|------------|--------|-----------|------------------|------|---------|--|
| | Estimates | SE | Z | Estimates | SE | Z | Estimates | SE | Z | |
| Height | 0.09 | 0.01 | 5.92 * | 0.20 | 0.03 | 7.13 * | 0.03 | 0.00 | 32.58 * | |
| Morphology | - | - | - | 1.21 | 0.38 | 3.19 * | 0.60 | 0.14 | 4.17 * | |
| Mechanism | -1.27 | 0.43 | -2.98 * | 1.03 | 0.36 | 2.88 * | - | - | - | |
| Height + Morphology | - | - | - | -0.09 | 0.04 | -2.00 * | -0.01 | 0.00 | -2.24 * | |
| Height + Mechanism | 0.02 | 0.04 | 0.64 | -0.16 | 0.04 | -4.04 * | - | - | - | |
| Morphology + Mechanism | - | - | - | -0.86 | 0.83 | -1.03 | - | - | - | |
| Height + Morphology + | | | | 0.16 | 0.08 | 1 07 * | | | | |
| Mechanism | - | - | - | 0.10 | 0.08 | 1.97 * | - | - | - | |

Figure legends

FIGURE 1. In Ubatuba, in a dense and very rich rainforest, trees without avoidance mechanisms (like fast growth) have larger diameters. The logistic model showed that these trees also carry fewer lianas.

5 FIGURE 2. In Paulo de Faria, in a seasonally dry tropical forest, trees with avoidance morphologies, like peeling bark, (A, C) or avoidance mechanisms, like fast growth, (B, D) are larger. Trees with a combination of size and mechanism or morphology have fewer lianas, as shown by the logistic model.

FIGURE 3. Trees with morphologies to avoid lianas, like peeling bark, generally have larger

10 diameter (A) or height (B). The logistic model demonstrated that these trees also have fewer lianas in Bauru, a savanna woodland site.



Figure 1.



Figure 2.



Figura 3.



Capítulo 3 - Trait matching or neutrality in liana-tree interaction?

Trait matching or neutrality in liana-tree interaction?³

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³ Artigo segue as normas de Perspectives in Plant Ecology, Evolution and Systematics.

Abstract

In spite of one liana species may interact with all tree species in a community, some constraits may limit the number of interaction of a liana species. These constraits may result on a gradient of number of interactions of liana and tree species. Our aim was to investigate the processes originating

- 5 the variation of number of interaction of liana and tree species in liana-tree networks. We investigated two processes: (a) neutral interaction, in which abundance is the major determinant of number of species interaction; and (b) trait matching, in which liana and tree traits determine the species number of interaction. To investigate interaction neutrality we compared the observed number of interaction of lianas and trees with those generated by null models according to species
- 10 abundance. To investigate trait matching we used multiple regression with number of interaction as the response variable, whereas height, exfoliation bark, spines, fast growth and palm architecture (for trees) and diameter and climbing mode (for lianas) were explanatory variables. The abundance strongly explained the number of interactions of trees and lianas, whereas only height of trees and trendillar climbing mode of lianas explained the number of interactions. This result indicates the
- 15 importance of abundance on the number of interactions of a species.

Key-words: abundance, character displacement, degree, network, nested, climber

Introduction

5

One liana species potentially may interact with all tree species in a community. However, some constraits may limit the number of interaction of a liana species, like characters from trees that hamper liana occupation. These characters may include tree height, which is generally positively related to liana presence (Carsten et al., 2002; Nesheim and Økland, 2007; Carrasco-Urra and Gianoli 2009; Ding and Zang, 2009; Jimenez-Castillo and Lusk, 2009; Homeier et al., 2010; this

- thesis, chapter 2). This positive relationship may be due to tree age: larger trees may be older and, therefore provide more opportunities and time for liana colonization (Pérez-Salicrup et al., 2001; Malizia and Grau, 2006; Campanello et al., 2007). The facilitation process may also explain this
- 10 pattern, i.e., once a liana reaches the canopy, newly arriving lianas can be favored by the shortcut to reach the highest trees (Pinard and Putz, 1994). Other variables influencing liana infestation are related to tree morphology capable of avoiding lianas, such as spines or thorns, and bark smoothness, roughness, and exfoliation. Spines, for example, may abscise due to liana weight (Maier, 1982), and spiny trees host fewer lianas. Trees with smoothing or exfoliating bark also have
- 15 fewer lianas (Campanello et al., 2007). Another variable which influences liana presence is tree mechanisms, like fast growth, shedding of leaves and branches, emergence of closed palm leaves, and the hosting of protective insects are considered mechanisms that avoid lianas. For example, palms are generally less susceptible to liana infestation when compared to non-palms (Maier, 1982; Putz, 1980; Putz, 1984; Campanello et al., 2007) because new leaves emerge closed from the
- 20 terminal bud, grow vertically, and then spread out and lean over (Putz, 1980). From the liana perspective, some variables may also influence their capacity to colonize trees, such as the climbing mode. Lianas with tendrils are found in mid-sized and small trees, because these trees offer thinner branches that tendrils may easily encircle (Carsten et al., 2002). Another variable is liana size: lianas invest on growth by allocating more resources to root and stem elongation and fewer resources to

structural support (Schnitzer and Bongers, 2002). Therefore, lianas with larger diameter would be older and, consequently, occupy more trees.

Sfair et al. (this thesis, chapter 2) showed that tree size, mechanisms and morphologies to avoid lianas influence liana presence on the individual level. On the species level, these variables may also be important, because they may characterize species groups. For example, species of the Myrtaceae family generally have exfoliating bark and, consequently, would have fewer lianas (Campanello et al., 2007). As another example, species from the genus *Cecropia* are fast-growing trees and generally have fewer lianas (Campanello et al., 2004). Sfair et al. (2010) proposed that tree species with fewer lianas should have some traits that would decrease or hinder their occupation by

5

10 lianas. Additionally, generalist trees and liana species would have traits that would promote their association. These trait differences among species would result in a gradient of number of interactions (Sfair et al, 2010).

However, a simpler variable may explain the number of interactions of a species: its abundance. The most linked species are more abundant than the least linked ones, which are

- 15 generally rare in the local community. This interaction neutrality would result from random encounters among individuals (Krishna et al., 2008; Vázquez et al., 2009a). Therefore, all individuals would have the same interaction probability and in comparison with rare species the abundant species would interact more frequently and with more species (Vázquez et al., 2009a). If species interact according to their abundance, we expect that abundance would explain the variation
- 20 of the number of interactions among species. However, if the number of interactions is a consequence of trait matching factors, such as liana diameter and climbing mode and tree diameter, mechanisms and morphologies to avoid lianas, then these variables would explain species number of interaction better than abundance.

Our aim was to investigate the processes originating the number of interactions in liana-tree networks by testing the following hypotheses: (a) if the interaction is determined by trait matching, then liana and tree traits determine species number of interactions (trait matching hypothesis); but (b) if the interaction between lianas and trees is neutral, then abundance is the major determinant of species degree (interaction neutrality hypothesis).

Material and Methods

Sites sampled

5

We sampled lianas and trees rooted within plots in three different sites in the state of São

- Paulo, southeastern Brazil. These sites have different plant formations, to which different sampling designs were applied, considering the peculiarities of each community, such as average height, diameter, and density of lianas and trees. In all three sites, the sampled area corresponded to 1 ha divided into 100 plots of 10 x 10 m each (contiguous in the rain and seasonal forests, and random in the savanna woodland).
- The first site (23°21'54"- 59"S and 45°05'02"- 04"W, 348-394 m above sea level) is a tropical rainforest in the municipality of Ubatuba, in the Parque Estadual da Serra do Mar, a conservation unit of 47,500 ha. We surveyed all dead and living plants with perimeter at breast height (PBH) \geq 15 cm (Rochelle et al., *unpublished*) and all lianas with diameter at breast height (DBH) \geq 1 cm (van Melis and Martins, *unpublished*). The second site (19°55'-58'S and 49°31'-32'W; 400-495 m above
- sea level) is a fragment of 435.73 ha of tropical seasonally dry forest (Rezende et al., 2007a) in the municipality of Paulo de Faria. We excluded plots with densely tangled lianas, and sampled living trees with DBH ≥ 3 cm and lianas with DBH ≥ 1 cm. The third site (22°19'41"-21'06"S and 48°59'49"-49°01'12"W, 519-603 m above sea level is a fragment of 321.71 ha of savanna woodland in the municipality of Bauru. We sampled all living trees with DBH ≥ 0.1 cm and all lianas with

stem diameter at soil height (DSH) \ge 0.1 cm (Weiser, 2007). For further detail of each sampled area, see Sfair et al. (2010).

Eliminating the outliers

Some outliers were eliminated from our analyses. In the Rainforest, *Euterpe edulis* Mart.
(Arecaceae) was a very abundant palm with 180 individuals but only two interactions. In the
Woodland Savanna, we did not consider the abundant trees *Psychotria capitata* Ruiz & Pav.
(Rubiaceae) and *Actinostemon klotzschii* (Didr.) Pax (Euphorbiaceae) with 330 and 325 individuals
and with nine and eight interactions, respectively (see anexo 2). We excluded these species of the
next analysis because the inclusion of these species increases the variation of the regression analysis.

Trait matching hypothesis

In all sites, we recorded some tree and liana features that were previously reported in the literature as determinant of liana climbing. We recorded five variables for trees: (a) height; (b)

15 exfoliating bark, (c) spines or thorns, (d) fast growth, (e) palm architecture. We considered tree height as a proxy for tree size. Fast growth was not used in the analysis of Bauru data due to lack of information. For statistical models of lianas, we considered (a) diameter and (b) climbing mode: twiners, tendrillar or scrambling lianas. Since information on the climbing mode for some species were missing in Ubatuba, we considered undetermined climbing mode as another category. The

20 undetermined class of climbing mode of lianas comprised 17.64% of all liana species.

In the multiple regression analysis the number of interactions was the response variable whereas traits were considered explanatory variables. The best regression model was chosen by backward procedure, which selects the most favorable explanatory variables using variable deletion (Crawley, 2007). We used the AIC (Akaike's Information Criterion) to choose the best model. AIC

penalizes any superfluous variable in the model, so when comparing two models lower AIC indicates the best fit (Crawley, 2007).

Interaction neutrality hypothesis

- 5 To investigate in detail whether abundance is related to liana and tree species number of interactions, we created a matrix in which the column corresponded to liana species, while rows represent tree species. For each liana and tree species, relative abundance is known. For each matrix cell, the entry represented the respective relative abundance of its column and row. Therefore, we created a matrix in which the cell occupation probability was proportional to the relative abundance
- 10 of the respective liana and tree species. When the cell content represented an abundant liana (column) and an abundant tree (row), the probability of filling was higher. In other words, abundant species had higher probability to interact than rarer species. We filled the cells with 1's in respect their probability, i.e., cells with higher values received 1 and cells with lower values, 0 (zeros). We considered the same matrix fill (connectance) as the original matrix as the cut off for high versus
- 15 low. So, we have a matrix, in which the interaction between lianas and trees is solely due to relative abundance of the paired species. We called this matrix as "abundance model" (Vázquez et al., 2009b).

For each species of the abundance model, we calculated the number of interaction of a species, which is the sum of rows or columns. We used linear regression to correlate the number of

20 inteactions from the abundance matrix with the respective liana or tree species abundance. We also used linear regression to correlate the original species number of interactions to their abundance. To achieve normality, we log-transformed ($\log x + 1$) all the variables. So, we had two linear regressions, one referring to the observed and the other referring to the expected number of inteactions values, whereas the independent variable was the same (abundance). If the abundance

was the only variable explaining species number of interactions, we would expect no difference between the two slopes. These two lines (Figs. 1 and 2) were compared using the differences between slopes (b) and tested using a t-test, which compares the regression coefficients and the standard error (Zar, 1999). If the lines have the same slope, the line elevation (a) is compared (Zar, 1999). The differences between slopes were significant in all cases and we did not compare the line elevation.

Results

5

Ubatuba was the richest site (66 liana and 210 tree species), followed by Bauru (39 liana and 10 140 tree species) and Paulo de Faria (45 liana and 87 tree species). However, only 125, 119, and 64 tree species, respectively, had associated lianas in those sites. The proportion of tree species that were free from lianas varied in each community: 40.47% in Ubatuba, 26.43% in Paulo de Faria, and 15% in Bauru.

15 Trait matching hypothesis

For trees in Rainforest and Seasonal Forest, height influenced the number of interactions: taller species are more prone to liana occupation (Table 1). The best model in Rainforest included height, exfoliating bark, fast growth and the combination of height and exfoliating bark. In the Seasonal Tropical Forest and Woodland Savanna, the best models included only height (Table 1).

20 For lianas, in these both sites, the best model included diameter and trendillar and scrambling climbing mode, whereas in Ubatuba, the best model included none of the traits (Table 2). In Seasonal Forest, lianas species with tendrils climb on more tree species (Table 2).

Neutrality hypothesis

For all sites, the number of inteactions was positively and significantly related to liana and tree abundance (Table 3). However, the error variance values were greater for the observed number of interactions values than for the number of interactions values expected if abundance was the only

- 5 important variable, indicating that there was at least 50% of non-explained variation in the regression between original data and abundance. Additionally, the error variance for lianas abundance versus original or abundance number of interactions were smaller than for trees, probably because lianas must climb a tree to reach the forest canopy, i.e, there are no lianas without an interaction. The exception is Bauru, where the error variance value was greater for abundance versus
- 10 the expected number of interactions values (Table 3).

Even after the log-transformation of data, the most abundant species had fewer number of interactions than predicted by the regression line (Figs. 1 and 2). In other words, the number of interactions of the most abundant liana and tree species had a tendency towards stabilization, except in Ubatuba (Figs. 1 and 2).

- 15 The t-test was significantly different for all comparisons, probably because the regression slope of abundance model was higher than observed number of interactions (Table 3). This result indicates that tree and liana species with high observed number of interactions had fewer links than expected by the abundance models; and, conversely, tree and liana species with small number of interactions had more links than expected by the abundance models (Figs. 1 and 2). Therefore, the
- 20 abundance models did not explain completely the species number of interactions.

Discussion

Abundant tree and liana species have more interactions than rarer species. In addition, there is a stabilization of number of interactions for abundant species even after log-transformation of data.

Many different liana species climb the abundant tree species. As abundance of these tree species increases, the probability of encounter between lianas and trees increases. However, at very high abundance, the tree species start to encounter rarer liana species. Rarer species are hard to link in a stochastic interaction, so there is a stabilization of number of interactions. For example, the

5 abundant tree species *Bathysa mendoncaei* K.Schum. had 147 individuals in the Rainforest, but 23 links. However, another abundant tree *Eriotheca pentaphylla* (Vell.) A. Robyns in the Rainforest, with 62 individuals, showed 21 links, only two fewer links than *B. mendoncaei* (see anexo 2).

The strong relation between abundance and number of interactions may be interpreted in two ways. First, species have higher number of interactions because they are abundant. Second, they are

- 10 abundant, because, having higher number of interactions, they have access to more resources (Santamaría and Rodríguez-Gironés, 2007), such as light. In spite of we had adopted the first interpretation in this work, because number of interactions is a response variable, the second interpretation is also possible for lianas. Lianas species with higher number of interactions must occupy more tree canopies, having higher number of interactions and acquiring more energy.
- 15 Consequently, they also would produce more fruits, increasing their abundance. The second interpretation is not valid for trees species, because lianas are generally harmful to them, decreasing their fruit production (Kainer et al., 2006; Fonseca et al., 2009) and growth (Clark and Clark, 1990; Ladwig and Meiner, 2009), and increasing their mortality (Grogan and Landis, 2009). So, the increased number of interactions means more lianas species attached to trees, decreasing tree access
- 20 to resources and making tree species less abundant. The first interpretation (higher number of interactions because trees are more abundant) is more reasonable in this case.

The trait analysis indicates that the traits selected in this study are not important for the interaction of the liana and tree species. The exceptions are height of trees and trendillar climbing mode of lianas: taller trees and trendillar lianas have more interactions than smaller trees and other

kind of climbing mode. Previously studies also confirmed that taller trees lianas have more interactions than smaller trees (Carsten et al., 2002; Nesheim and Økland, 2007; Carrasco-Urra and Gianoli 2009; Ding and Zang, 2009; Jimenez-Castillo and Lusk, 2009; Homeier et al., 2010; this thesis, chapter 2). The importance of tendrillar lianas in the seasonal forest may be related to this low canopy forest (Lopes et al., 2008), since lianas with this structure are associated to mid-sized and small trees, which have thinner branches that tendrils may easily encircle (Carsten et al., 2002). The few significant traits and combination of traits may explain the strong relationship between abundance and number of interactions: a small part of the variation is not explained by abundance. This small part may be partially explained by height of trees or trendillar climbing mode of lianas,

10 but also may be explained by phylogenetic relationship, micro-habitat variation and forest structure (this thesis, chapter 2).

Trait matching and neutral variables have been used to explain the structure of mutualistic networks (Vázquez et al., 2009a). For example Vázquez et al. (2009b) found that both abundance and complementarity in spatiotemporal distribution contribute to some network pattern, like

15 nestedness. The abundance and trait variables, like morphological constraints, are also able to produce asymmetry in mutualistic networks (Stang et al., 2007). In our work, we described that the abundance is heavily related to the number of interactions of liana and tree interaction. Probably some structure of liana-tree interaction, like nestedness, could also be explained by abundance. Future research will explore the role of liana and tree variables on network structure.

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Figure Captions

Fig. 1. Relationship between abundance and number of interactions for tree species in the three sites sampled. The filled dots represent the original number of interactions values. The unfilled dots represent the number of interactions of the abundance model. The straight line represents the

regression line between the original number of interactions and the respective species abundance.
 The dashed line represents the number of interactions from the abundance model and the respective species abundance.

Fig. 2. Relationship between abundance and number of interactions for liana species in the three sites sampled. The filled dots represent the original number of interactions values. The unfilled

10 dots, the number of interactions of abundance model. The straight line represents the regression line between the original number of interactions and the respective species abundance. The dashed line represents the number of interactions fr the abundance model and the respective species abundance.

Fig. 1.



Log₁₀ (Abundance+1)





Log₁₀(Abundance+1)





| 2 | Table 1. Multi | ple regression | results for all three | areas sampled for trees. | *p < 0.05 |
|---|----------------|----------------|-----------------------|--------------------------|-----------|
| | | | | | |

| | Rainforest | | | Seas | onal For | rest | Woodl | Woodland Savanna | | | | |
|---------------------------|------------|-------|---------|----------|----------|---------|----------|------------------|-------|--|--|--|
| | Estimate | SE | t | Estimate | SE | t | Estimate | SE | t | | | |
| Height | 0.044 | 0.017 | 2.483 * | 0.575 | 0.212 | 2.712 * | 0.352 | 0.201 | 1.749 | | | |
| Exfoliating bark | 0.636 | 0.381 | 1.671 | - | - | - | - | - | - | | | |
| Fast Growth | -0.308 | 0.163 | -1.88 | - | - | - | - | - | - | | | |
| Height + Exfoliating bark | -0.075 | 0.039 | -1.904 | - | - | - | - | - | - | | | |

4 Table 2. Multiple regression results for all three areas sampled for lianas. We included only the climbing mode "tendril" because all

| | Rainforest | | | Seas | sonal Fore | st | Woodland Savanna | | | | |
|----------|------------|----|---|----------|------------|---------|------------------|--------|--------|--|--|
| | Estimate | SE | t | Estimate | SE | t | Estimate | SE | t | | |
| Diameter | - | - | - | 4.764 | 2.557 | 1.863 | 7.086 | 4.605 | 1.539 | | |
| Tendril | - | - | - | 15.408 | 7.032 | 2.191 * | -0.672 | 18.173 | -0.037 | | |
| Scramble | - | - | - | 13.675 | 7.709 | 1.774 | 11.575 | 18.339 | 0.631 | | |
| | | | | | | | | | | | |

5 other climbing modes were non-significant (* p < 0.05).

7 Table 3. Regression parameters between the abundance and the original number of interactions and the abundance and the number of

| 8 | interactions from abundance models | The t-Test between | the two regression sl | slopes were significative for all c | ases. |
|---|------------------------------------|--------------------|-----------------------|-------------------------------------|-------|
|---|------------------------------------|--------------------|-----------------------|-------------------------------------|-------|

| | Original | | | | | Abundar | t-Test | | | | | |
|------------------|--------------------|---------|---|-------|---|--------------------|----------|---|-------|--------|------|---------|
| | Equation | F | p | R² | | Equation | F | р | R² | t | D.F. | р |
| Trees | | | | | | | | | | | | |
| Rainforest | y = 0.684x - 0.176 | 296.970 | 0 | 0.570 | X | y = 0.894x - 0.412 | 1112.777 | 0 | 0.832 | 4.393 | 448 | < 0.001 |
| Seasonal Forest | y = 0.446x - 0.011 | 125.108 | 0 | 0.595 | X | y = 0.972x - 0.21 | 927.219 | 0 | 0.916 | 2.563 | 170 | 0.0112 |
| Woodland Savanna | y = 0.569x - 0.005 | 742.112 | 0 | 0.845 | x | y = 0.753x - 0.387 | 1423.111 | 0 | 0.913 | 6.377 | 272 | < 0.001 |
| Lianas | | | | | | | | | | | | |
| Rainforest | y = 0.842x + 0.107 | 945.226 | 0 | 0.937 | X | y = 1.261x - 0.428 | 2010.183 | 0 | 0.969 | 10.669 | 128 | < 0.001 |
| Seasonal Forest | y = 0.687x + 0.25 | 520.244 | 0 | 0.924 | X | y = 1.022x - 0.288 | 546.720 | 0 | 0.927 | 6.323 | 86 | < 0.001 |
| Woodland Savanna | y = 0.647x + 0.296 | 701.625 | 0 | 0.950 | X | y = 0.906x - 0.193 | 333.531 | 0 | 0.900 | 4.690 | 74 | < 0.001 |

Capítulo 4 - Processes involved in networks of antagonistic liana-tree interaction
Running Head: Processes on antagonistic networks

Title: Processes involved in networks of antagonistic liana-tree interaction ^{4*}

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^{4*}Artigo segue as normas de *Ecology*.

ABSTRACT

The processes that influence mutualistic networks comprise basically neutral (abundance) and trait complementarity factors. Our aim was to determine the processes that result in nestedness of liana-tree network, an antagonistic network. We developed a new metric: the species contribution for nestedness and used statistical modeling to investigate how neutral and species traits variables shape the species contribution for nestedness for three areas in Southeastern Brazil. We showed the higher the abundance, the higher species contribution for nestedness in all areas, indicating the importance of the random encounter of liana and tree species. However, neutral and traits also influenced nestedness, a similar result found in some mutualistic networks. The species contribution for nestedness depends not only the species, but also the environmental features.

Key-words: antagonism; climber; host-tree, liana; mutualism; nestedness; phorophyte; species contribution for nestedness, vine.

INTRODUCTION

In a network, nestedness is a non-random structure in which species with fewer interactions (specialists) interact with specific subsets of the species with which the generalists interact. As a consequence of the nested pattern, generalist species tend to interact with each other, establishing a dense core of interactions (Bascompte et al. 2003). This pattern is very common in mutualistic networks, like pollination and frugivory (Bascompte et al. 2003), ant and extra-floral nectaries (Guimarães et al. 2006), fish and cleaning symbionts (Guimarães et al. 2007), and anemonefish and host sea anemone systems (Ollerton et al. 2007). Nestedness can be influenced by different processes, such as species phenotypes, spatial distribution, and sampling effects (Vázquez et al. 2009a, Vázquez et al. 2009b).

Two basic processes may result in the nested structure on mutualistic networks. The first one is neutrality, i.e., all individuals are assumed to be ecologically equivalent (Hubbell 2001). Therefore, interactions shaped by neutral processes would occur if all individuals show the same probability of interaction (Krishna et al. 2008). In this case abundant species would have more interactions than rare ones (Krishna et al. 2008, Vázquez et al. 2009a). These abundant species would be the generalists (have more interactions), whereas the rare species would be specialists (have fewer interactions) in a nested network. In spite of abundance explaining nestedness well (Dupont et al. 2003), other processes can play an important role in network structure. Vázquez et al. (2009a) called these processes trait matching, i.e, the correspondence of phenotypic traits of animals and plants. For example, long corollas that exclude animals with short proboscides (Vázquez et al. 2009a). In spite of the combination of different trait matching explains better nestedness in mutualistic networks than abundance does (Santamaría and Rodrígues-Gironés 2007), there is increasing evidence the structure of nested networks is shaped by a complex interplay between neutral and trait matching processes (Krishna et al. 2008, Vázquez et al. 2009b, Chamberlain et al. 2010).

Antagonistic networks, such as parasite-host and herbivory systems, are more prone to

specialization and compartmentalization than to nestedness (Prado and Lewinsohn 2004, Thompson 2006, Thébault and Fontaine 2010). Trophic networks, like herbivore-plant systems, are modular and have lower connectance than mutualistic networks with similar diversity (Thébault and Fontaine 2010). However, some studies also found nestedness in antagonistic networks, such as parasite-host systems (Rohde et al. 1998, Zelmer et al. 2004, Timi and Poulin, 2007, Graham et al. 2009). In fact, nestedness in parasitic networks might be associated to the same patterns shaping nestedness in mutualisms: abundance and trait similarity (Graham et al. 2009).

The interaction between lianas and trees is characterized as antagonistic, since they compete, especially belowground for nutrients (Schnitzer et al. 2005; Toledo-Aceves and Swaine 2008). The structure of interaction between lianas and trees was described as nested (Sfair et al. 2010). As mutualistic networks, we propose that the neutral and trait matching variables also explain nestedness in antagonistic networks: in liana-tree interactions, not only abundance would play an important role, but also variables that promote or inhibit liana occupation (this thesis, chapter 2). These variables include tree size, for example, since the larger the tree the higher the number of lianas harbored (Ding and Zang 2009, Jimenez-Castillo and Lusk 2009, Homeier et al. 2010; see this thesis (chapter 2) for a review of tree traits that promote liana occupation). Other variables include spines, peeling bark, fast growing and palm architecture (this thesis, chapter 2). Since these traits influence the liana occurence, we hypothesize the same traits shape nestedness on liana-tree network. For example, a tree species with traits that promote liana occupation may be a species that strongly contributes to nestedness.

Our aim was to identify the processes that result in nestedness in liana-tree antagonistic networks. The processes are divided into two classes: neutral (abundance) and traits matching processes, like liana and tree size, mechanisms and morphologies of trees to avoid lianas, and liana climbing mode.

METHODS

Species contribution to nestedness

The network of interaction between lianas and trees is represented by a matrix, in wich lianas are rows and trees, columns. The contribution of each species for nestedness (ni) is based on the metric NODF (Almeida-Neto et al. 2008). As NODF, the individual contribution to nestedness (ni) takes into account the two properties of nested pattern: the decreasing number of presences (1's) between rows (columns) and the percentage of presences that occurs at identical positions between pairs of rows (columns). We describe in details how to calculate ni for the species represented in the lianas, but the same procedure can be applied to the trees.

To compute the nestedness contribution of a liana species *i* we first contrast the number of interactions of species i with trees with number of interactions of all other liana species. If the number of interactions of species i is equal to the number of interactions a liana species j, the pairwise nestedness is $ni_{ij} = 0$. Thus, this zero represents the lack of contribution of the pair of species *ij* in generating nestedness, since there is no decreasing fill between them (Almeida-Neto et al. 2008). If the number of interactions of both species differs, the pair might contribute to nestedness in two distinct ways. First, if the species *i* establishes more interactions than species *j*, ni_{ij} will be the proportion of interactions of the species *j* with the same tree species that also interact with species *i*. This proportion depicts the proportion of interactions of liana species *j* that are nested in the interactions of species *i*. Alternatively, if the species *j* has more interactions than species i, ni_{ij} will be the proportion of interactions of the species *i* with the same tree species that also interact with species *j*.

The contribution of a species to nestedness is computed for each species:

$$ni = \sum_{j=1, i\neq j}^{L} ni_{ij}$$

In which ni is the individual contribution of a species to nestedness and L is the number of liana species in the network, quantifying its importance in generating nestedness on the matrix as a whole. As mentioned above, the same procedure would allow computing the nestedness for individual tree species.

Sampled sites

We sampled lianas and trees rooted within plots in three different sites (a tropical rain forest, a tropical seasonally dry forest and a savanna woodland), all in the state of São Paulo, Southeastern Brazil. These sites have different plant formations, to which different sampling designs were applied, considering the peculiarities of each community, such as average height, diameter, and density of lianas and trees. For example, a tropical rain forest generraly has bigger trees than the other formations. In all three sites, the sampled area was 1 hectare (ha), divided into 100 plots of 10 x 10 m each.

The first site is a tropical rainforest in the municipality of Ubatuba (hereafter Rainforest; 23°21'54"- 59"S and 45°05'02"- 04"W, 348-394 m above sea level), in the Parque Estadual da Serra do Mar, a conservation unit of 47,500 ha. We surveyed all dead and living plants with PBH (perimeter at breast height) \geq 15 cm (Rochelle 2008) and all lianas with DBH (stem diameter at breast height) \geq 1 cm (van Melis 2008). The second site is a fragment of 435.73 ha of tropical seasonally dry forest (hereafter Seasonal Forest; 19°55'-58'S and 49°31'-32'W; 400-495 m above sea level, Rezende et al. 2007a) in the municipality of Paulo de Faria. We sampled living trees with DBH \geq 3 cm and lianas with DBH \geq 1 cm, and excluded plots with densely tangled lianas. The third site is a fragment of 321.71 ha of savanna woodland in the municipality of Bauru (hereafter Woodland Savanna; 22°19'41"-21'06"S and 48°59'49"-49°01'12"W, 519-603 m above sea level). We sampled all living trees with DBH \geq 0,1 cm and all lianas with DSH (stem diameter at soil height) \geq 0,1 cm (Weiser 2007). For further detail of each sampled area, see Sfair et al. (2010).

Data analysis

For all sites, we recorded tree and liana features that were previously reported in literature as determinants of liana climbing (this thesis, chapter 2). We recorded four groups of variables for trees: (a) abundance; (b) diameter; (c) morphology (peeling and spiny bark) and (d) mechanisms: successional status (pioneer and non-pioneer; sensu Swaine and Whitmore 1988), growth habit (palms and tree-ferns), and protective insects. For example, bigger trees are more prone to liana infestation (this thesis, chapter 2). We considered tree height as a proxy of tree size. Successional status variable were not used in the model of Bauru analysis because data were missing, since pioneer trees concept is meaninglessin savanna. We also used these variables for lianas (a) abundance, (b) diameter, and (c) climbing mode. Climbing mode group includes twiners, tendrillar, and scrambling lianas. In Ubatuba, some climbing modes for some species were missing, and we considered as new category: undetermined climbing mode. The model employed median of height for each species of trees and lianas, respectively. Abundance and diameter of trees from Rainforest and Seasonal Forest lianas from Rainforest, Seasonal Forest, and Woodland Savanna, and ni, abundance and diameter of trees of Woodland Savanna were log-transformed to achieve normality. We considered abundance as neutral variable and diameter, mechanisms and morphologies to avoid lianas and climbing mode as traits.

Analysis was by multiple regression, in which ni was the response variable. The variables tree abundance, diameter, mechanism and morphology, and liana abundance, diameter and climbing mode were the explanatory variables. The best regression model was chosen by backward procedure, which selects the most favorable explanatory variables using variable deletion. We used the AIC (Akaike's Information Criterion) to choose the best model. AIC penalizes any superfluous parameter in the model, so when comparing two models, lower AIC indicated the best fit (Crawley 2007).

RESULTS

For trees in the Rainforest and the Seasonal Forest, the traits and abundance are both important for the structure of interaction between trees and lianas. For trees in The Rainforest, the best model included all variables, except morphology and its interactions and the interaction between diameter and mechanism ($R^2 = 0.394$, F = 8.251, p < 0.001; Table 1). Abundant trees with mechanisms to avoid lianas, like palm architecture or fast growth, contributed more to nestedness, whereas abundant and bigger trees with the same mechanisms, contributed less to nestedness. (Table 1). In the Seasonal Forest the best model included all variables ($R^2 = 0.609$, F = 8.262, p < 0.001; Table 1). In this site, abundante trees contributed negatively to nestedness, whereas trees with mechanisms to avoid lianas, contributed positively. The combination of traits and abundance returned intriguing results: abundant and larger trees contributed more to nestedness, as well as larger trees with mechanisms and morphologies to avoid lianas. On the other hand, larger trees with mechanisms to avoid lianas and trees with mechanism and morphologies contributed less to nestedness (Table 1). However, in the Woodland Savanna, the best model included only abundance ($R^2 = 0.626$, F = 195.8, p < 0.001; Table 1): abundant trees contributed more to nestedness than rarer species (Table 1).

For lianas, we found the opposite pattern: in the Rainforest ($R^2 = 0.505$, F = 12.26, p < 0.001) and the Seasonal Forest (($R^2 = 0.795$, F = 166.8, p < 0.001), only the abundance was significant: abundant lianas contributed to nestedness. In the Woodland Savanna ($R^2 = 0.728$, F = 10.05, p < 0.001) traits and abundance were importante. Twiner lianas contributed to nestedness, as well trendillar lianas that were also larger and abundant, whereas larger trendillar lianas contributed less to nestedness (Table 2).

DISCUSSION

We found that both abundance and traits influence nestedness on antagonistic networks. However, the significance of traits and neutral variables depends on the site sampled: in the Rainforest and the Seasonal Forest for trees and lianas in the Woodland Savanna, traits plus abundance are influenced ni, whereas trees in the Woodland Savanna and lianas in the Rainforest and the Seasonal Forest only abundance contributed to nestedness. This different nestedness explanation for different life-forms (lianas and trees) is also found in mutualistic networks: abundance of plants does not explain nestedness on pollinator-plant networks in Tenerife, but the abundance of animals does. Those authors suggest that floral morphology and flower-visitor behavior may influence network structure (Dupont et al. 2003).

One intriguing result is the non-significant influence of tree morphology to avoid lianas in the Rainforest. At this same site, tree morphology does not play an important role determining lianas presence (this thesis, chapter 2). This is a dense forest, where light is a limiting factor. Consequently, lianas search for any well-lit tree in a shady forest. In this case the forest structure influences the liana presence and could be more important than individual tree morphologies. Therefore, the morphology variable is not significative for ni. Nevertheless, mechanisms to avoid lianas are important, probably because of the abundant palm *Euterpe edulis* Mart. This species comprises 11.10% of all trees in Ubatuba. Palms are a growth form that may decrease the probability of liana occupation, since new leaves emerge from the terminal bud, grow vertically, and then spread out and lean over (Putz 1980).

Abundance alone may predict the nestedness in mutualistic networks (Dupont et al. 2003, Krishna et al. 2008). However, networks based on the neutral model are more nested than expected by null models traditionally used. Forbidden links incorporated into the analysis decrease the nestedness, which reaches a more realistic value (Krishna et al. 2008). In our work, we show that nestedness of an antagonistic network is also explained by both neutral and trait matching processes, but abundance is present in all models. Similarly, this thesis (chapter 3) showed that abundance is also important for species degree. In this case, more abundant lianas would interact with more trees and vice-versa (this thesis, chapter 3). Santamaría and Rodríguez-Gironés (2007) pointed out that, even if a neutral model

explains the structure of interaction very well, some problems arise from this generalization. First, it is not clear if generalist species are generalists because they are abundant or they are abundant because, being generalists, they have access to more resources. Second, this affirmation excludes forbidden links, which is supported by empirical data (Santamaría and Rodrígues-Gironés 2007). The combination of traits may complement one another. For example, complementary traits (like plant and animal phenology and nectar sugar concentration) relax the trend of high nestedness in barrier models (i.e., length of corolla tube and proboscis), and barrier models relax the low connectance and the dependence of random effects of complementary traits (Santamaría and Rodrígues-Gironés 2007). In the Seasonal Forest, for example, species with the combination of morphologies and mechanisms and the combination of diameter and mechanism to avoid lianas are negatively related to ni, i.e., the combination of variables decreases nestedness. On the other hand, species with the combination of diameter, mechanisms and morphologies contribute positively to nestedness. These results indicate that, although the abundance was present in all models, analyzing each model carefully shows that different species influence ni in different ways.

The R² of the statistical models assumed values higher than 39%, indicating that abundanceand traits chosen explain ni relatively well. The unexplained variation may be due to other ecological and evolutionary processes (Bascompte and Jordano 2007), such as spatial distribution of species (Vázquez et al 2009b). The spatial distribution of lianas is highly influenced by gap formation (Malizia and Grau 2008), indicating that forest structure also plays an important role in liana-tree interaction. In this thesis (chapter 2) showed that tree features promoting or avoid lianas act jointly with forest structure, particularly light availability. Light is a limiting factor in Ubatuba, a shady forest, where light may be more important than tree features for liana climbing. In Paulo de Faria and Bauru, the forests are more open, with low canopy (this thesis, chapter 2). Probably the processes that influence ni fit worse in the Rainforest than the Seasonal Forest and the Woodland Savanna because of the importance of forest

structure on liana-tree interaction. Another variable that may influence ni is phylogenetic constraint. Phylogenetic signal, under certain scenarios, can contribute to nestedness of mutualistic networks. It is closely related to trait complementarity, since related species tend to have similar structures (Rezende et al. 2007b). Future study could test the influence of phylogenetic signal on the network structure in antagonistic networks.

We developed a new metric: the species contribution for nestedness, ni. Using this metric, we show that the processes that influence nestedness on mutualistic networks are similar to antagonistics networks. This similarity is about abundance and trait matching processes in mutualistic networks. We further propose that nestedness on liana-tree networks is not only dependent of species features, but also of the forest structure.

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Table 1. Multiple regression results for all three areas sampled for trees. We show the results for the best model given by the backward deletion of variables. *p < 0.05. S. E. is the standard error.

| | Rainforest | | | Seasonal Forest | | | Woodland Savanna | | |
|-----------------------------------|------------|--------|---------|-----------------|--------|---------|------------------|--------|---------|
| | Estimate | S. E. | t value | Estimate | S. E. | t value | Estimate | S. E. | t value |
| Intercept | 13.886 | 9.924 | 1.399 | 63.064 | 12.276 | 5.137* | 3.384 | 0.0428 | 78.95* |
| Abundance | -8.804 | 10.496 | -0.839 | -8.488 | 3.911 | -2.170* | 0.174 | 0.012 | 13.99* |
| Diameter | 0.950 | 2.651 | 0.358 | -5.385 | 5.084 | -1.059 | - | - | - |
| Mechanism | -5.538 | 9.076 | -0.610 | 87.934 | 27.423 | 3.207* | - | - | - |
| Morphology | - | - | - | 4.647 | 13.382 | 0.347 | - | - | - |
| Abundance x Diameter | 5.974 | 3.698 | 1.616 | 6.681 | 1.695 | 3.942* | - | - | - |
| Abundance x Mechanism | 28.032 | 13.683 | 2.049* | -5.479 | 2.876 | -1.905 | - | - | - |
| Diameter x Mechanism | - | - | - | -27.209 | 8.096 | -3.361* | - | - | - |
| Diameter x Morphology | | | | -3.273 | 5.506 | -0.594 | - | - | - |
| Mechanism x Morphology | - | - | - | -72.610 | 27.722 | -2.619* | - | - | - |
| Abundance x Diameter x Mechanism | -13.338 | 5.651 | -2.360* | - | - | - | - | - | - |
| Diameter x Morphology x Mechanism | - | - | - | 25.412 | 9.395 | 2.705* | - | - | - |

Table 2. Multiple regression results for all three areas sampled for lianas. We show the results for the best model given by the backward deletion of variables. * p < 0.05; S. E. is the standard error.

| | Ŭ | Ubatuba | | | Paulo de Faria | | | Bauru | | |
|------------------------------------|----------|---------|---------|----------|----------------|---------|----------|--------|---------|--|
| | Estimate | S. E. | t value | Estimate | S. E. | t value | Estimate | S. E. | t value | |
| Intercept | 7.716 | 2.923 | 2.640* | 21.536 | 2.530 | 8.511* | 53.119 | 10.286 | 5.164* | |
| Abundance | 7.397 | 0.990 | 7.470* | 11.431 | 0.885 | 12.915* | 2.291 | 1.993 | 1.150 | |
| Diameter | -0.426 | 3.350 | -0.127 | - | - | - | 23.952 | 13.996 | 1.711 | |
| Climbing mode: tendril | - | - | - | - | - | - | -5.396 | 10.925 | -0.494 | |
| Climbing mode: twiner | - | - | - | - | - | - | 13.820 | 5.848 | 2.363* | |
| Abundance x Diameter | - | - | - | - | - | - | -4.296 | 2.961 | -1.451 | |
| Abundance x Climbing mode: tendril | - | - | - | - | - | - | 4.464 | 2.264 | 1.972 | |
| Diameter x Climbing mode: tendril | -0.705 | 4.283 | -0.165 | - | - | - | -39.617 | 14.465 | -2.739* | |
| Abundance x Diameter x Climbing | - | - | - | - | - | - | 9.334 | 3.271 | 2.854* | |
| Mode:tendril | | | | | | | | | | |

Capítulo 5 - A theoretical approach to the management of lianas

Title: A theoretical approach to the management of lianas⁵

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⁵ Artigo segue as normas de *Forest Ecology and Management*.

Lianas decrease tree fruit production, inhibit tree growth, and increase tree mortality. Lianas also stall gaps and slow forest recovery after a perturbation. Using mathematical simulations, we have investigated the best way to manage lianas in a forest dominated by this growth habit. We built a network in which lianas interact with trees and simulated three patterns of liana cutting: from the most linked to the least linked species, from the least linked to the most linked species, and at random. Cutting randomly or from the least to the most linked lianas were the worst method. The best approach was cut from the most- to the least-linked lianas because cutting 50% of the most linked species released nearly 50% of all tree species. To release 50% of the individuals of all trees, the most abundant liana species should be removed. This method may change the forest dynamics, most likely by the promotion of slow growing trees and the acceleration of forest recovery. However, lianas may fall after cutting, killing seedlings and saplings. Future research should evaluate the costs of the method proposed.

Keywords: climber, gap, management, network, perturbation, vine.

1. Introduction

Lianas (woody climbers) are a very abundant growth habit in tropical forests, particularly in seasonally dry tropical forests (Schnitzer, 2005; DeWalt et al. 2010). Lianas reduce tree fruit production (Kainer et al., 2006; Fonseca et al., 2009), inhibit tree growth rate (Campanello et al., 2007a), and increase tree mortality (Grogan and Landis, 2009). Most studies focus on the impact lianas exert on particular tree species, generally those with some economic importance. For example, two studies show that liana load decreases Brazilian nut tree production (Kainer et al., 2006) and inhibits timber tree growth (Grogan and Landis, 2009).

The importance of lianas is also related to forest disturbance: lianas may be more abundant in fragment edges, probably as a consequence of lateral light penetration and support availability (Laurance et al., 2001; Arroyo-Rodríguez and Toledo-Aceves, 2009). The availability of light and support also explains why lianas are more abundant (Madeira et al., 2009) and have more biomass (Letcher and Chazdon, 2009) in intermediate stages of succession. Therefore, gaps increase liana density and richness (Schnitzer and Carson, 2001) and liana stem proliferation (Schnitzer et al., 2004). Liana proliferation may change the forest dynamics, slowing down forest regeneration after a perturbation, since lianas would promote pioneer trees and stall gaps in a low-canopy stage (Schnitzer et al., 2000).

When the forest regeneration of natural areas is compromised by lianas, the management of this life-growth seems necessary. Most studies have focused on economically important trees, mainly on timber trees (Grogan and Landis, 2009). However, the cutting of lianas with the whole forest in mind, not just one tree species, could accelerate forest regeneration. For example, cutting lianas and bamboos increases the solar radiation that reaches the understory (Campanello et al., 2007b), which in turn increases mean tree growth rate (Gerwing, 2001) and contributes to an

increased abundance of herbaceous plants, sapling survival, and growth rates in general (Campanello et al., 2007a).

Sfair et al. (2010) described the interaction between trees and lianas in a given community is nested. This structure has a core of species that tend to interact with each other (generalists) and a group of species with few interactions that tend to interact with the core (specialists). Therefore, there is a gradient in the number of interactions among different species in a forest community (Sfair et al., 2010). Memmott et al. (2004) showed that a nested structure is robust for species loss: only the extinction of the most linked species increases the probability of a second extinction. Nested community study (Fortuna and Bascompte, 2006). Similarly, simulations of liana loss using network theory may suggest an approach to the best management of a liana-infested forest. Based on the study by Memmott et al. (2004), we expect that cutting the most-linked liana species would release more tree species and, consequently, be a more efficient strategy to liana management. We aimed to identify the best best management strategy of cut lianas by analyzing species loss simulations in liana-tree networks.

2. Material and Methods

We sampled lianas and trees rooted within the plots of three different sites, all in the state of São Paulo, in southeastern Brazil. The first site (23°21'54"-59"S and 45°05'02"-04"W; 348-394 m above sea level) is a tropical rainforest in the municipality of Ubatuba (hereafter Rainforest), in the Parque Estadual da Serra do Mar, a conservation unit of 47500 ha. This site has no evidence of large perturbations, and we did not detect any gaps in the sampled area. The second site (19°55'-58'S and 49°31'-32'W, 400-495 m above sea level) is a 435.73 ha fragment of seasonally dry tropical forest in the municipality of Paulo de Faria (hereafter Seasonal Forest). In the late 1970s,

this fragment suffered a 30% reduction in area and, in the mid-1980s, 50 ha were flooded after the construction of a dam. Since 1981, there has been no record of anthropogenic perturbation at this site, such as logging or fire. The third site (22°19'41"-21'06"S and 48°59'49"-49°01'12"W, 519-603 m above sea level) is a 321.71-ha fragment of savanna woodland in the municipality of Bauru (hereafter Savanna Woodland). This area has evidence of cassava and others types of plantation around 1990. For further information about the areas sampled, see Sfair et al. (2010).

For each area, we constructed a bipartite network, in which dots represent lianas and trees, and lines connecting these dots represent the interactions between dots (for details, see Sfair et al., 2010). These networks were used to simulate liana management by cutting all individuals of a particular liana species. Following Memmott et al. (2004), we used three different algorithms to remove lianas in each network: (1) we systematically removed lianas from few interactions to more interactions; (2) we systematically removed lianas from the most-linked to the least-linked species; and (3) we randomly removed lianas without replacement. The third process was repeated one thousand times. Then, we estimated the percentage of tree species without lianas according to these liana cutting patterns.

These simulations were performed using quantitative matrices of interaction instead of binary matrices. The quantitative matrices have all observed interaction between two species, instead of only the presence or absence of interaction. The results of the mathematical simulations do not differ from those obtained withbinary networks, but are closer to reality. We added all interaction frequencies for each liana and tree species. To know whether species abundance could be replaced by the sum of the interaction frequencies in the following analysis, abundance and interaction frequency were related through regression analysis. We also log-transformed tree species data for all three areas to produce normality and variance homogeneity. As abundance and number of interactions are positively related, a very abundant species with few interactions may increase the error in the regression analysis. For this reason, in the Rainforest we excluded the outlier palm *Euterpe edulis* Mart. (Arecareceae), a very abundant palm tree (180 individuals) with only two interactions with liana species.

The most effective method of liana cutting was used as a basis to estimate the percentage of trees that would be free from lianas. We were interested in how many liana species should be removed to release as many trees as possible from liana interaction. We utilized the species frequency of interaction as a surrogate for species abundance, since both variables are strongly correlated.

3. **Results**

The Rainforest was the richest site, with 219 species of trees and 66 species of lianas. The Savanna Woodland had 140 species of trees and 39 species of lianas; and the Seasonal Forest, 86 species of trees and 45 of lianas. The Savanna Woodland had the largest density of trees (11,173 trees ha⁻¹) and lianas (2793 lianas ha⁻¹). The Rainforest had 1876 trees/ha and 526 lianas/ha. The Seasonal Forest had 1416 trees ha⁻¹ and 1427 lianas ha⁻¹. The Savanna Woodland and the Seasonal Forest are considered liana forests due to the great abundance of lianas in relation to their richness. The Rainforest had a greater richness of lianas and trees and a lower abundance of lianas, and we did not consider this site as a liana forest.

The three different algorithms produced different patterns of trees released from lianas. The first strategy, removal from the least to the most interacting liana species was the least effective management procedure (Fig 1). In both the Rainforest and the Seasonal Forest, we had to remove approximately 80% of the liana species to release only about 20% of trees species (Fig. 1a, 1b). In the Woodland Savanna, the slope was even more abrupt: we had to remove almost all the liana species to obtain an effective decline in trees loaded with lianas (Fig. 1c). The third strategy,

random removal of lianas, was more effective than the first strategy, producing a steady decline in trees occupied by lianas. Likely as a result of the fewer number of interactions in the Rainforest, the decline was faster in this site than in the Seasonal Forest and the Woodland Savanna (Fig. 1). However, the most effective procedure of liana removal was thes second strategy, beginning the cutting from the most-linked and proceeding to the least-linked liana species. This method ensured that the cutting of nearly half of all liana species would free nearly half of the tree species from lianas (Fig. 1).

The frequency of interactions was a good surrogate for liana species abundance in the Rainforest ($R^2 = 0.988$; F = 2622.707; p < 0.001) and trees ($R^2 = 0.757$; F = 299.842; p < 0.001); similarly in the Seasonal Forest, the frequency of interactions was predictive for trees ($R^2 = 0.810$; F = 162.314; p < 0.001) and lianas ($R^2 = 0.999$; F = 26976.356; p < 0.001) and in the Woodland Savanna for trees ($R^2 = 0.953$; F = 1388.294; p < 0.001) and lianas ($R^2 = 0.958$; F = 846.7; p < 0.001). These results mean that the most-linked liana and tree species were also the most abundant. Therefore, if the frequency of interactions is a good surrogate for abundance, we can extend the validity of our results to include liana abundance. There was an abrupt decline in the number of trees released when we cut the lianas species (Fig. 2). Few liana species were involved in most attachments to trees, and cutting all individuals of these liana species released most of the trees. In the Rainforest, cutting the seven most abundant species releases half of the trees (Fig. 2a). In the Savanna Woodland (Fig. 2c) and the Seasonal Forest (Fig. 2b), cutting the fourth and fifth dominant liana species, respectively, releases 50% of the trees from lianas.

4. Discussion

Cutting the most-linked liana species may be a good strategy for managing lianas. According to our models, the proportion of liana species removed is almost proportional to the tree species

released from lianas. Considering this, we must focus on the most linked liana species to release half of the trees. As the interaction frequency is significantly related to species abundance, removing the most linked species mean that we should remove the most abundant liana species. To reduce the overall costs of liana cutting, Vidal et al. (1997) suggested cutting lianas based on features such as aggressiveness, which refers to those liana species that interconnect many tree crowns and have the ability to resprout vigorously from fallen stems. However, this information is absent for many liana species (Vidal et al., 1997). We suppose that probably the most abundant liana species are the most aggressive ones and the management approach we propose encompasses the suggestion by Vidal et al. (1997). Further, the costs of liana cutting can be high (Pérez-Salicrup et al. 2001) and focusing on the most abundant species, which should include training people to recognize these species, would bring expenses down. Cutting few liana species would facilitate training and is simpler than the method suggested by Vidal et al. (1997).

The method we propose would not drive liana species to extinction, because some individuals are often missed, generally the most slender ones (Pérez-Salicrup et al., 2001). In addition, many lianas reproduce clonally, which may be an adaptation to high disturbance regimes, such as gaps (Gerwing and Uhl, 2002). After a disturbance, lianas can fall from their hosts and grow new roots (Nabe-Nielsen and Hall, 2002). In addition, canopy openings favor liana seed germination (Gerwing, 2006). Although the response to logging varies according to the liana species in ways related to reproduction (Gerwing, 2006), lianas may reproduce vigorously after cutting and it may be necessary to manage them continuously.

In an undisturbed forest, such as the Rainforest, management is unnecessary. This site is an extensive forest with a high richness of lianas and trees. Consequently, the simulation showed that we should cut more liana species to release the same number of trees when compared to the Seasonal Forest and the Woodland Savanna. The least- to most-connected liana species method is

more effective in this site when compared to both the Seasonal Forest and the Woodland Savanna, even though this strategy is a poor solution. These results advocate for the relative inefficient of liana cutting methods in Ubatuba. Further, Ubatuba is a rich forest, with 66 liana species and no perturbation recorded. Therefore, we feel that it is not necessary to manage lianas in a wellstructured and rich forest such as Ubatuba.

Trees without lianas produce more fruits (Kainer et al., 2006), grow faster (Campanello et al., 2007a), and are less prone to dying (Grogan and Landis, 2009). Therefore, trees released from lianas would enjoy competitive advantages over trees with lianas, a situation that could change forest dynamics. Slow-growing trees generally have more lianas than pioneers (Putz, 1980, 1984; Campanello et al., 2007a). Schnitzer and Carson (2010) showed that slow-growing tree species grew faster in gaps without lianas than in gaps with lianas. Thus, liana management would favor the reproduction, growth, and survival of slow-growing trees. Moreover, liana abundance is related to forest succession: lianas are more abundant in intermediate stages of succession where both support and light are available (Madeira et al., 2009). Although it has more light, a disturbed area, such as gaps, has fewer support trees and is not a favorable site for lianas. A well-structured forest, with tall trees and a closed canopy, also has few lianas due to its shady environment (Madeira et al., 2009). In liana-dominated patches, the successional transition to a higher-stature forest occurs very slowly (Gerwing, 2001). Therefore, liana cutting would favor slow-growing trees, which would eventually form a well-structured forest. However, cutting lianas may lead to two immediate consequences. There will be a negative effect, since lianas may fall and kill tree seedlings and saplings, thus creating fuel for fires (Pérez-Salicrup, 2001; Gerwing, 2001). This effect would change forest regeneration by decreasing tree species recruiting. Additionally, there will be a positive effect, with soil enrichment from liana decomposition. We estimate that a balance between negative and positive effects on forest regeneration after liana cutting might be

considered. Future research can clarify these effects and the successional status after liana cutting according to the method we proposed.

5. Conclusion

We provided a theoretical model for liana management. Empirical works have previously proposed cutting every liana in a plot (Gerwing, 2001), a procedure that decreases liana abundance when compared to control plots (Gerwing and Vidal, 2002). However, lianas play important roles in the vegetation, such as providing arboreal pathways and food for vertebrates (Emmons and Gentry, 1983) and maintaining the diversity of phytophagous beetles (Ødegaard, 2000). In addition, some lianas have a flowering time complementary to that of trees, thus providing food resources to pollinators throughout the year (Morellato and Leitão-Filho, 1996). Arboreal rodents use lianas as conduits for moving within the canopy and from the canopy to the ground, and this increases the removal rate of seeds, i.e., liana density increases seed dispersal by arboreal rodents (Kilgore et al., 2010). Therefore, cutting all lianas in a plot would result in serious consequences to the animal community. The method we propose would reduce this impact, because we focus on the most abundant species and, consequently, we do not suggest the removal of all the lianas. The consequences of this procedure for forest regeneration should be evaluated. We anticipate that the regeneration process would cause progression to a well-structured forest and maintain liana richness. However, management costs must be calculated. We believe that a focus on the most abundant liana species would cost less than cutting all lianas in a plot. Future research should determine the costs of the procedure we propose, including the costs of training people to cut lianas.

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Figure Captions

Fig. 1. Cutting patterns for the three sample areas: (A) Rainforest, (B) Seasonal Forest, and (C) Woodland Savanna. The square represents cutting from the least-linked to the most-linked lianas; the filled dot, random cutting; and the clear dot, cutting from the most-linked to the least-linked lianas. The error bars of random cutting are very small and are not shown.

Fig. 2. Proportion of trees released after cutting lianas for (A) Rainforest, (B) Seasonal Forest, and (C) Woodland Savanna.. Cutting the most abundant species released most of the trees. Each filled dot represents one liana species.

Fig. 1



Proportion of liana species removed


Conclusões gerais

1. Estudos anteriores mostraram que lianas competem com árvores por nutrientes e luz. Entretanto, tais estudos focaram apenas lianas e árvores interagindo par a par. Essa tese mostra que há uma estrutura na interação entre lianas e árvores quando consideramos o conjunto de espécies em uma comunidade: Assim como as redes de interações mutualísticas, as redes antagonísticas de interação entre lianas e árvores também possui o **padrão** aninhado, ou seja, espécies que interagem com muitas outras espécies e espécies que interagem com poucas espécies e preferencialmente com espécies com muitas interações.

2. Baseando-se em estudos com redes mutualísticas, foi possível estudar os processos que levam ao aninhamento e às possíveis implicações de uma rede aninhada. De maneira similar, ambos os tipos de redes provêm dos mesmos **processos** neutros e relacionados aos caracteres. Nessa tese consideramos caracteres como presença de espinhos, casca decídua, crescimento rápido e arquitetura de palmeiras.

3. A estrutura aninhada é importante, pois fornece pistas de como fazer o manejo de lianas: deve-se privilegiar o corte de espécies de lianas com muitas interações. Como há uma forte relação entre número de interações e abundância de espécies, recomendamos que sejam focadas as espécies mais abundantes de lianas. Cortando as espécies de lianas com mais interações, um maior número de árvores ficaria livre de lianas com um menor esforço e um menor custo de pessoal para fazer o manejo. Portanto, a estrutura aninhada de interação entre árvores e lianas **implicaria** em sugestões de baixo custo para o manejo de lianas em florestas tomadas por esse hábito.

4. Além disso, essa tese abordou outros aspectos de ecologia de lianas. Em uma revisão sobre os caracteres de árvores que inibem a ocupação por lianas, mostramos que, as variáveis como abundância, tamanho, presença de espinhos, arquitetura e casca esfoliante são de extrema importância. A associação entre variávies indica que elas agem conjuntamente com a estrutura da floresta, particularmente com a disponibilidade de luz, na ocupação por lianas. Há também um

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gradiente que vai de espécies muito bem armadas a espécies totalmente desprotegidas contra a ocupação pode lianas;

Diante do exposto, futuros trabalhos poderiam explorar de forma mais aprofundada algumas questões levantadas nessa tese:

5. Haveria maior taxa de especiação em florestas sombreadas? Ou florestas sombreadas constituiriam áreas que atrairiam muitas espécies de um conjunto regional de espécies de lianas? Uma maneira de investigar essas questões seria cruzar dados de origem filogenética com a distribuição geográfica dos principais gêneros de trepadeiras;

6. Os padrões de diversidade de lianas seguem os mesmos padrões de árvores? Essa tese mostra que há um padrão nesse sentido (anexo 1). Entretanto novas análises levando em consideração dados multivariados de variáveis ambientais devem ser realizadas. Essa tarefa será possível com novos levantamentos realizados no Brasil;

7. Aplicar a sugestão de manejo de lianas em comunidades reais. Será possível prever se o manejo de lianas promove espécies de crescimento lento, bem como se a riqueza de lianas é mantida na comunidade. Também será possível estudar se os benefícios à comunidade animal são mantidos.

8. Como a distribuição espacial afeta a estrutura de interação entre árvores e lianas? Lianas que ocupam um espaço amplo devem interagir com mais espécies do que lianas que possuem uma distribuição espacial mais restrita. Haveria uma correspondência entre a estrutura da rede e a ocupação de microhábitats por lianas e árvores?

9. Espécies de lianas filogeneticamente similares interagem com espécies de árvores também filogeneticamente similares? Estudos com redes mutualísticas mostram que o aninhamento é em parte explicado por origem comum entre espécies.

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Anexo 1 - Is climber diversity related to tree diversity? – The role of heterogeneity on climber diversity Is climber diversity related to tree diversity? – The role of heterogeneity on climber diversity⁶

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⁶ Artigo segue as normas de *Global Journal of Biodiversity Science and Management* (submetido).

The richness and abundance of climbers vary among communities and may depend on soil Abstract properties, climate, perturbation history and variables of community structure. Our aim was to test the hypothesis that, in spite of the influence of these variables, climber diversity may also be related to tree diversity. We gathered data from a rainforest site, three sites of seasonal semideciduous forest, and two sites of savanna with different physiognomies in SE Brazil. Diversity descriptors were represented by species abundance distribution (SAD), richness, and Shannon index (H'). We compared trees for richness using rarefaction analysis, for SAD using Kolmogorov-Smirnov test, and for H' using t-test with Bonferroni sequential correction. The same analyses were performed for climbers. In addition, we compared floristic similarity of climbers and trees among the sites using modified Sørensen's index for abundance. The relationship among the diversity descriptors between climbers and trees was tested with linear regression. The diversity descriptors varied similarly among the sites, indicating that trees and climbers respond in similar way to the variation of other factors. We suppose that the major variable influencing the similar variation of diversity of trees and climbers is a fragmentation process. For example, continuous forests would have more richness than fragmented ones. Tree H' showed a significant positive relationship with climber richness; the other descriptors did not show any significant relationship. Shannon H' is a heterogeneity index that considers both richness and SAD, attaining maximum values when the species number is high and all the species have similar abundances. We propose that a) the greater the tree H', the greater the heterogeneity of the tree community; b) this heterogeneity would be expressed by many different combinations of traits favorable or unfavorable to climbers; c) each combination would appear with some abundance; and d) this heterogeneity would enhance the number of potential niches for climbers, thus promoting climber richness.

Keywords Abundance Heterogeneity Liana Shannon Index Richness

Introduction

The distribution patterns of organisms both at community and population levels have been addressed by many authors (Brown, 1984). However, these distributions patterns are hard to explain because of many variables influencing them (Schnitzer, 2005; Ricklefs, 2006). One way to overcome the great complexity of this issue is to focus on a particular group, such as trees, herbs, or climbers (Schnitzer, 2005). Climbers are more abundant (number of individuals, Schnitzer, 2005) and richer (number of species, van der Heidjen and Phillips, 2009) in tropical than in temperate systems. In tropical systems, climbers are favored by a stronger dry season, because they can access deep soil water and do not suffer xylem embolism (Meinzer *et al.*, 1999; Schnitzer, 2005), keeping their leaves during the unfavorable season (Putz and Windsor, 1987). In consequence, climbers invest in growth, while trees shed their leaves and decrease growth rate during a dry season (Meinzer *et al.*, 1999; Schnitzer, 2005).

Climber abundance and richness may also be related to perturbation (Senbeta *et al.*, 2005; DeWalt *et al.*, 2006; Muthuramkumar *et al.*, 2006), which can be caused by humans, such as deforestation (Laurance *et al.*, 2001), or by natural events, such as hurricanes (Allen *et al.*, 1997) and gap formation (Schnitzer *et al.*, 2000). Gaps, for example, have high temperatures and low humidity, creating conditions similar to seasonally dry tropical forests, which are favorable to climber growth (Schnitzer, 2005). In gaps, climbers decrease growth of non-pioneer and promote growth of pioneer trees (Schnitzer *et al.*, 2000; Campanello *et al.*, 2007). Schnitzer *et al.* (2000) proposed that climber diversity in tropical forests is kept high by gap formation, because in shaded sites germination rates of climber species is low (Sanches and Válio, 2002). However, climber abundance may be higher in intermediate successional phases, because the canopy is low and light is plentiful, promoting climber growth (Madeira *et al.* 2009). For this reason, liana density may be more related to forest structure than soil and climate factors (Van der Heidjen and Phillips, 2008). On the other hand, Nesheim and Økland (2007) stated that nutrient and light availability would be important during the initial stages of climber development, but tree traits would become more important when climbers start to ascend.

Research addressing abundance and richness of climbers generally emphasize the role of factors such as climate, soil, and perturbation related to forest structure. In this work, we propose a relationship between diversity of climbers and trees. Few works focus on tree diversity as a variable that can influence climber diversity: Watanabe and Suzuki (2008) found a positive relationship between rattans and trees diversity, and Caballé and Martin (2001) observed that low abundance and high richness of trees were related with low richness and abundance of climbers

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through time. Therefore, tree diversity can influence climber diversity, since, for example, greater abundance of trees can provide more support availability and, therefore, increase climber abundance.

Our aim was to test the hypothesis that diversity of climbers is related to diversity of trees. To address this issue, we considered species abundance distribution (SAD), richness, and Shannon's H' index of heterogeneity as descriptors of diversity, and investigated whether the descriptors of climbers and trees are different among six sites in southeastern Brazil and related to each other in each site.

Materials and Methods

Data collection

We sampled six sites in southeastern Brazil (Fig. 1), consisting of rainforest, seasonal forest and savanna, which are the most important tropical vegetation formations covering the greatest area in the Neotropics. In each of these sites the sample design was adapted to the vegetation peculiarities. Ubatuba (23°21'59''S and 45°05'03''W) is a tropical wet forest (Köppen's (1948) Af climate). This site is a relatively continuous forest of 47500 ha. At an altitude of 348 - 395 m, the annual mean temperature is 20.25 °C and the annual mean precipitation is 2624 mm. In 1 ha, Rochelle (2008) sampled all trees with PBH (perimeter at breast height) > 15 cm and van Melis (2008), all lianas (woody climbers) with DBH (diameter at breast height) > 1 cm.

Paulo de Faria (19°57'S e 49°31'W, 400 - 495 m altitude) is a seasonally dry tropical forest, with Aw climate (Köppen, 1948). The annual mean temperature is 27 °C and the annual mean precipitation, 1405 mm. In the fragment with total area of 435.73 ha, all trees with DBH \geq 3cm and lianas with DBH \geq 1cm were sampled (Rezende, 2005). Both samples corresponded to a grid of 100 contiguous plots of 10 x 10 m each, thus making up 1 ha.

Itirapina (22°13`S e 47°51`W, 762 m of altitude) is a dense savanna, with a fragment area approximately 60 ha. The climate is Cwa (Köppen, 1948), with annual mean temperature of 21.4 °C and annual mean precipitation of 1394.3 mm. Polo (*in prep.*) considered all trees and lianas with DSH (diameter at soil height) > 3 cm and > 1cm, respectively, in two separate grids of 100 contiguous plots of 5 x 5 m, each one making up 0.5 ha.

São Carlos (21°57'S e 47°50'W, 850 m of altitude) is a seasonal dry tropical forest fragment of 112 ha (Hora and Soares, 2002, Silva and Soares, 2002). The climate is Cwa-Awa (Köppen, 1948), with mean annual temperature of 25.4 °C and mean annual precipitation of 1440 mm. Silva and Soares (2002) sampled all trees with DBH \geq 5 cm in

1 ha of non-contiguous plots with 0.02 ha each and Hora and Soares (2002) sampled all lianas with $DBH \ge 2.5$ cm in 0.75 ha of non-contiguous plots of 0.01 ha.

Bauru (22°20'30''S e 49°00'30''W, 510 to 540 m of altitude) is a woodland savanna covering a 321.71 ha fragment. The climate is Cwag (Köppen, 1948), with mean annual temperature of 22.4 ° C and mean annual precipitation of 1306 mm (Weiser 2007). Weiser (2007) sampled all trees with DBH \ge 0.1 cm and all lianas with DSH \ge 0.1 cm in 1 ha (Weiser 2007).

Lavras (21°19'25.2" S e 44°59'53.1" W, 920 to 1180 m of altitude) is a seasonal dry tropical forest, characterized by Cwa climate (Köppen, 1948) with mean annual temperature of 19.4 and mean annual precipitation of 1529.5 mm (Castro, 2004; Appolinário, 2008). The sampling included three forest fragments with total area of 48.9 ha. All trees with DSH \geq 5cm were sampled in 54 plots of 200 m² (total of 1.08 ha) by Castro (2004), while Appolinário (2008) sampled all climbers with DBH \geq 1 cm in 52 of the 54 plots.

Data analysis

We considered richness, species abundance distribution (SAD) and Shannon's H' heterogeneity index as diversity descriptors. By using these three descriptors we were able to take into account several aspects included in the concept of diversity: not only the number of individuals (abundance) and the number of species (richness), but also the relationship between these two variables (H'). According to McGill *et al.* (2007), in spite of information loss, these descriptors complement each other: richness and H' are univariate and easily understandable variables, and SAD, although more complicated, provides more information, such as the discrimination of rare, intermediate, and abundant species.

We tested for a difference of richness of climbers and trees among the sites with rarefaction analysis using the accumulated number of individuals as sampling effort (Gotelli and Colwell, 2001; Magurran, 2004). The rarefaction curve was constructed by random sampling of N individuals repeated 1000 times (Hurlbert 1971; Krebs 1999) with confidence interval of 95% (Hurlbert, 1971; Krebs, 1999; Gotelli and Colwell, 2001) using Analytic Rarefaction 1.3 software (Holland, 2003). We plotted the rarefaction curve up to 606 individuals for trees, since the smallest sample had 604 individuals in São Carlos (Fig. 2). The rarefaction curve for climbers was plotted up to 550 individuals, since the smallest sample had 528 individuals in São Carlos (Fig. 3).

SAD is the distribution of the observed number of individuals of each species in a community (McGill *et al.*, 2007). According to Tokeshi (1999), SAD is a detailed representation of the community, whereas species richness is

more basic information. We compared the SADs among all sites with Kolmogorov-Smirnov test, following Magurran (2004).

We considered the logarithm of base *e* for Shannon heterogeneity index (Magurran 2004) and compared the values with an adapted t-test (Hutcheson, 1970; Zar, 1999), applying Bonferroni sequential correction (Rice, 1989; Sokal and Rohlf, 2003). This correction decreases the Type I error among all comparisons (Sokal and Rohlf, 2003; Gotelli and Ellison, 2004).

We compared tree and climbers species similarity among all sites with Sørensen index modified by Chao *et al.* (2005). The modified Sørensen index takes into account the species abundance in each sample and is based on the probability of two random individuals, each from one sample, belonging to the same species (Chao *et al.*, 2005). This index is also less sensitive to sample size and considers the species estimate for each site (Chao *et al.*, 2005). For this reason, for each comparison we made 1000 replications. We used Spade software for calculations of modified Sørensen index (Chao and Shen, 2003), which reduces the bias when a substantial number of species is missing (Chao *et al.*, 2006).

We tested for the relationship between climbers and trees with simple linear regression analysis. The explanatory variables were the descriptors of tree diversity and the response-variables were the descriptors of climber diversity. We also used Bonferroni sequential correction to decrease Type I error of multiple tests with the same set of values (Sokal and Rohlf, 2003; Gotelli and Ellison, 2004).

Results

Trees

Tree richness was not significantly different among Bauru, São Carlos and Paulo de Faria, but was significantly smaller in Itirapina and greater in Ubatuba and Lavras (Fig. 2). SAD for trees in Ubatuba differed from all other samples (Table 1). The values of H' differed among all sites, except between Paulo de Faria and Bauru (Table 1). Ubatuba had the greatest and Itirapina had the smallest H' (Table 2). Generally, tree species were different among all sites, demonstrating an overall floristic similarity lower than 10%. However, São Carlos and Paulo de Faria had 61.17% species in common, Bauru and Itirapina had 63.32%, Lavras and Itirapina had 28 %, and Lavras and Bauru had 48.80% species in common (Table 3). These results were expected, since São Carlos and Paulo de Faria are

seasonally dry tropical forests, whereas Bauru and Itirapina are savannas. The standard error was relatively small, indicating high precision of the data (Chao *et al.* 2006).

Climbers

The rarefaction results for climbers (Fig. 3) were similar to those for trees (Fig. 2): richness did not differ among Bauru, São Carlos, Paulo de Faria and Lavras, and Itirapina had fewer and Ubatuba more species than the other sites (Fig. 3). As for trees, SAD for climbers was different in Ubatuba compared to all other sites (Table 4). We also found differences between Paulo de Faria and Itirapina and between Itirapina and São Carlos (Table 4). The Shannon index was different among all sites, except between Paulo de Faria and Bauru, between Paulo de Faria and Lavras and between Bauru and Lavras (Table 5). The floristic similarity of climbers among all sites was similar to that of trees: the greatest values were between the savannas Itirapina and Bauru (65.41%) and between the seasonally dry forests Paulo de Faria and São Carlos (40.66%; Table 3). Generally, the Sørensen index was smaller than 20% among all other comparisons, implying a low similarity among sites (Table 3). The standard error was also small (less than 0.04), indicating high precision of the data (Chao *et al.* 2006).

Relationship among diversity descriptors

We found a significant positive correlation only between tree H' and climber richness (Table 6). However there was no significant correlation between tree abundance and climber abundance, tree richness and climber richness, climber richness and tree abundance, climber abundance and tree richness, climber abundance and tree H', climber H' and tree abundance, climber H' and tree richness, or between tree H' and climber H' (Table 6).,.

Discussion

The variation of richness, abundance, and Shannon index among the sites were similar for trees and climbers, indicating that the same factors affect the diversity descriptors of climbers and trees similarly. One of these factors might be anthropogenic fragmentation, since forest fragments generally have lower plant richness than continuous areas (Laurance, 2008). With the exception of Ubatuba, all the other sites were fragments with different areas and shapes. Being a relatively continuous forest, Ubatuba had the greatest species richness. Also, Ubatuba had the lowest values of floristic similarity with other sites. Most tree species in the Brazilian Atlantic rainforest, such as Ubatuba,

have restricted distribution (Scudeller *et al.*, 2001, Caiafa and Martins, 2010), implying high floristic dissimilarity to other forest types. The inclusion of environmental heterogeneity in the sample can also yield high species richness, as was the case at Lavras, once different fragments and ecological corridors (Castro, 2004) were sampled. The species richness in a fragment is also dependent on matrix characteristics, edge influence, and perturbation history (Laurance, 2008), all factors that could explain the much lower richness of climbers and trees in Itirapina. This cerrado small fragment is surrounded by a 30-m wide firebreak, separating it from plantations of *Pinus elliottii* and *Eucalyptus saligna* (personal observation).

Our hypothesis that abundance, richness, and H' of climbers would be related to tree diversity descriptors was only partially confirmed, because the only significant relationship among diversity descriptors we found was that between tree H' and climber richness. We propose that H' can be considered an indicator of internal heterogeneity of the community and that the more heterogeneous the community is, the greater the number of climber species. Environmental heterogeneity may be created by both abiotic variables -- such as topography, temperature, precipitation, and substrate – and biotic variables, such as evapotranspiration (Wilson, 2000). Therefore, it is possible to regard the forest as a mosaic of resource availability (Grace, 1991) shared among species, thus contributing to their coexistence (Ricklefs, 1977). More heterogeneous environments can support more diversity than less heterogeneous ones (Rosenzweig, 1995; Lundholm and Larson, 2003; Pausas et al., 2003; Leigh et al., 2004; Dufour et al., 2006). For example, in South Africa Thuiller et al. (2006) showed that topographic heterogeneity could improve plant richness both by increasing the number of niches in space and by keeping the number of niches relatively stable in time. Environments with microtopographic heterogeneity also have higher species abundance, higher biomass, and more rare species (Vivian-Smith, 1997). Spatial heterogeneity can influence diversity both by increasing the number of habitats types and by affecting ecological processes – such as dispersal and competition (Dufour et al., 2006) – through the spatial configuration of habitats. The environmental heterogeneity was shown also to be positively related to diversity in theoretical (Palmer, 1992) as well as in practical studies with animal diversity (Tews et al., 2004).

Similarly, the increased heterogeneity of the tree community would yield an increased heterogeneity of traits of the potential supports for climbers, since tree species have characters that promote or avoid climber occupation. Among the tree characters inhibiting climbers Putz (1984) recognized palm architecture, spiny trunk, fast growing, ant mutualism, dead leaves retention, and exfoliating bark. For example, in a semideciduous forest in Argentina, Campanello *et al.* (2007) found that palms were 69.5% less infested by climbers. Besides, some palms, such as *Bactris* spp., have spiny trunk that hinder occupation by climbers, probably due to the abscission of the spines under liana

weight (Maier, 1982). Tree species with large leaves, flexible trunk (Putz, 1984), or with exfoliating bark (Talley *et al.*, 1996; Campanello *et al.*, 2007) also have fewer climbers. Putz (1984) suggested that climbers hinder shadetolerant and slow-growing trees, and promote indirectly the pioneer species. Pioneer species, such as *Cecropia* spp., do not have lianas (Putz, 1984; Campanello *et al.*, 2004), and in species of this genus, symbiotic ants remove climbers by cutting their apical meristems (Janzen, 1969). On the other hand, other tree characters, such as slow growth (Putz 1984), rough bark (Carsten *et al.*, 2002), and multiple stems (Reddy and Parthasarathy, 2006) promote climber occupation.

A complementary explanation about the relationship of H' of trees and richness of climbers is the biotic interaction hypothesis (Currie et al., 2004). This hypothesis states that speciation rate is due to biotic interaction, which increases opportunities for evolutionary diversification in some sites (Currie et al., 2004). For example, many plant species of temperate climates are pollinated and dispersed by wind, whereas most tropical species are pollinated and dispersed by animals. The evolution of tropical flowers and diaspores is related to the evolution of animal pollinators and dispersers, thus leading to an increase of richness of animals and plants in the tropics (Schemske, 2002). In an analogus way, a high Shannon index represents similar relative abundances of the species, combined with a high number of species. If trees have a high H', then the tree community present many different combinations of traits that promote or inhibit their occupation by climbers, and the different combinations of traits occur with high, similar relative abundances. Therefore, from the viewpoint of the climbers, the tree community would represent a gradient ranging from totally favorable trait combinations to totally unfavorable trait combinations. This gradient of favorableness would occur not only along space but also along time, since communities have spatial structure and also temporal dynamics. The combination of spatial and temporal variation of favorableness/unfavorableness would imply high heterogeneity, thus allowing speciation towards a larger number of climber species, according to this biotic interaction hypothesis. Additionally, Sfair et al. (2010) showed that the interaction structure between lianas (woody climbers) and host-trees is nested. In spite of negative interaction between lianas and trees, nestedness also characterizes mutualistic and facilitation networks. In these cases, nestedness may decrease competition and increase diversity (Bastolla et al., 2009, Verdú and Valiente-Banuet, 2008). We predict that nestedness also increases diversity in liana-tree networks. According to the biotic interaction hypothesis, we propose that the heterogeneity of tree traits and the great number of their different combinations influence positively not only the speciation rate of climbers, thus increasing climber richness, but also their coexistence, thus maintaining climber richness.

Conclusion

Climber abundance may vary according to climate (Schnitzer, 2005) and forest structure (van der Heijden and Phillips, 2008). For example, sites with short or absent dry season have more climber richness (van der Heijden and Phillips, 2009). In this study we found a relation between the diversity of climbers and trees, particularly the richness of climbers and the diversity index of trees. We propose that a larger heterogeneity of the tree community represents a large number of potential sites for climbers, thus increasing their richness. It is possible that sites with different dry season durations (van der Heijden and Phillips, 2009) combined with tree heterogeneity can enhance the rates of climber speciation.

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| | Ubatuba | Paulo de Faria | Itirapina | São Carlos | Bauru | Lavras |
|----------------|----------|----------------|-----------|------------|-----------|-----------|
| Ubatuba | | 4741.23 * | 6430.88 * | 3659.24* | 8425.55 * | 5690.26 * |
| Paulo de Faria | -19.71 * | | 979.18 | 795.35 | 536.12 | 1622.78 |
| Itirapina | -35.55 * | 11.41 * | | 1517.09 * | 1339.97 | 3073.66 * |
| São Carlos | 13.74 * | -3.53 * | -13.56 * | | 1512.93 | 861.08 |
| Bauru | -25.93 * | -0.095 | 19.32 * | -4.24 * | | 3070.20 |
| Lavras | -10.64* | 14.19 * | 37.92 * | 7.48 * | 24.89 * | |

Table 1 Kolmogorov-Smirnov test for SAD (in **bold**) and t-Test for Shannon H' indices for trees among the six sites(*p < 0,05).

Table 2 Abundance (individuals.ha⁻¹), richness (species.ha⁻¹) and Shannon H' diversity index (nats.individual⁻¹) with their respective variance for trees in the six sites.

| | Ubatuba | Paulo de Faria | Itirapina | São Carlos | Bauru | Lavras |
|-------------|-------------------------|-------------------------|-------------------------|-------------------------|------------------------|-------------------------|
| Richness | 207 | 87 | 82 | 77 | 140 | 157 |
| Abundance | 1876 | 1419 | 4662 | 604 | 11173 | 5179.42 |
| H' | 4.48 | 3.58 | 3.15 | 3.79 | 3.56 | 4.012 |
| Variance H' | 9.83 x 10 ⁻⁴ | 9.74 x 10 ⁻⁴ | 3.18 x 10 ⁻⁴ | 1.56 x 10 ⁻³ | 1.4 x 10 ⁻⁴ | 2.54 x 10 ⁻⁴ |

| | Ubatuba | Paulo de Faria | Itiranina | São Carlos | Bauru | Lavras |
|----------------|-----------------|---------------------|--------------------|--------------------|-----------------------|--------------------|
| | Obatuba | Taulo de Falla | mapma | Sao Carlos | Dauru | Lavias |
| Ubatuba | | 0.031 (±0.006) | $0.028(\pm 0.003)$ | 0.064 (±0.010) | 0.077 (±0.008) | 0.083 (±0.015) |
| Paulo de Faria | 0 | | 0.009 (±0.003) | 0.611 (± 0.058) | 0.079 (±0.009) | 0.075 (± 0.012) |
| Itirapina | 0 | 0.076 (± 0.012) | | $0.021(\pm 0.005)$ | 0.633 (±0.019) | $0.280(\pm 0.018)$ |
| São Carlos | 0.036 (± 0.009) | 0.406 (± 0.016) | 0.022 (±0.010) | | 0.016 (±0.003) | 0.058 (±0.015) |
| Bauru | 0 | $0.147 (\pm 0.007)$ | 0.654 (±0.036) | 0.088 (±0.013) | | 0.498 (±0.013) |
| Lavras | 0 | 0.093 (± 0.008) | 0.101 (±0.008) | 0.104 (±0.013) | 0.187 (±0.009) | |

 Table 3 Floristic similarity indicated by Sørensen index (± standard error) among all sites, considering trees (results in bold) and climbers.

| | Ubatuba | Paulo de Faria | Itirapina | São Carlos | Bauru | Lavras |
|----------------|---------|----------------|-----------|------------|-----------|-----------|
| Ubatuba | | 1864.11 * | 1276.47 * | 1604.30 * | 1662.00 * | 2166.50 * |
| Paulo de Faria | 6.91 * | | 417.97 * | 283.98 | 123.70 | 259.33 |
| Itirapina | 25.90 * | -27.13 * | | 383.14 * | 338.42 | 395.34 |
| São Carlos | 2.88 * | 3.56 * | -23.06 * | | 214.83 | 432.91 |
| Bauru | 7.75 * | -0.35 | 33.08 * | -4.13 * | | 231.17 |
| Lavras | 7.60 * | -2.24 | 17.11 * | 4.79 * | -2.22 | |

Table 4 Kolmogorov-Smirnov test values for SAD (in **bold**) and t-Test for Shannon indices of climbers among thesix sites (*p < 0,05).

Table 5 Abundance, richness and Shannon diversity index (nats.individual⁻¹) of climbers with their respective variance value for the six sampled areas.

| | Ubatuba | Paulo de Faria | Itirapina | São Carlos | Bauru | Lavras |
|--------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|------------------------|
| Richness/ha | 65 | 45 | 25 | 45 | 39 | 51 |
| Abundance/ha | 526 | 1427 | 2778 | 528 | 2793 | 711.43 |
| Shannon H' | 3.42 | 2.98 | 1.91 | 3.20 | 2.96 | 2.877 |
| Variance H' | 2.46 x 10 ⁻³ | 8.33 x 10 ⁻⁴ | 6.74 x 10 ⁻⁴ | 2.27 x 10 ⁻³ | 3.16 x 10 ⁻⁴ | 2.3 x 10 ⁻³ |

| Tree | | Climber | Intercept | Regression Coefficient | Adjusted R ² | F | Р |
|---------------|---|---------------|-----------|------------------------|-------------------------|--------|----------|
| Abundance | x | Abundance | 455.066 | 2.534 | 0.367 | 3.899 | 0.1195 |
| Richness | x | Richness | -9.278 | 2.984 | 0.4652 | 5.349 | 0.0818 |
| Abundance | x | Richness | 8883.5 | -105.1 | -0.09114 | 0.5824 | 0.4879 |
| Richness | x | Abundance | 147.90429 | -0.01570 | -0.1176 | 0.4737 | 0.5291 |
| Shannon Index | x | Abundance | 4.2515375 | -0.0003355 | 0.5486 | 7.075 | 0.0564 |
| Shannon Index | x | Richness | 2.249313 | 0.033616 | 0.9489 | 93.88 | 0.0006 * |
| Abundance | x | Shannon Index | 9665 | -1906 | -0.1689 | 0.2774 | 0.6262 |
| Richness | x | Shannon Index | -20.64 | 50.36 | 0.06631 | 1.355 | 0.3091 |
| Shannon Index | x | Shannon Index | 1.7171 | 0.7072 | 0.5738 | 7.73 | 0.0498* |

Table 6 Regression analysis results among diversity descriptors of climbers and trees (*p< 0,05) after sequential</th>Bonferroni correction.



Fig. 1 The six sampled sites in southeastern Brazil.



Fig 2 Rarefaction curves for trees until 606 individuals. Continuous lines represent averages and dotted line,

confidence intervals of 95%.



Fig. 3 Rarefaction curves for climbers until 550 individuals. Continuous lines are the mean resample and dotted line, confidence interval of 95%.

Anexo 2 - Descritores das redes complexas

Tabela 1. Principais descritores de redes para as três áreas estudadas nessa tese. Para maiores informações veja (Rezende 2005), Weiser (2007), van Melis (2008) e Rochelle (2008). Alguns valores podem ser diferentes dos trabalhos originais devido a atualizações na identificação de espécies. FOD = Floresta Ombrófila Densa, Ubatuba; FES = Floresta Estacional Semidecídua, Paulo de Faria; Cerradão = Bauru.

| | FOD | FES | Cerradão |
|-------------------------------------|-------|--------|----------|
| Árvores | | | |
| Nº indivíduos | 1878 | 1419 | 11173 |
| N° de espécies | 219 | 86 | 140 |
| Nº de espécies com ligações | 125 | 64 | 119 |
| Nº de ligações/espécie com ligações | 3.672 | 10.313 | 8.025 |
| NODF | 0.213 | 0.629 | 0.531 |
| Lianas | | | |
| Nº indivíduos | 526 | 1427 | 3035 |
| N° de espécies | 66 | 45 | 39 |
| Nº de espécies com ligações | 66 | 45 | 39 |
| N° de ligações/espécie | 6.955 | 14.667 | 24.487 |
| NODF | 0.199 | 0.495 | 0.699 |
| Rede | | | |
| Nº de espécies na rede | 191 | 109 | 158 |
| Nº de ligações | 459 | 660 | 955 |
| Nº de ligações/espécie | 2.403 | 6.055 | 6.044 |
| Conectância | 0.056 | 0.229 | 0.206 |
| NODF | 0.210 | 0.585 | 0.547 |

| Espécie | N°de ligações | Espécie | Nº de ligações |
|--|---------------|-------------------------------|----------------|
| Bathysa mendoncaei | 23 | Mollinedia schottiana | 3 |
| Eriotheca pentaphylla | 21 | Ocotea paranapiacabensis | 3 |
| Sloanea guianensis | 21 | Pausandra morisiana | 3 |
| Indeterminada 1 | 19 | Roupala brasiliensis | 3 |
| Virola bicuhyba | 12 | Sorocea hilarii | 3 |
| Garcinia gardneriana | 11 | <i>Virola</i> sp. | 3 |
| Calyptranthes grandifolia | 10 | Alseis floribunda | 2 |
| Coussarea meridionalis var. porophylla | 10 | Annonaceae | 2 |
| Faramea pachyantha | 10 | Ardisia martiana | 2 |
| Hieronyma alchorneoides | 10 | Brosimum lactescens | 2 |
| Morta | 10 | Buchenavia kleinii | 2 |
| Pouteria psammophila | 10 | Cordia taguahyensis | 2 |
| Ecclinusa ramiflora | 9 | Couepia venosa | 2 |
| Mollinedia triflora | 9 | Cupania vernalis | 2 |
| Hirtella hebeclada | 8 | Eugenia batingabranca | 2 |
| Rustia formosa | 8 | Eugenia cerasiflora | 2 |
| Brosimum sp. | 7 | Eugenia prasina | 2 |
| Tetrastylidium grandifolium | 7 | Euplassa cantareirae | 2 |
| Eugenia kleinii | 6 | Euterpe edulis | 2 |
| Eugenia neoaustralis | 6 | Guarea macrophylla | 2 |
| Marlierea tomentosa | 6 | Indeterminada 6 | 2 |
| Pouteria grandiflora | 6 | Indeterminada 7 | 2 |
| Pseudopiptadenia warmingii | 6 | Licania kunthiana | 2 |
| Rudgea recurva | 6 | Miconia cinnamomifolia | 2 |
| Trichilia silvatica | 6 | Myrcia aethusa | 2 |
| Cryptocarya saligna | 5 | Myrciaria floribunda | 2 |
| Guapira opposita | 5 | Nectandra grandiflora | 2 |
| Licania hoehnei | 5 | Pouteria caimito | 2 |
| Marlierea glazioviana | 5 | Pseudopiptadenia leptostachya | 2 |
| Brosimum guianense | 4 | Sloanea sp. | 2 |
| Cupania oblongifolia | 4 | Spondias purpurea | 2 |
| Eugenia cuprea | 4 | Tabebuia serratifolia | 2 |
| Eugenia oblongata | 4 | Aniba viridis | 1 |
| Guapira hirsuta | 4 | Cabralea canjerana | 1 |
| Guapira venosa | 4 | Calyptranthes pileata | 1 |
| Indeterminada 2 | 4 | Calyptranthes strigipes | 1 |
| Marlierea suaveolens | 4 | Campomanesia phaea | 1 |
| Mollinedia oligantha | 4 | Cariniana estrellensis | 1 |
| Mouriri sp. | 4 | Citronella paniculata | 1 |
| Plinia rivularis | 4 | Cordia sellowiana | 1 |
| Aegiphila sellowiana | 3 | Coussarea accedens | 1 |
| Cryptocarya mandioccana | 3 | Coussarea porophylla | 1 |
| Eugenia excelsa | 3 | Daphnopsis schwackeana | 1 |
| Jacaratia spinosa | 3 | Erythroxylum pulchrum | 1 |
| Marlierea silvatica | 3 | Eugenia melanogyna | 1 |
| Micropholis compta | 3 | Fabaceae | 1 |

Ombrófila Densa (Ubatuba).

Continua na próxima página

Continuação Tabela 2

| Espécie | N°de ligações | Espécie | N° de ligações |
|---------------------------------|---------------|-------------------------|----------------|
| Faramea picinguabae | 1 | Cedrela fissilis | 0 |
| Ficus obtusiuscula | 1 | Chomelia sp. | 0 |
| Guatteria sp. | 1 | Chrysophyllum flexuosum | 0 |
| Heisteria silvianii | 1 | Chrysophyllum viride | 0 |
| Indeterminada 4 | 1 | Copaifera trapezifolia | 0 |
| Indeterminada 5 | 1 | Cryptocarya moschatta | 0 |
| Jacaranda sp. | 1 | Cyathea atrovirens | 0 |
| Leandra acutiflora | 1 | Cyathea phalerata | 0 |
| Mabea piriri | 1 | Cyathea sp. 2 | 0 |
| Malouetia arborea | 1 | Cyatheaceae | 0 |
| Matayba guianensis | 1 | Dahlstedtia pinnata | 0 |
| Matayba inelegans | 1 | Dunalia arborescens | 0 |
| Maytenus ilicifolia | 1 | Endlicheria paniculata | 0 |
| Maytenus sp. | 1 | Erythroxylum | 0 |
| Meriania calyptrata | 1 | Eugenia fusca | 0 |
| Miconia dodecandra | 1 | Eugenia linguaeformis | 0 |
| Mollinedia engleriana | 1 | Eugenia multicostata | 0 |
| Mollinedia lamprophylla | 1 | Eugenia plicata | 0 |
| Mollinedia uleana | 1 | Eugenia schulziana | 0 |
| Myrceugenia myrcioides | 1 | Eugenia sp. 1 | 0 |
| Myrcia guianensis | 1 | Eugenia sp. 10 | 0 |
| Myrcia tijucensis | 1 | Eugenia sp. 3 | 0 |
| Neomitranthes glomerata | 1 | Eugenia sp. 4 | 0 |
| Ocotea elegans | 1 | Eugenia sp. 5 | 0 |
| Ocotea laxa | 1 | Eugenia ternatifolia | 0 |
| Ocotea odorifera | 1 | Faramea sp. | 0 |
| Picramnia ciliata | 1 | Ficus insipida | 0 |
| Platymiscium floribundum | 1 | Guatteria nigrescens | 0 |
| Rudgea vellerea | 1 | Hillia parasitica | 0 |
| Siparuna brasiliensis | 1 | <i>Hymenaea</i> sp. | 0 |
| Stephanopodium organense | 1 | Ilex theaezans | 0 |
| Urbanodendron bahiense | 1 | Indeterminada 10 | 0 |
| Alibertia sp. | 0 | Indeterminada 3 | 0 |
| Alsophila sternbergii | 0 | Indeterminada 8 | 0 |
| Amaioua intermedia | 0 | Indeterminada 9 | 0 |
| Andira ormosioides | 0 | Inga capitata | 0 |
| Astrocaryum aculeatissimum | 0 | Inga marginata | 0 |
| Attalea dubia | 0 | <i>Inga</i> sp. | 0 |
| Bactris setosa | 0 | Inga sp. 2 | 0 |
| Bathysa australis | 0 | Inga striata | 0 |
| Byrsonima ligustrifolia | 0 | Lauraceae sp. | 0 |
| Calycorectes acutatus | 0 | Lauraceae sp. 2 | 0 |
| Calyptranthes lanceolata | 0 | Licaria armeniaca | 0 |
| Calyptranthes lucida | 0 | Marlierea excoriata | 0 |
| Calyptranthes urbani | 0 | <i>Marlierea</i> sp. | 0 |
| Campomanesia schlechtendahliana | 0 | Matayba intermedia | 0 |
| Casearia decandra | 0 | Matayba silvatica | 0 |
| Casearia sylvestris | 0 | Matayba sp. | 0 |
| Cecropia glaziovi | 0 | Miconia cabucu | 0 |
| Cecropia sp. | 0 | Miconia petropolitana | 0 |

Continua na próxima página

Continuação Tabela 2

| Espécie | N° de ligações |
|--------------------------|----------------|
| Miconia sp. | 0 |
| Miconia tristis | 0 |
| Moraceae | 0 |
| Myrocarpus frondosus | 0 |
| Myrtaceae sp. | 0 |
| Neomitranthes sp. | 0 |
| Ocotea dispersa | 0 |
| Ocotea venulosa | 0 |
| Pera glabrata | 0 |
| Piper xylosteoides | 0 |
| Plinia edulis | 0 |
| Posoqueria latifolia | 0 |
| Protium heptaphyllum | 0 |
| Pseudopiptadenia sp. | 0 |
| Psychotria patentinervia | 0 |
| Quiina glazovii | 0 |
| Quiina magalanogomesi | 0 |
| Rapanea hermogenesii | 0 |
| Rollinia sericea | 0 |
| Rollinia sp. | 0 |
| Rubiaceae | 0 |
| Rudgea jasminoides | 0 |
| Sapium glandulosum | 0 |
| Schefflera calva | 0 |
| Solanum sp. | 0 |
| Terminalia januarensis | 0 |

Ombrófila Densa (Ubatuba).

| Espécie | Nº de ligações |
|---|----------------|
| Adenocalymma comosum | 46 |
| Condylocarpon ishtmicum | 32 |
| Forsteronia australis | 31 |
| Forsteronia refracta | 30 |
| Machaerium declinatum | 20 |
| Forsteronia sp. | 19 |
| Marcgravia polyantha | 19 |
| Elachyptera micrantha | 16 |
| Heteropsis rigidifolia | 16 |
| Paullinia carpopodea | 16 |
| Dalbergia frutescens | 12 |
| Heteropterys nitida | 12 |
| Polybotrya semipinnata | 12 |
| Mikania lundiana | 10 |
| Wilbrandia ebracteata | 10 |
| Strychnos brasiliensis | 9 |
| Chondodendron platyphyllum | 7 |
| Tetrastylis ovalis | 7 |
| Arrabidaea sp. | 6 |
| Machaerium lanceolatum | 6 |
| Machaerium uncinatum | 6 |
| Paullinia bicorniculata | 6 |
| Paullinia trigonia | 6 |
| Pristimera celastroides | 6 |
| Pfaffia paniculata | 5 |
| Solanum sp. 1 | 5 |
| Trigonia nivea | 5 |
| Bauhinia microstachya var. microstachya | 4 |
| Bauhinia surinamensis | 4 |
| Coccoloba sp. | 4 |
| Icacinaceae | 4 |
| Macfadyena uncata | 4 |
| Mendoncia velloziana | 4 |
| Mikania sp. 2 | 4 |
| Abuta selloana | 3 |
| Dioclea sp. | 3 |
| Mikania sp. 1 | 3 |
| Passiflora sidaefolia | 3 |
| Paullinia seminuda | 3 |
| Prestonia riedelli | 3 |
| Salacia elliptica | 3 |
| Acacia sp. | 2 |
| Anthodon decussatum | 2 |
| Aristolochia paulistana | 2 |

| Espécie | N° de ligações |
|--------------------------|----------------|
| Hippocratea nervosa | 2 |
| Hyperbaena domingensis | 2 |
| Machaerium dimorphandrum | 2 |
| Malpighiaceae 1 | 2 |
| Malpighiaceae 2 | 2 |
| Tontelea martiana | 2 |
| Tontelea miersii | 2 |
| Acacia tenuifolia | 1 |
| Adenocalymma sp. | 1 |
| Cheiloclinium serratum | 1 |
| Cissampelos fasciculata | 1 |
| Cissus paullinifolia | 1 |
| Dalbergia lateriflora | 1 |
| Heteropterys sp. | 1 |
| <i>Hiraea</i> sp. | 1 |
| Malpighiaceae 3 | 1 |
| Morta | 1 |
| Paragonia sp. | 1 |
| Paullinia spicata | 1 |
| Peritassa hatschbachii | 1 |
| Schwartzia brasiliensis | 1 |
| Solanum sp. 2 | 1 |

Tabela 4. Espécies de árvores e o seu respectivo número de interações na Floresta

| Estacional Semidecídua | (Paulo | de Faria) | • |
|------------------------|--------|-----------|---|
|------------------------|--------|-----------|---|

| Espécie | N°de ligações | Espécie | N° de ligações |
|-------------------------------|---------------|---------------------------------------|----------------|
| Machaerium paraguariense | 32 | Acalypha diversifolia | 4 |
| Cariniana estrellensis | 27 | Coccoloba latifolia | 4 |
| Diatenopteryx sorbifolia | 23 | Ocotea diospyrifolia | 4 |
| Inga marginata | 23 | Abrus arboreus | 3 |
| Chrysophyllum gonocarpum | 21 | Machaerium oblongifolium | 3 |
| Nectandra cissiflora | 20 | Trichilia casaretti | 3 |
| Unonopsis guatterioides | 20 | Urera baccifera | 3 |
| Eugenia florida | 19 | Aspidosperma parvifolium | 2 |
| Hymenaea pubescens | 19 | Genipa americana | 2 |
| Sapium glandulosum | 19 | Ocotea corymbosa | 2 |
| Terminalia argentea | 19 | Sweetia fruticosa | 2 |
| Astronium graveolens | 18 | Terminalia brasiliensis | 2 |
| Casearia gossypiosperma | 18 | Actinostemon klotzschii | 1 |
| Inga vera | 17 | Attalea phalerata | 1 |
| Trichilia claussenii | 17 | Ficus citrifolia | 1 |
| Trichilia hirta | 16 | Luehea grandiflora | 1 |
| Aloysia virgata | 15 | Phyllostylon brasiliense | 1 |
| Guarea kunthiana | 15 | Pouteria gardneri | 1 |
| Cedrela fissilis | 14 | Syagrus oleracea | 1 |
| Guarea guidonia | 14 | Tabebuia roseoalba | 1 |
| Pterogyne nitens | 14 | Acacia polyphylla | 0 |
| Albizia hassleri | 13 | Agonandra brasiliensis | 0 |
| Psidium sartorianum | 13 | Allophylus edulis | 0 |
| Simira sampaioana | 13 | Ardisia latipes | 0 |
| Trichilia catigua | 13 | Bauhinia ungulata | 0 |
| <i>Cordia</i> sp. | 12 | Campomanesia guazumifolia | 0 |
| Rhamnidium elaeocarpum | 12 | Casearia aculeata | 0 |
| Ceiba pubiflora | 11 | Cupania vernalis | 0 |
| Jacaratia spinosa | 11 | Eugenia ligustrina | 0 |
| Aralia excelsa | 10 | Eugenia moraviana | 0 |
| Casearia mariquitensis | 10 | Hexachlamys sp. | 0 |
| Casearia rupestris | 10 | Ixora heterodoxa | 0 |
| Piptadenia gonoacantha | 10 | Machaerium minutiflorum | 0 |
| Protium heptaphyllum | 10 | Machaerium villosum | 0 |
| Guazuma ulmifolia | 9 | Manihot pilosa | 0 |
| Rollinia dolabripetala | 9 | Myracrodruon urundeuva | 0 |
| Annona cacans | 8 | Myrcia tomentosa | 0 |
| Enterolobium contortisiliquum | 8 | Piper arboreum | 0 |
| Anadenanthera macrocarpa | 7 | Pterodon emarginatus | 0 |
| Alibertia macrophylla | 6 | Randia armata | 0 |
| Celtis iguanaea | 6 | Trema micrantha | 0 |
| Piper amalago | 6 | Trichilia pallida | 0 |
| Tabebuia impetiginosa | 6 | · · · · · · · · · · · · · · · · · · · | - |
| Guanira areolata | 5 | | |

Estacional Semidecídua (Paulo de Faria).

| Espécie | N° de ligações |
|----------------------------|----------------|
| Dolichandra quadrivalvis | 44 |
| Anthodon decussatum | 43 |
| Forsteronia pubescens | 43 |
| Forsteronia pilosa | 42 |
| Arrabidaea triplinervia | 40 |
| Urvillea laevis | 38 |
| Arrabidaea chica | 32 |
| Secondatia sp. | 24 |
| Serjania lethalis | 23 |
| Adenocalymna bracteatum | 22 |
| Combretum discolor | 22 |
| Bauhinia microstachya | 20 |
| Amphilophium paniculatum | 17 |
| Urvillea uniloba | 17 |
| Pyrostegia venusta | 16 |
| Lundia obliqua | 15 |
| Tanaecium selloi | 15 |
| Arrabidaea leucopogon | 14 |
| Carolus chlorocarpus | 14 |
| Dolichandra unguis-cati | 14 |
| Serjania hebecarpa | 13 |
| Cissus campestris | 11 |
| Heteropterys dumetorum | 11 |
| Tynanthus elegans | 11 |
| Banisteriopsis lutea | 10 |
| Cissampelos glaberrima | 10 |
| Serjania laruotteana | 10 |
| Dasyphyllum flagellare | 9 |
| Guettarda guianensis | 8 |
| Cardiospermum grandiflorum | 7 |
| Serjania caracasana | 7 |
| Pleonotoma tetraquetrum | 6 |
| Tanaecium pyramidatum | 5 |
| Arrabidaea pulchella | 4 |
| Fabaceae sp. | 4 |
| Tetrapterys sp. | 4 |
| Rhynchosia phaseoloides | 3 |
| Serjania communis | 3 |
| <i>Serjania</i> sp. | 2 |
| Wilbrandia longisepala | 2 |
| Harmsiopanax sp. | 1 |
| Heteropterys argyrophaea | 1 |
| <i>Hiraea</i> sp. | 1 |
| Machaerium oblongifolium | 1 |
| Pfaffia paniculata | 1 |
| Espécie | Nº de ligações | Espécie | Nº de ligações |
|----------------------------|----------------|--------------------------|----------------|
| Ocotea pulchella | 31 | Vatairea macrocarpa | 6 |
| Vochysia tucanorum | 30 | Brosimum gaudichaudii | 5 |
| Miconia albicans | 29 | Carvocar brasiliense | 5 |
| Tanirira guianensis | 29 | Myrcia multiflora | 5 |
| Yylonia aromatica | 29 | Vochysia cinnamomea | 5 |
| Myrsine umbellata | 27 | Zevheria montana | 5 |
| Congiba langsdorfii | 27 | Acosmium subalagans | 5 |
| Coussarea hydrangeifolia | 20 | Agginhila lhotskiana | 4 |
| Rudaga viburnoidas | 20 | Rauhinia rufa | 4 |
| Cordiara macrophylla | 23 | Bursonima nachuphulla | 4 |
| Earamaa montavidansis | 23 | Campomanasia pubascans | 4 |
| Purameu monieviaensis | 21 | Componanesia pubescens | 4 |
| Qualea coradia | 20 | Couepia granaijiora | 4 |
| Siparuna guianensis | 20 | Erioineca gracuipes | 4 |
| Pera glabrata | 19 | Eugenia aurata | 4 |
| Ocotea corymbosa | 18 | Lajoensia pacari | 4 |
| Ocotea puberula | 18 | Lamanonia ternata | 4 |
| Platypodium elegans | 18 | Machaerium brasiliense | 4 |
| Protium heptaphyllum | 18 | Ouratea spectabilis | 4 |
| Qualea grandiflora | 18 | Plenckia populnea | 4 |
| Myrcia tomentosa | 17 | Senna silvestris | 4 |
| Machaerium acutifolium | 16 | Syagrus flexuosa | 4 |
| Styrax camporum | 16 | Trichilia pallida | 4 |
| Terminalia glabrescens | 16 | Ixora venulosa | 3 |
| Coccoloba mollis | 15 | Kielmeyera variabilis | 3 |
| Plathymenia reticulata | 15 | Lithraea molleoides | 3 |
| Qualea multiflora | 15 | Miconia stenostachya | 3 |
| Erythroxylum subracemosum | 14 | Ocotea minarum | 3 |
| Roupala brasiliensis | 14 | Pseudobombax longiflorum | 3 |
| Terminalia argentea | 14 | Stryphnodendron obovatum | 3 |
| Qualea parviflora | 13 | Tabebuia aurea | 3 |
| Anadenanthera peregrina | 12 | Amaioua guianensis | 2 |
| Myrcia venulosa | 12 | Andira vermifuga | 2 |
| Lacistema hasslerianum | 11 | Annona cacans | 2 |
| Symplocos pubescens | 11 | Bredemeyera floribunda | 2 |
| Ixora gardneriana | 10 | Brosimum guianense | 2 |
| Symplocos nitensvar.nitens | 10 | Byrsonima verbascifolia | 2 |
| Annona coriacea | 9 | Chrysophyllum marginatum | 2 |
| Gochnatia polymorpha | 9 | Connarus suberosus | 2 |
| Guettarda viburnoides | 9 | Curatella americana | 2 |
| Luehea grandiflora | 9 | Dalbergia miscolobium | 2 |
| Psychotria capitata | 9 | Eugenia punicifolia | 2 |
| Actinostemon klotzschii | 8 | Fagara rhoifolia | 2 |
| Bowdichia virgilioides | 8 | Guapira areolata | 2 |
| Myrcia guianensis | 8 | Guapira hirsuta | 2 |
| Schefflera vinosa | 8 | Guapira salicifolia | 2 |
| Aspidosperma tomentosum | 6 | Kielmeyera rubriflora | 2 |
| Eugenia hiemalis | 6 | Matayba elaeagnoides | 2 |
| Ficus citrifolia | 6 | Miconia langsdorffii | 2 |
| Guapira noxia | 6 | Sapium obovatum | 2 |

Tabela 6. Espécies de árvores e o seu respectivo número de interações no Cerradão (Bauru).

Continua na próxima página

Continuação Tabela 6

| Espécie | N° de ligações |
|-----------------------------|----------------|
| Aspidosperma cylindrocarpon | 1 |
| Annona crassiflora | 1 |
| Byrsonima coccolobifolia | 1 |
| Byrsonima intermedia | 1 |
| Calyptranthes concinna | 1 |
| Daphnopsis utilis | 1 |
| Dimorphandra mollis | 1 |
| Enterolobium gummiferum | 1 |
| Erythroxylum tortuosum | 1 |
| Gochnatia barrosii | 1 |
| Guapira opposita | 1 |
| Heteropterys sp. | 1 |
| Licania humilis | 1 |
| Lopimia malacophylla | 1 |
| Myrcia uberavensis | 1 |
| Pouteria ramiflora | 1 |
| Psidium guineense | 1 |
| Strychnos pseudoquina | 1 |
| Syagrus romanzoffiana | 1 |
| Vernonia rubriramea | 1 |
| Zeyheria tuberculosa | 1 |
| Agonandra excelsa | 0 |
| Bauhinia forficata | 0 |
| Bauhinia ungulata | 0 |
| Byrsonima crassifolia | 0 |
| Byrsonima laxiflora | 0 |
| Campomanesia adamantium | 0 |
| Casearia sylvestris | 0 |
| Cedrela fissilis | 0 |
| Cybistax quinquefolia | 0 |
| Davilla sp. | 0 |
| Dendropanax cuneatus | 0 |
| Diospyros hispida | 0 |
| Eugenia bimarginata | 0 |
| Himatanthus obovatus | 0 |
| Hymenaea stigonocarpa | 0 |
| Myrcia bella | 0 |
| Ocotea velloziana | 0 |
| Piptocarpha rotundifolia | 0 |
| Pseudolmedia laevigata | 0 0 |
| Senna rugosa | 0 |
| Tocovena formosa | Õ |

| Espécie | N° de ligações |
|---------------------------|----------------|
| Serjania lethalis | 66 |
| Forsteronia glabrescens | 64 |
| Stizophyllum riparium | 54 |
| Banisteriops anisandra | 52 |
| Serjania reticulata | 50 |
| Secondatia densiflora | 48 |
| Banisteriops argyrophylla | 45 |
| Temnadenia violacea | 45 |
| Distictella mansoana | 44 |
| Securidaca rivinaefolia | 39 |
| Diplopterys pubipetala | 34 |
| Forsteronia velloziana | 34 |
| Smilax fluminensis | 32 |
| Gouania latifolia | 28 |
| Banisteriops stellaris | 27 |
| Prestonia coalita | 26 |
| Smilax polyantha | 26 |
| Mascagnia cordifolia | 25 |
| Odontadenia lutea | 25 |
| Arrabidaea pulchella | 22 |
| Doliocarpus dentatus | 22 |
| Chiococca alba | 19 |
| Ipomoea tuberosa | 19 |
| Strychnos bicolor | 17 |
| Arrabidaea triplinervia | 16 |
| Macfadyena dentata | 15 |
| Arrabidaea craterophora | 11 |
| Arrabidaea pulchra | 11 |
| Passiflora alata | 11 |
| Heteropterys syringifolia | 7 |
| Dolichandra unguis-cati | 3 |
| Memora peregrina | 3 |
| Passiflora suberosa | 3 |
| Pyrostegia venusta | 3 |
| Smilax campestris | 3 |
| Heteropterys umbellata | 2 |
| Mansoa difficilis | 2 |
| Cissus erosa | 1 |
| Serjania gracilis | 1 |

Tabela 7. Espécies de lianas e o seu respectivo número de interações no Cerradão (Bauru).

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