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ZULQARNAIN

“LIANA AND PHOROPHYTE PAIRWISE ANALYSIS ALONG THE GRADIENT IN A FRAGMENT OF SEMIDECIDUOUS FOREST”

“ANÁLISE DE PARES DE LIANA E FORÓFITO AO LONGO DE UM GRADIENTE EM UM FRAGMENTO DA FLORESTA ESTACIONAL SEMIDECÍDUA”

CAMPIANS

2014

UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

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Thesis presented to the Institute of Biology of UNICAMP to obtain the Degree of Doctor in Plant Biology.

Tese apresentada ao Instituto de Biologia da UNICAMP para obtenção do Título de Doutor em Biologia Vegetal.

Este exemplar corresponde à redação final da Tese defendida pelo candidato
Zulqarnain
e aprovada pela Comissão Julgadora.

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Ficha catalográfica
Universidade Estadual de Campinas
Biblioteca do Instituto de Biologia
Mara Janaina de Oliveira - CRB 8/6972

Zulqarnain, 1982-
Z84a Análise de pares de Liana e Forófito ao longo de um gradiente em um fragmento da floresta estacional semidecídua / Zulqarnain. – Campinas, SP : [s.n.], 2014.

Orientador: Fernando Roberto Martins.
Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Analise de regressão. 2. Competição. 3. Coocorrência de plantas. 4. Filogenia. 5. Atributos funcionais. I. Martins, Fernando Roberto,1949-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Informações para Biblioteca Digital

Título em outro idioma: Liana and Phorophyte pairwise analysis along the gradient in a fragment of semideciduous forest
Palavras-chave em inglês:
Regression analysis
Competition
Plants co-occurrence
Phylogeny
Functional traits
Área de concentração: Biologia Vegetal
Titulação: Doutor em Biologia Vegetal
Banca examinadora:
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Marcelo Carnier Dornelas
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Data de defesa: 20-02-2014
Programa de Pós-Graduação: Biologia Vegetal

Campinas, 20 de fevereiro de 2014

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Resumo

Em florestas tropicais, a relação entre lianas e suas árvores-suporte (forófitos) representa uma importante interação antagônica. Em interações antagônicas a capacidade individual de um organismo de usar recursos aumenta, ao passo que a do outro organismo que interage decresce como resultado da interação. Cerca de 69% de todos os sistemas antagonisticos têm sinal filogenético, tendo em vista que interações entre espécies podem ser moldadas pela bagagem filogenética recebida como herança de seus antepassados. Por entretanto interações entre espécies variam de acordo com gradientes ambientais e o padrão de coocorrência de espécies de plantas em pequenas escalas espaciais muda com as condições ambientais. Portanto, o objetivo geral desta tese é avaliar a ocorrência de algum grau de especialização em lianas e forófitos e verificar a probabilidade de coocorrências entre lianas ou entre lianas e forófitos varia com a posição na encosta ou com a variação de variáveis do solo ao longo da encosta. A área focal deste trabalho foi um fragmento da Floresta Estacional Semidecídua no município de Campinas, mas em primeiro capítulo também pesquisou outros três fragmentos, (i) Floresta Ombrófila no município de Ubatuba, (ii) Cerradão no município de Bauru, e (iii) Floresta Estacional Semidecídua no município de Paulo de Faria, em estado de São Paulo, no sudeste do Brasil. No capítulo (1) observou que em florestas ombrófila e estacionais, lianas e forófitos com alta originalidade filogenética tenderam a interagir com um conjuntos de espécies muito distintas. Por outro lado constatou-se que nos bosques de cerrados, lianas e forófitos com altas originalidade filogenética tenderam a interagir com conjuntos comuns de espécies. No segundo capítulo (2), mostramos que lianas coocorrem aleatoriamente no forófito, mas também observamos a existência de uma tendência de que lianas com mecanismos de escalada semelhantes facilitam a escalada de outra liana a escalar a árvore hospedeira. Por contudo não encontramos lianas coocorrência ao longo de gradientes ambientais. No capítulo (3), observamos que as variáveis selecionadas (fatores topoedáficos e diversidade filogenicas dos forófitos) não explicaram a variacão na freqüência de coocorrência das lianas- forófitos. Por constatamos que lianas têm um comportamento oportunista para subir nas árvores e diversidade filogenicas usuando como proxy para atributos de árvores não são importantes para as lianas. Argumentamos que as diferenças ambientais entre florestas e savanas mediaram processos evolutivos distintos nas interações liana-forófito. Os processos estocásticos são o fator dominante gerando padrão de co-ocorrência entre lianas e lianas-forófito.

Palavras-chave: (1) Analise de regressão (2) Competição (3) Coocorrência de plantas (4)

Filogenia (5) Atributos funcionais.

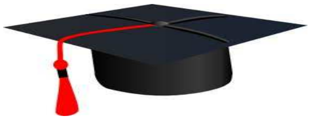
Abstract

Liana and host tree (phorophyte) represent an important antagonistic interaction in tropical forest. In antagonistic interactions the individual ability of using nutrient resources increases whereas the ability of interacting individual decreases as a result of interaction. About 69 % of all antagonistic systems have phylogenetic signal, considering that species interactions can be shaped by phylogenetic baggage that species received as an inheritance from their ancestors. However species interactions vary according to environmental gradients hence the co-occurrence pattern of the plant species in small spatial scales also changes with environmental conditions. Therefore, the aim of this thesis was to evaluate some degree of specialization between lianas and phorophytes and probability of co-occurrences among lianas as well lianas and phorophytes along the slope or the variation of soil variables along the slope. The focal area of this work was a fragment of tropical semideciduous forest in the muncipality of Campinas, but in the first chapter we also surveyed three other fragments (i) Tropical Rain Forest in the muncipality of Ubatuba, (ii) Woodland Savanna in the municipality of Bauru and (iii) the tropical semideciduous forest in the municipality of Paulo de Faria, in the state of São Paulo, in southeastern Brazil. In chapter (1) we observed that in tropical rain forest and seasonal forests, lianas and phorophyte with high phylogenetic originality tended to interact with a set of very distinct species. Moreover it was found that in the woodland Savanna, lianas and phorophytes with high phylogenetic originality tended to interact with common sets of species. In chapter (2) we showed that lianas co-occur randomly on the host tree, but we also observed an existence of a tendency that lianas with similar climbing mechanisms facilitate other liana climbing the host tree. But we did not find role of environmental gradients in lianas co-occurrence. In chapter (3), we observed that selected variables (topoedaphic factors and phylogenetic diversity of phorophyte), also did not explain the variation in the frequency of liana-phorophyte co-occurrence. But we found that lianas have an opportunistic behavior and phylogenetic diversity using as proxy for tree traits are not important to the lianas. We argued that environmental differences in forests and savannas mediated distinct evolutionary processes in structuring liana-phorophyte interactions. The stochastic processes are the dominant factor generating pattern of co-occurrence among lianas and liana and host tree.

Key Words: (1) Regression analysis (2) Competition (3) Plants co-occurrence (4) Phylogeny (5) Functional traits.

SUMÁRIO

Dedication



To Dear Co-Supervisor Late Dr. Igor Aurelio Silva and

Supervisor Prof. Dr. Fernando Roberto Martins

I know that without you it would have never been possible!

THANK YOU!

Acknowledgement

- First of all I bow down my head to the Omnific, Omniscient, Omnipotent and Omnipresent **AL-MIGHTY ALLAH** who provided me the opportunity of exploring the texture of his natural beauties. All respect to all the **Holy Messengers and Prophet Muhammad (P.B.U.H)** for enlightening our conscious with the essence of faith.
- I owe a deep depth of heartiest regards to my research supervisor **Prof. Dr. Fernando Roberto Martins** and **Co-Supervisor Late Dr. Igor Aurelio Silva**, whose excellent supervision, valuable suggestions, constant encouragement and precious attention throughout the course of this study resulted in the successful completion of this research work.
- I am indebted to all the honorable members of my defense committee for accepting the invitation..
- I wish to express my sincere gratitude to the members of the Postgraduate Program of Plant Biology **Prof. Dr. Sandra Carmello-Guerreiro, Prof. Dr. Marcelo Carnier Dornelas, Maria Roseli de Melo** at UNICAMP for her guidance and help at every stage of my PhD.
- The whole work was carried out with the excellent facilities made available at the State University of Campinas UNICAMP, Institute of Biology (IB). I am here to say thank you UNICAMP and thank you IB for giving me the environment to flourish in life.
- My special thanks are extended to all my lab friends especially Andre Rodrigo Rich, Andre Rochelle, Anna Abrahão, Arildo Dias, Fernanda, Gabriela Atique, Graham Zemunik, Julia Caram Sfair, Juliano Van Melis, Junior Ferreira, Luciana Franci, Maira Padgurschi, Marcelo Freire, Mario Jose Marques, Millene Silvestrini, Valdivino lima dos Santos for providing me valuable assistance, moral support and smiling moments during the whole work.
- I am extremely grateful to my Pakistani friends, especially Abdul Qayum Khan and his Family, Abdul Aziz, Abdur Rahim, Abidullah, Adnan Khan, Ali Riaz, Anwar Iqbal, Atlas Khan, Faizanullah, Farhadullah, Hamidullah, Hikmatullah Jan, Jasim Khan, Khalid Ahmad, Khalid Ahmed, Kifayatullah, Mehmood Alam, Mohibullah Shah, Naseer Ahmad, Syed Badshah, Umar Nishan, Ziarat Shah, for being so supportive during all the time.
- Where would I be without my family? It is an honor for me to take this opportunity to thank my affectionate, sympathetic and respectable parents who brought me up with their love; my wife, kids and sisters for their love, prayers and support throughout my career. My sincerest

thanks to my brothers Fasih Ur Rahamn, Muhammad Pervez and their wives and all my relatives for their patience, assistance, continuous support and encouragement during the completion of this work and my PhD.

- I would like to give my heartfelt appreciations to my friends Prof. Dr. Muhammad Habib and his family, Nadir Habib, Eva, Danilo Damas and Maria elena, Gabriel Jeronomy Curti and his family, Ibrahim Waagner and his family, Joao Marcondes and his family and Islamic society of Campinas for helping me learn so much about the social life in Brazil.
- I feel obliged for the confidence shown on me by awarding me PhD fellowship by the Academy of Sciences for the Developing World (TWAS) and Brazillian National Council for Scientific and Technological Development (CNPq).
- Finally I am thankful to all those who helped in the realization of this work in any way directly or indirectly.
- May God give me the strength to serve Science and humanity!

Zulqarnain

Introdução Geral

Informações recentes sobre a história evolutiva e relações filogenéticas têm levantado muitas perguntas sobre causas e efeitos da organizada e diversidade de comunidades (Vamosi et al. 2008; Cavender-Bares et al. 2009). Várias teorias têm sido propostas sobre como as comunidades ecológicas são organizada. Hubbell (2001) propôs que a montagem de comunidades seria o resultado de processos totalmente neutros, e que a coocorrência de espécies seria uma resultante estocástica. Mas, para a teoria clássica, a montagem de comunidades seria determinada por filtros ambientais e por exclusão competitiva (Weiher e Keddy 1999). A competição ocorre quando plantas vizinhas disputam o mesmo fóton de luz, o mesmo íon de nutriente e o mesmo espaço (Grime 1973, 2001). De acordo com uma terceira teoria, fatores históricos regulariam o processo de montagem da comunidade, e eventos passados desempenhariam um papel importante (Ricklefs e Schluter 1993). Atualmente, os efeitos relativos dos processos neutros, dos relacionados com nicho e dos processos históricos como agentes reguladores da montagem de comunidades e da coexistência de espécies estão sob debate (Tilman 2004; McGill 2011), principalmente porque também pode ocorrer facilitação entre espécies. A facilitação é um tipo de interação, na qual um indivíduo de uma espécie melhora o ambiente local para um indivíduo de outra espécie, especialmente sob condições ambientais adversas (Callaway 1995; Bruno et al. 2003). Assim, atributos fenotípicos das espécies são importantes direcionadores do tipo de interações que elas podem estabelecer entre si.

Espécies filogeneticamente aparentadas tendem a assemelhar-se na maioria dos atributos fenotípicos (Blomberg et al. 2003) e conservam atributos ancestrais que influenciam a maneira como interagem com outras espécies (Gomez et al. 2010). Como espécies aparentadas tendem a acoplar-se ao ambiente de maneira semelhante, fatores ambientais influenciam a relação filogenética das espécies que coocorrem (Webb et al. 2002). Assim, a avaliação do padrão filogenético de comunidades também é importante para explicar a ocorrência simultânea de espécies de plantas. Se os atributos funcionais forem conservados na evolução das linhagens de espécies (Ackerly 2003; Reich et al. 2003) e a filtragem ambiental for o processo ecológico dominante (Weiher e Keddy 1995; Webb 2000), espera-se que as espécies coocorrentes sejam estreitamente aparentadas. Neste caso, as distâncias filogenéticas entre as espécies coocorrentes serão mais curtas que as esperadas ao acaso, e o padrão filogenético resultante será uma estrutura filogenética agregada (Webb et al. 2002). Por outro lado, se os atributos funcionais forem filogeneticamente conservados e a competição por recursos limitantes for o principal processo ecológico envolvido na montagem de comunidades, as espécies mais proximamente aparentadas tendem a ser eliminadas e a apresentar baixo nível de coocorrência devido à exclusão competitiva de uma ou mais espécies semelhantes (Leibold 1998). Neste caso, as distâncias filogenéticas entre as espécies são mais longas que as esperadas ao acaso, gerando uma estrutura filogenética dispersa (Webb et al. 2002).

Entre os ecossistemas do mundo, as florestas tropicais estão atualmente atraindo muita atenção dos ecólogos, não só por causa de sua diversidade de espécies, mas também por causa de sua composição e estrutura complexas. Um dos componentes dessa complexidade é a heterogeneidade de habitats, que influencia a distribuição espacial das espécies (Fowler 1988; Terborgh 1992). Variações topográficas locais (ângulo de inclinação do terreno, posição na encosta, face de exposição da vertente) podem gerar grande heterogeneidade de micro-habitats (Moody e Meentemeyer 2001; Takyu et al. 2002) e têm sido consideradas como fatores principais no controle da diversidade de espécies de plantas (Enoki 2003). Além da radiação solar (Hayes et al. 2007) e dos regimes de perturbação (Hunter e Parker 1993; Nagamatsu e Miura 1997), a topografia é um dos fatores mais importantes que afetam as condições de água e nutrientes no solo (Brubaker et al. 1993; Gessler et al. 2000; Hazlett e Foster 2002; Roy e Singh 1994). Já está bem estabelecido que o comprimento do declive, o ângulo de inclinação e a configuração da encosta afetam a natureza e distribuição das propriedades do solo. Algumas das relações entre a inclinação do relevo e a formação do solo podem ser muito refinadas. Por exemplo, Jenny (1941) percebeu um tipo de solo diferente para cada grau de inclinação do terreno. Além disso, Ellis (1938) relatou que alterações relativamente pequenas no relevo afetavam a penetração de água no solo juntamente com a profundidade e natureza do solo. Essa variação no ambiente influencia a intensidade e a importância das interações bióticas (Greenlee e Callaway 1996; Goldberg e Novoplansky 1997), pois a competição e a facilitação podem ocorrer simultaneamente entre as espécies situadas num gradiente, em que o fluxo lateral de água pode trazer mais nutrientes para a parte inferior da encosta.

Assumindo que as interações entre espécies variam de acordo com gradientes ambientais e que o padrão de coocorrência de espécies de plantas em pequenas escalas espaciais muda com as condições ambientais (Collins e Klahr 1991), decorre que a distribuição espacial reflete tanto interações entre espécies no uso de recursos quanto seu sucesso reprodutivo (Condit et al. 2000 ; Gotzenberger et al. 2011). As interações podem produzir benefícios mútuos, como, por exemplo, a polinização (mutualismo: Bascompte e Jordano 2007). Podem produzir também benefícios unilaterais, sem prejuízo nem benefício para o outro organismo, como no caso de epífitas (comensalismo: Burns 2007; Silva et al. 2010). Mas, podem produzir benefícios unilaterais com prejuízo para o outro organismo, como na herbivoria (Prado e Lewinsohn 2004). Neste caso, uma das espécies age por autobenefício, e são geradas interações antagônicas, em que a capacidade individual de um organismo de usar recursos aumenta, ao passo que a do outro organismo que interage decresce como resultado da interação (Rico 2001).

Em florestas tropicais, a relação entre lianas e suas árvores-suporte (forófitos) representa uma importante interação antagônica, uma vez que lianas e forófitos competem entre si por luz e nutrientes (Kainer et al. 2006; Campanello et al. 2007). Lianas são trepadeiras lenhosas que germinam no solo, mas não podem sustentar a posição ereta e necessitam de apoio para atingir o dossel e obter luz adequada. Elas constituem um importante componente de florestas tropicais (Schnitzer e Bongers 2002). Lianas têm caules muito especializados chamados sarmentos que buscam ativamente um suporte por meio de caules volúveis, gavinhas, ganchos, ou raízes adventícias (Hegarty 1991; Putz e Holbrook 1991). Embora a interação entre o forófito e a liana seja antagônica, uma liana já estabelecida num forófito pode facilitar a escalada do mesmo forófito por outras lianas (Campanello et al. 2007). Assim, as interações entre lianas podem ser tanto de competição (quando competem por um mesmo forófito) ou de facilitação (quando a presença de uma liana no forófito facilita a escalada do forófito por outra liana).

A distribuição e abundância de lianas são afetadas por vários fatores ambientais (Schnitzer e Bongers 2002). Pesquisas de campo têm sugerido que a abundância de lianas está relacionada com a fertilidade do solo (Laurance et al. 2001), a água do solo (Ibarra-Manríquez e Martínez-Ramos 2002) e com a abertura do dossel (Babweteera et al. 2000). Os regimes de perturbação também parecem afetar a distribuição de lianas (Babweteera et al. 2000; Kouam'e et al. 2004). Distúrbios como a queda de árvores podem aumentar a abundância de lianas, em parte devido ao aumento da disponibilidade de luz (DeWalt et al. 2000; Hegarty e Caball'e 1991; Putz 1984). Como lianas geralmente são dependentes de árvores com tronco de pequeno diâmetro para apoio (e.g., Darwin 1867; Putz e Chai 1987), a densidade de lianas é freqüentemente maior em clareiras e na fase de construção do que em florestas maduras (e.g., Putz 1984b; Hegarty e Clifford 1991; Oliveira-Filho et al. 1997; Madeira et al. 2009). A arquitetura e outros caracteres das árvores também podem influenciar na ocorrência de lianas, posto que algumas árvores têm características favoráveis a lianas e outras têm características que evitam lianas (Putz 1984b; Campbell e Newbery 1993).

Neste trabalho estudamos uma encosta no interior de um fragmento da Floresta Estacional Semidecídua no município de Campinas, estado de São Paulo, no sudeste do Brasil. Nessa encosta ocorre uma série de solos, que vai desde um Latossolo profundo na parte inferior menos inclinada até um Neossolo Litólico raso na parte superior muito inclinada. Como o clima regional é tropical estacional, assumimos que a parte superior da encosta tenha condições mais estressantes que a parte inferior, na qual corre um rio. A hipótese do gradiente de estresse (Bertness e Callaway 1994; Greenlee e Callaway 1996; Brooker et al. 2008) prediz que o tipo de interação entre as espécies varia desde o predomínio de facilitação nas condições mais estressantes até o predomínio de competição nas condições mais favoráveis.

Aceitando a hipótese do gradiente de estresse, esperamos encontrar maior número de lianas por forófito na parte superior da encosta, em decorrência do predomínio da facilitação entre espécies de lianas nas condições mais estressantes do solo raso em terrenos mais inclinados. Por entretanto, esperamos encontrar menor número de lianas por forófito na parte inferior da encosta em decorrência do predomínio da competição entre espécies de lianas nas condições mais favoráveis do solo profundo em terrenos menos inclinados. O predomínio da competição é indicado por uma dispersão filogenética das espécies de lianas coocorrentes num mesmo forófito. Por contudo, se o padrão filogenético das espécies de lianas coocorrentes num mesmo forófito for agregado, a presença das lianas seria decorrente da filtragem ambiental.

Neste caso, esperamos encontrar uma correlação significativa da abundância das lianas com variáveis abióticas.

Como lianas e forófitos têm interações antagônicas (Sfair et al. 2010), esperamos encontrar algum grau de especialização em lianas e forófitos. Cerca de 69% de todos os sistemas antagonisticos têm sinal filogenético (Gómez et al. 2010), pois interações entre espécies podem ser moldadas pela bagagem filogenética recebida como herança de seus antepassados (Thompson 1994). Caso isse ocorra, esperamos que o grau de especialização de lianas e forófitos possa ser conservado filogeneticamente, ou seja, neste caso, as espécies de lianas proximamente aparentadas mostrariam um grau de especialização mais semelhante que espécies de lianas distantemente aparentadas, o mesmo sendo esperado para os forófitos.

Buscamos encontrar de coocorrência de lianas e forófitos numa comunidade florestal. Investigamos como a probabilidade de coocorrências entre lianas ou entre lianas e forófitos varia com a posição na encosta ou com a variação de variáveis do solo ao longo da encosta. Tentamos também entender qual força de interação (competição ou facilitação) prevalece ao longo dos gradientes ambientais que promovem o padrão de coocorrência de lianas e forófitos.

Organização da tese

O Capítulo 1 foca o padrão filogenético na interação entre lianas e forófitos. Mostramos que, em quatro áreas no sudeste brasileiro (um fragmento de cerradão, dois fragmentos da Floresta Estacional Semidecídua e um fragmento da Floresta Ombrófila Densa), os processos evolutivos que estruturam as interações liana-forófito foram diferentes em florestas e savanas. Encontramos um padrão oposto nas interações de espécies com grande originalidade filogenética. Nas florestas tropicais (ombrófila, estacional) as espécies mais originais coocorreram com maior freqüência com conjuntos muito distintos de espécies. No entanto, no cerradão as espécies mais originais coocorreram com os conjuntos mais comuns de espécies. Na floresta estacional, também observamos uma pequena tendência de lianas originais ocorrerem em um pequeno número de espécies de forófitos e de lianas aparentadas compartilharem espécies semelhantes de forófitos. Este sinal filogenético na interação de espécies de liana e forófito em florestas estacionais sugere que as condições peculiares do ambiente nessas florestas limitam até certo ponto a capacidade de divergência de espécies de lianas na utilização de espécies de forófitos.

O Capítulo 2 evidencia o padrão de interação filogenética entre lianas e lianas ao longo de gradientes ambientais. Considerando a influência relativa da filogenia e dos gradientes ambientais, esperamos que lianas coocorrentes num mesmo forófito seja mais relacionadas filogeneticamente do que o esperado por acaso e que respondesssem à variação de variáveis abióticas ao longo de um gradiente. Mostramos que espécies de lianas estreitamente relacionadas coocorreram com maior frequência nas mesmas espécies de forófitos. Concluímos que a limitação da dispersão e caracteres fenotípicos das árvores são os principais fatores associados ao padrão de coocorrência de lianas em microescala.

O Capítulo 3 avalia no padrão de coocorrência entre lianas e forófitos. Considerando o papel dos atributos das forófitos e gradientes ambientais a hipótese de que a frequencia do coocorrência de lianas e forófitos (1) ser devido a variação dos atributos entre forófito (2) responder a gradientes ambientais. Nós investigamos a freqüência de coocorrência das lianas-forófito com as medidas de diversidade filogenética usando como um proxy para a diversidade functional. Observou-se que lianas subiu nas árvores, independentemente de suas características funcionais. Argumentamos que processos estocásticos, como limitação de dispersão teve papel alto em padrão de coocorrência das liana-forófito em micro escala.

Esta tese possui quarto apêndices, **(1)** lista de mecanismos de escalada de lianas nas estudaram quatro fragmentos (um fragmento de cerradão, dois fragmentos da Floresta Estacional Semidecídua e um fragmento da Floresta Ombrófila Densa) no Sudeste do Brasil. **Apêndice 2** Abundância lianas e seus mecanismos de escalada no fragmento estudado (Floresta Estacional Semidecídua, no município de Campinas) no Sudeste do Brasil. **Apêndice 3** contém pares significativos de lianas coocorrendo na árvore hospedeira no fragmento estudado (Floresta Estacional Semidecídua, no município de Campinas) no Sudeste do Brasil. **Apêndice 4** contém a diversidade filogenética e distância média filogenética de espécie de forófito em cada parcela do fragmento estudado (Floresta Estacional Semidecídua, no município de Campinas) no Sudeste do Brasil.

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Chapter 1: Phylogenetic structure of liana-phorophyte interactions in tropical forests

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Abstract

We assessed the influence of phylogenetic relatedness of species on the structure of the liana-phorophyte interactions. Considering that closely related species tend to have similar niches, we expected (1) closely related lianas to co-occur in similar phorophyte species and (2) phylogenetically distinct lianas, with their unique set of features, to occur on a distinct set of phorophytes. We sampled four highly diverse forest sites in SE Brazil (a tropical rainforest, a savanna woodland and two tropical seasonal forests) and sought for (1) a phylogenetic signal in climbing traits of lianas; (2) a phylogenetic signal in the liana-phorophyte interaction by testing the correlation between (a) phylogenetic distances and similarity of interacting species and (b) the phylogenetic originality of species and number of their interactions; and (3) a positive relationship between phylogenetic originality and the distinctiveness of the interactions. We found phylogenetic signal in climbing mechanisms of liana species. In the seasonal forest, we also observed a slight tendency of closely related lianas to share similar phorophyte species and of original lianas to occur on a small number of phorophyte species. However, when we evaluated the interactions of species with high phylogenetic originality, we found an opposing pattern in forests and savanna. In forests, the phylogenetically original liana species co-occurred more frequently with very distinct assemblages of phorophytes. However, in the woodland savanna, the phylogenetically original liana species co-occurred conversely with more common sets of phorophyte species. We argued that environmental differences in forests and savannas mediated distinct evolutionary processes in structuring liana-phorophyte interactions.

Key Words: Atlantic forest, Climbing traits, Originality, Plant interactions, Quantile regression.

Introduction

Species interactions are a major component of the rich biological communities (Loreau et al. 2001; Fordyce 2006; Bascompte and Jordano 2007). Network of these interactions is non random when they occurs only within specialist subset of species (e.g. Compartmentalized, Dicks et al. 2002). The interactions may be nested when the generalist species tend to interact with each other and forming a dense core of interactions (Bascompte et al. 2003). Nestedness varies with different processes, such as sampling effects, spatial distribution and species phenotypes (Vázquez et al. 2009a; Vázquez et al. 2009b; Rezende et al. 2007). Because species interactions are the outcome of phenotype complementarity (Jordano 1987; Jordano et al. 2003; Stang et al. 2006). Phenotypic complementarity is the functional matching between the interacting species in such a way that they physically fit with one another (Rezende et al. 2007; Vázquez et al. 2009a). For example the proboscis length of pollinators fitness to the length of corolla make interactions among the pollinator and the flower of the plants (Vázquez et al. 2009a). Therefore, phenotype complementarity has a greater contribution to the nested pattern of interactions (Rezende et al. 2007). Nested interactions may also be antagonistic in which the ability of one individual increases with the decrease in the interacting ability of another individual (Graham et al., 2009).

An important antagonistic interaction occurs in tropical forests between lianas and host plants or phorophytes (Schnitzer and Bongers 2002; Sfair et al. 2010). Lianas are woody climbers that compete with phorophytes above ground for light and below ground for nutrients, decreasing phorophyte fecundity (Kainer et al. 2006) and growth rate (Campanello et al. 2007). Lianas depend on phorophytes for support to reach the canopy and get suitable light conditions to grow (Putz 1984a). Therefore, phorophyte species may be understood as a stable, important set of resources for liana species (Sfair and Martins 2011). In the liana-phorophyte interplay, species morphological features have a very important role (Hegarty 1991).

The species with infrequent and rare features in a community are thought to be more distinct than those species with common features (Vane-Wright et al. 1991; Pavoine et al. 2005). Thus, the average rarity of the species features in the community defines the species’ originality (sensu Pavoine et al. 2005). In other words, the whole contribution of a species to the feature richness of the community depends on its originality (Pavoine et al. 2005). The originality will be well distributed when most of the species contribute most of the features and when few species contribute less traits then the originality will be concentrated into few species (Pavoine et al. 2005). Trait frequency ranges from exclusive (present in only one species) to very common (present in most species, Pavoine et al. 2005). Mouillot et al. (2008) reported 52 % phenotypic original species in fish phylogeny and Pavoine et al. (2005) also described 50 % original species in carnivores phylogeny. However rare species in the community have larger impact on the community function than common species (Lyons et al 2005). In phylogenetic trees, the branch lengths represent the expected number of features that species have inherited from their common ancestor (May 1990; Nee and May 1997). Therefore, the branch length of a single species may be used as a proxy for the number of its features (Pavoine et al. 2005). This phylogenetic originality may play an important role in the structure of liana and phorophyte assemblages. Because species with distinct sets of features have particular niches with low functional overlap with the rest of the species (Mouillot et al., 2005). Therefore, original lianas should occur on distinct tree species.

Some tree species have adopted certain characteristics like exfoliating bark and palm architecture that avoid lianas and some trees have characteristics like rough and fissured barks favor lianas (Putz 1984a; Pinard and Putz 1992). The traits related to habitat use are generally conserved in lineages of species (Prinzing et al. 2001; Losos 2008) and evolutionary closely related species resemble in their phenotype traits (Bloomberg et al. 2003). Therefore, the interactions between lianas and phorophyte may be shaped by phylogenetic baggage that organisms inherit from their ancestors (Thompson 1994). In other word the interaction between lianas and phorophyte may be due to conserved traits in lianas and phorophyte species lineages. Phylogeny is an important tool for assessing the mutualistic interactions among plant and animals and facilitation network among plants and plants (Rezende et al. 2007; Verdú and Valient-Banuet 2011). The species may have retained their ancestral traits which are related to their specialized interactions (Gómez et al. 2010). Therefore, we expect that liana species may have conserved certain traits that are specialized for the phylogenetic closely related phorophyte species, and the phorophyte species may have conserved certain characteristics that favor phylogenetic closely related liana species.

We studied four different tropical forests in southeastern Brazil to investigate the phylogenetic pattern of liana-phorophyte interactions. Considering that closely related plant species tend to have similar niches (Prinzing et al. 2001; Losos 2008), closely related lianas are expected to co-occur on similar phorophyte species and lianas may have conserved strategy for using this support to reach the canopy.. Likewise, phylogenetically original lianas, with their unique set of features, are expected to occur on distinct phorophyte sets. Although there are some studies on co-occurrence of lianas and phorophytes (e.g. Sfair et al. 2010; Blick and Burns 2011), there is no study assessing the phylogenetic relationships between lianas and phorophytes. In this paper we tried to find the difference concerning phylogenetic structure of liana-phorophyte interaction among different tropical vegetation types, such as rainforest, seasonal forest and woodland Savana. Therefore, to seek these different structures in different vegetation formation we sought to answer the following questions: (1) Do liana species conserve climbing traits in their lineage? (2) Do phylogenetic closely related liana species climb on similar phorophyte species? (3) Do phylogenetic closely related phorophyte species assemble similar liana species? (4) Is the number of interactions related to the phylogenetic originality of liana and phorophyte? (5) Is the distinctiveness of phorophyte and liana sets related to the phylogenetic originality of lianas and phorophytes, respectively?

Methods

Study sites and sampling

We surveyed four tropical forest sites in São Paulo state, southeastern Brazil, in three different vegetation types: a rainforest, savanna woodland, and two seasonal forest sites. (1) The rainforest is located in the Serra do Mar State Park, which has 4,700 ha in the northern coast of the state, in Ubatuba municipality (23º21’S, 45º05’W). The regional climate is rainy tropical without dry season (Af; Koeppen 1948; Sfair et al. 2010). The mean annual temperature is 20.6 ºC, and the mean annual rainfall is 2,320 mm. (2) The savanna woodland has 321.71 ha in Bauru municipality (22º19’S, 48º59’W). The regional climate is rainy tropical with a short dry season (Cwa; Koeppen 1948; Sfair et al. 2010). The mean annual temperature is 22.6 ºC, and the mean annual rainfall is 1,331 mm. (3) One site of seasonal forest has 245 ha in Campinas municipality (22º50’S, 46º55’W) in the central region of the state (hereafter, central seasonal forest). The regional climate is rainy tropical with long dry winter (Cwa; Koeppen 1948; Cielo-Filho et al. 2007). The mean annual temperature is between 22 ºC and 24 ºC , and the mean annual rainfall is 1,372 mm. (4) The other site of seasonal forest has 435.73 ha in Paulo de Faria municipality (19º55’S, 49º31’W), in the northern boundary of the São Paulo state (hereafter, northern seasonal forest). The regional climate is also rainy tropical with long dry winter (Aw; Koeppen 1948; Sfair et al. 2010). The mean annual temperature is 24 ºC, and the mean annual rainfall is 1,245 mm.

In all sites, 100 plots of 10 m × 10 m each were settled down to sample liana and phorophyte species. Depending on the characteristics of each plant community, such as average height, diameter, and density of lianas and trees, different sampling designs were applied to include the greatest number of plant species. For example, the trees in the savanna woodland are generally thinner than those in the rainforest; therefore few phorophytes would be sampled if the rainforest sampling method was adopted in the savanna plots. Thus, in the rainforest site, we surveyed plants with trunk diameter at breast height DBH ≥ 7.5 cm and lianas with DBH ≥ 1 cm. In the woodland savanna site, we surveyed plants with DBH ≥ 0.3 cm and lianas with DSH (stem diameter at soil height) ≥ 0.1 cm (Weiser 2007). We sampled this smallest diameter because of the presence of few very young lianas and phorophytes in the site. In the central seasonal forest, we sampled trees with DBH ≥ 5 cm and lianas with DSH (stem diameter at soil height) ≥ 1 cm, whereas in the northern seasonal forest we sampled trees with DBH ≥ 3 cm and lianas with DBH ≥ 1 cm. We excluded the unidentified lianas and those tree species without lianas from our phylogenetic analysis.

We observed three climbing mechanisms of the lianas from published articles (Santos et al. 2009; Tibiriçá et al. 2006): (1) tendrillers, lianas with a specialized stem, leaf or petiole with a thread-like shape that is used for support and attachment; (2) twinners, lianas climbing by twisting and embracing around the support; and (3) scramblers, lianas with long slender stem that help them to grip neighboring stems. We computed the proportion of phorophyte species in relation to all tree species in each forest site, i.e. the net proportion of phorophytes (Campanello et al. 2007). We also described floristically the four sites by comparing the similarity of liana and phorophyte species among them by means of Jaccard index.

Phylogenetic data

Considering all the species sampled in the sites, we constructed two phylogenetic trees, one for all species of lianas and the other for all species of phorophytes (Fig1, 2. Phylogenetic tree of liana and phorophyte species families). We used the PHYLOMATIC software, a phylogenetic toolkit for the assembly of phylogenetic trees (Webb and Donoghue 2005). The phylogenetic trees were based on the information from the current PHYLOMATIC reference tree (R20080417; Megatree), which is based on information from several published phylogenies (Webb and Donoghue 2005). PHYLOMATIC takes as input a list of taxa with family and genus informations based on modern APG III (Angiosperm Phylogeny Group 2009) classification, matches the taxa to the most resolved position possible in any of a set of master trees in the database (the ‘Megatrees’), and returns the phylogeny (Webb and Donoghue 2005). Polytomies in family nodes (e.g. Bignoniaceae, Fabaceae, Apocynaceae) were resolved by evenly spacing the genus node above the family node following several published molecular phylogenies (e.g. Lohmann 2006; Simon et al. 2009; Livshultz et al. 2007). We used the BLADJ (branch length adjustment) averaging algorithm of the PHYLOCOM software package to assign the branch lengths of the phylogenetic trees (Webb et al. 2011). BLADJ fixes the root node at a specified age and sets the length of all other branches by evenly spacing the undated nodes among the dated nodes and between dated nodes and terminal nodes (Webb et al. 2011). The branch length was based on the minimum ages of nodes for orders, genera and families considering fossil data (Wikström et al. 2001).

Phylogenetic analysis

First, we analyzed whether there was phylogenetic signal in climbing mechanism (tendril, twining and scrambler) of liana species (Appendix 1), i.e., whether closely related lianas share the same climbing mechanism. Phylogenetic signal refers to the situation in which ecological similarity between species is related to phylogenetic relatedness; this is the expected outcome of Brownian motion divergence (Losos 2008). We tested whether there was a phylogenetic signal by comparing the minimum number of trait state changes across the tree to a null model (999 randomizations), in which the character states were randomized in the tips of the tree (Maddison and Slatkin 1991). If related species are similar to each other, the number of trait state changes will be lower than expected by chance (Maddison and Slatkin 1991). We did this analysis with the ‘phylo.signal.disc’ function in the R environment (R development core team 2011), which was developed *ad hoc* by E.L. Rezende and corresponds to the ‘fixed tree, character randomly reshuffled model’ proposed by Maddison and Slatkin (1991).

For each site we calculated the phylogenetic distance within all pairs of liana species to find whether more closely related liana species shared more similar phorophyte sets. We computed the phylogenetic distances between species in each liana pair with the PHYDIST function of the PHYLOCOM software package (Webb et al. 2011). To calculate the similarity (Jaccard index) between the sets of phorophyte species scaled by each liana species in the liana pair considered we used the ‘vegan’ package (Oksanen et al. 2011) in the R environment (R development core team 2011). To test for the significance of the relationship between liana phylogenetic distance and phorophyte similarity we used quantile regressions (Cade et al. 1999). If distantly related lianas occur on different phorophyte sets, a broad range of similarity values is expected between phorophyte sets. Therefore, the similarity between the phorophyte sets may have increased variance with decreasing liana relatedness, in such a way that a triangular relationship with a negative sloping hypotenuse may arise. In these cases, quantile regressions are recommended (Cade et al. 1999). To perform the quantile regression we considered data points in the 0.95 and 0.75 (upper 5 % and 25 %) quantiles, using the ‘quantreg package’ (Koenker 2008) in the R environment (R Development Core Team 2011). We assessed the significance of the slopes of the quantile regression with bootstrapped standard errors (Koenker 2008). Then, similarly we investigated whether closely related phorophytes shared more similar sets of liana species. To perform this investigation we adopted the same procedure described above.

Phylogenetic originality

To test whether original liana species occur on distinct phorophyte sets we first analyzed the relationship between the phylogenetic originality of each liana species and the number of interactions it had with phorophyte species. We followed the method proposed by Pavoine et al. (2005) to calculate the originality of lianas. By summing the branches necessary to link liana pairs in the phylogenetic tree, we calculated the distance within each species pair. Then, we measured the originality by the probability distribution that maximizes quadric entropy (QE-based index, Pavoine et al. 2005). Finally, we used quantile regressions with data points in the 0.95 and 0.75 quantiles to test the relationship between the originality and the number of interactions (Cade et al. 1999). Similarly, we computed the originality of phorophyte species according to Pavoine et al. (2005). We also tested the relationship between the originality and the number of interactions of phorophytes by means of quantile regressions with data points in the 0.95 and 0.75 quantiles (Cade et al. 1999). We did all these analyses separately for each site.

At last, we compared the phylogenetic originality of lianas to a measure of the distinctiveness of their phorophyte sets. This distinctiveness measure (hereafter, interacting originality) was based on the phylogenetic originality index (Pavoine et al. 2005) and was calculated from a similarity dendrogram of the phorophyte sets for liana species. In as much as the originality is a measure of phylogenetic distinctiveness of the species (Pavoine et al. 2005), the interacting originality is a measure of the distinctiveness of the interaction of each liana regarding the phorophyte sets of all liana species. Therefore, liana species with higher interacting originality occur in distinct phorophyte assemblages. Then, we constructed a dendrogram of the similarity among phorophyte sets for liana species using Jaccard Index and complete linkage clustering (Legendre and Legendre 1998). We then followed the method described in Pavoine et al. (2005) to calculate both phylogenetic and interacting originality of lianas. To test the relationship between the two originality indices we used quantile regression analyses with data points in the 0.95 and 0.75 quantiles (Cade et al. 1999). We also computed the interacting originality of phorophyte species and performed quantile regressions to test for the significance of the relationship between phylogenetic and interacting originality. We did all these analyses separately for each site. We calculated originality indices with ade4 package (Chessel et al. 2012) and quantile regression analyses with 'quantreg' package (Koenkor 2008) in the R environment (R development core team 2011).

Results

We sampled 46 liana and107 phorophyte species in the rainforest; 39 liana and 118 phorophyte species in the savanna woodland; 50 liana and 94 phorophyte species in the central seasonal forest; and 39 liana and 60 phorophyte species in the northern seasonal forest. Among these forests, the savanna woodland had the highest proportion of phorophyte species (84.3%), whereas the net proportion of phorophytes was 56.2%, 64.4% and 69% in the rainforest and central and northern seasonal forests respectively. In general, the similarity of liana and phorophyte species among sites was low (lower than 25 %), even between the seasonal forest sites (Tables 1 and 2).

We found a significant phylogenetic signal in climbing traits of liana species. The observed number of character state change was lower than expected by chance ($P < 0.001$). The random mean of trait state change was 42, whereas the observed number of character state change was 16.

When we tested for the relationship between phylogenetic distances and similarity of lianas and phorophytes, most results were not significant (Table 3 and 4). We observed a significant slope only in the central seasonal forest, and it was negative (Table 3). Therefore, in seasonal forests, closely related lianas may share similar phorophyte assemblages. Most results were also not significant when we assessed the phylogenetic originality and the number of interactions between lianas and phorophytes (Table 5 and 6). Again, in the central seasonal forest, we observed a significant negative relationship between originality of phorophytes and number of interactions. Thus, species with higher originality interact with a lower number of tree species in seasonal forests (Table 6).

Nevertheless, more consistent results were found in the comparison between phylogenetic originality and interacting originality of lianas and phorophytes (Table 7 and 8). We found a positive relationship for lianas in the rain and central seasonal forests, but a negative relationship in the savanna woodland (Table 7). We also found this opposing pattern when we evaluated the phorophytes: we observed a positive relationship for phorophytes in the central seasonal forest, but a negative relationship in the savanna (Table 8). Thus, in rain and seasonal forests, lianas and phorophytes with greater phylogenetic originality tended to interact with very distinct species sets, whereas in the savanna lianas and phorophytes with greater phylogenetic originality tended to interact with common species sets.

Discussion

In general, our results support the conclusion that evolutionary processes structuring the liana-phorophyte interactions are different in forests and savannas, in which we found an opposing pattern in the interactions of species with high phylogenetic originality. In the rain and seasonal forests, the original species co-occurred more frequently with very distinct species sets. However, in the savanna the original species co-occurred with more common species sets. We argue that the environmental conditions in savannas might have selected tree species with common functional traits, such as bark thickness, that favor the occurrence of original liana species. In forests, those traits are rare and associated with very original phorophytes. In the seasonal forests, we also observed a slight tendency of original lianas to occur on a small number of phorophyte species and of closely related lianas to share similar phorophyte species. This phylogenetic signal in the liana-phorophyte interaction of seasonal forest species suggests that peculiar environmental conditions in seasonal forests limit to some extent the divergence of ability of liana species to use phorophyte species.

Net proportion of phorophytes and species similarity

We found a high net proportion of phorophytes in all forests, reinforcing that lianas are a key component in tropical forest biodiversity (Schnitzer and Bongers 2002). However, this proportion was higher in the savanna and seasonal forests. In general, the abundance of lianas in a forest is related negatively with precipitation (Richard et al. 2000; Graham et al. 2003). This is likely due to the light availability during the dry season, which favors the development of liana species (Richard et al. 2000; Graham et al. 2003) due to their higher efficiency to fix carbon and use water, even under low soil moisture availability (Cai et al. 2009). Tropical savannas and seasonal forests undergo annually a long period of drought, which may last 7 months in some areas (Oliveira-Filho and Fontes 2000; Gottsberger and Silberbauer-Gottsberger 2006). In rainforests, on the other hand, the light is limited by the canopies of tall trees and frequent cloud shadows (Schnitzer 2005). Thus, the higher percentage of trees with lianas in the savanna and seasonal forests may be a result of the longer dry season.

Although the richness of liana species is not high in savannas (Gottsberger and Silberbauer-Gottsberger 2006), our results showed that they are abundant and occur in most tree individuals. Some environmental conditions in savannas, such as nutrient-poor soils and frequent fires, have selected trees with thick and deep-fissured bark (Gottsberger and Silberbauer-Gottsberger 2006). Such a corky-fissured bark is a common characteristic of Brazilian savanna trees (Gottsberger and Silberbauer-Gottsberger 2006) and is expected to facilitate the climbing of liana species, mainly those with tendrils (Putz 1984a; Pinard and Putz 1992). In addition, savanna trees are smaller than rainforest tress and have slenderer trunks and branches (Hoffmann et al. 2003; Paine et al. 2010). For example, the canopies of savanna woodland trees rarely surpass 15 m in height (Salis et al. 2006), whereas the canopies of rain and seasonal forest trees may reach 30 m or more in height (Erik 1997). The occurrence of lianas, mainly those with tendrils, is greater in phorophytes with slenderer trunks and branches (Putz 1984a, Pinard and Putz 1992). Thus, the highest net proportion of phorophyte species in the savanna woodland may be associated with the commonness of some important characteristics among tree species, which in turn favor the occurrence of lianas.

We found a low floristic similarity among the sites, even between the seasonal forests. This result reinforces that geographic distance and environmental heterogeneity are important factors determining the composition of tropical forests (Oliveira-Filho and Fontes 2000). It is well documented that the spatial distribution of species is associated with the spatial variation of environmental factors, such as precipitation, climate, temperature and soil conditions (Oliveira-Filho and Fontes 2000; Oliveira-Filho et al. 2001). Likewise, liana species composition also varies with the geographic location, altitude and disturbance history (De Walt et al. 2000).

Phylogenetic signal

Our results for the phylogenetic signal in climbing mechanisms of lianas support the conclusion that there might have been a weak selective pressure for trait divergence among clades during their evolution in tropical forests. In general, lianas with similar climbing mechanism have the tendency of climbing on phorophyte species with similar functional characteristics (Putz 1984b). Twinning lianas, for instance, are highly adapted to climb on larger supports, since they curl around the tree (Putz 1984b; Peñalosa 1982). Likewise, lianas with specialized adhesive structures (aerial roots, adhesive discs) can climb on hosts that are capable of supporting the liana weight (Putz 1984b; Carter and Teramura 1988). Tendril lianas are restricted to phorophytes with slenderer trunk and branches (Putz 1984b). Thus, plants with different climbing mechanisms may not compete with each other for the same phorophyte species sets, and if it would be the case, then the selective pressures for trait divergence may have not been strong enough among clades to promote a great divergence in climbing mechanisms.

In the seasonal forests, we observed that closely related species tended to share similar phorophyte species and that the slope of the phylogenetic originality with the number of interactions was negative. This phylogenetic signal in the liana-phorophyte interaction suggests that the divergence of liana ability to use different phorophyte species is somewhat limited in seasonal forest species. Differently from rainforests, seasonal forests have peculiar characteristics following the seasonal climate, such as greater gap formation, lower soil water availability and higher light availability, which favor the establishment of lianas (Schnitzer et al. 2000; Nesheim and Økland 2007; Nogueira et al. 2010). This wide range of abiotic favorable conditions is a selective pressure that could be stronger for divergence of traits associated with establishment and use of abiotic resources rather than for traits associated with liana ability to use different phorophyte species, such as climbing mechanisms.

Phylogenetic and interacting originality

In forests, the liana species with greater phylogenetic originality occurred more frequently in distinct phorophyte sets. In contrast, in the savanna woodland, the liana species with greater phylogenetic originality occurred more frequently in common phorophyte sets. Species interactions are associated with phenotype complementarity between interacting species (Thompson 2005), in such a way that interaction and specificity between liana and phorophyte species are the result of phenotype matching between lianas and trees (Burns and Dowson 2005). For instance, in tropical forests, climber specificity is associated with tree characteristics, such as bark stability, water holding capacity and surface texture of trees (Benzing 1995). Environmental conditions in savannas, such as frequent fire, nutrient poor soils and strong seasonal drought, have selected tree species with very similar functional characteristics, such as twisted trees with corky-fissured bark and slow growth (Hoffmann et al. 2003; Gottsberger and Silberbauer-Gottsberger 2006). These functional characteristics are very common in savanna tree species, but they are rare in forest tree species (Hoffmann et al. 2003; Paine et al. 2010). Most forest tree species have smooth, peeling bark and poorly branched, monopodial trunk, which avoid liana species (Putz 1984b; Schnitzer and Carson 2001). Since twisted branch ramification, corky-fissured bark and slow growth favor the occurrence of lianas (Pinard and Putz 1992; Campanello et al. 2007), the opposing pattern of the interactions of lianas with high phylogenetic originality in the forests and savanna may thus be due to the commonness of these functional traits in savannas and their rarity in forests.

We also observed an opposing pattern in the interactions of phorophytes with high phylogenetic originality in the savanna woodland and forests. The phylogenetic conservatism of climbing mechanisms may explain partially why phorophytes with greater phylogenetic originality hosted distinct liana sets in forest, since closely related lianas that have the same climbing strategy are expected to share similar phorophyte species (Prinzing et al. 2001; Lossos 2008). In the savanna woodland, phorophytes with greater phylogenetic originality hosted conversely common liana sets. Considering that phorophyte species are a set of resources for lianas (Ollerton et al. 2007; Sfair and Martins 2011), this result points out that most liana species converged similar strategies to use phorophytes in the savanna woodland. However, it is hard to explain these opposing patterns relative to phorophyte originality without accounting for liana functional traits other than climbing mechanisms. Further studies should consider other functional aspects related to the liana ability of using phorophyte to test this hypothesis.

Acknowledgments

We are indebted to The Academy of Science for the Developing World (TWAS) and National Research Council (CNPq) for the scholarship granted to the first author and FAPESP for the scholarship granted to the second author.

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Table 1. Values of the Jaccard`s similarity index for liana species among sampled forest sites in southeastern Brazil.

Sampled sites	Rainforest	Savanna woodland	Central seasonal forest	Northern seasonal forest
Rainforest	-	0	0.11	0.08
Savanna woodland	0	-	0.07	0.13
Central seasonal forest	0.11	0.07	-	0.25
Northern seasonal forest	0.08	0.13	0.25	-

Table 2. Values of Jaccard`s similarity index for phorophyte species among sampled forest sites in southeastern Brazil.

Sampled sites	Rainforest	Savanna woodland	Central seasonal forest	Northern seasonal forest
Rainforest	-	0.03	0.11	0.03
Savanna woodland	0.03	-	0.09	0.08
Central seasonal forest	0.11	0.09	-	0.20
Northern seasonal forest	0.03	0.08	0.20	-

Table 3. Quantile regression between liana phylogenetic distances and phorophyte similarity in sampled forest sites, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) is given. The *P* values for bootstrapped standard errors are also given. Significant values at α = 0.05 are presented in bold.

Sampled sites	0.95 slope	*P* values	0.75 slope	*P* values
Rainforest	0	1	0	1
Savanna woodland	0	0.94	0.0002	0.06
Central seasonal forest	-0.0003	**0.02**	-0.0001	0.6
Northern seasonal forest	0.0001	0.59	0.0001	0.47

Table 4. Quantile regression between phorophyte phylogenetic distances and liana similarity in sampled forest sites, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) is given. The *P* values for bootstrapped standard errors are given.

Sampled sites	0.95 slope	*P* values	0.75 slope	*P* values
Rainforest	0	1	0	1
Savanna woodland	0	1	0	1
Central seasonal forest	0	1	0	1
Northern seasonal forest	-0.0003	0.64	0	1

Table 5. Quantile regression between phylogenetic originality of lianas and number of interactions in sampled forest sites, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) is given. The *P* values for bootstrapped standard errors are also given.

Sampled sites	0.95 slope	*P* values	0.75 slope	*P* values
Rainforest	0.004	0.43	-0.001	0.47
Savanna woodland	0	1	0	1
Central seasonal forest	-0.001	0.32	-0.0004	0.27
Northern seasonal forest	-0.002	0.13	-0.00004	0.94

Table 6. Quantile regression between phorophyte originality and number of interactions in sampled forest sites, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) is given. The *P* values for bootstrapped standard errors are also given. Significant values at α = 0.05 are presented in bold.

Sampled sites	0.95 slope	*P* values	0.75 slope	*P* values
Rainforest	0.005	0.09	-0.001	0.9
Savanna woodland	0.0001	0.53	0.0003	0.20
Central seasonal forest	-0.001	**0.02**	-0.0003	**0.01**
Northern seasonal forest	0.0001	0.96	0	1

Table 7. Quantile regression between phylogenetic originality and interacting originality of lianas in sampled in forest sites, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) is given. Significant *P* values (α = 0.05) for bootstrapped standard errors given in bold.

Sampled sites	0.95 slope	*P* values	0.75 slope	*P* values
Rainforest	2.72	**0.01**	-0.02	0.97
Savanna woodland	-0.57	**0.01**	-0.16	**0.01**
Central seasonal forest	3.67	**0.01**	1.09	**0.04**
Northern seasonal forest	-0.32	0.17	-0.05	0.65

Table 8. Quantile regression between phylogenetic originality and interacting originality of phorophytes in sampled forest sites, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) is given. Significant *P* values (α = 0.05) for bootstrapped standard errors given in bold face.

Sampled sites	0.95 slope	*P* values	0.75 slope	*P* values
Rainforest	-0.1	1.00	-0.06	0.65
Savanna woodland	-0.29	**0.01**	0.05	0.63
Central seasonal forest	-0.01	0.99	0.39	**0.01**
Northern seasonal forest	-0.66	0.29	0.002	0.94

Figure 1. Phylogenetic tree assembled for the Liana families in sampled forest sites in southeastern Brazil.

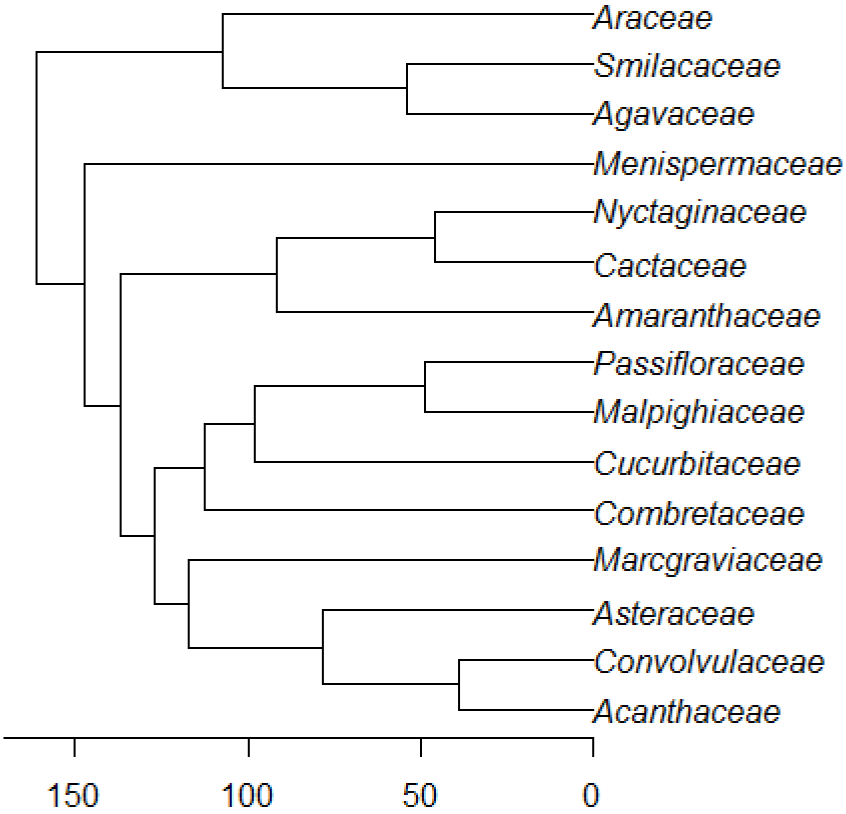
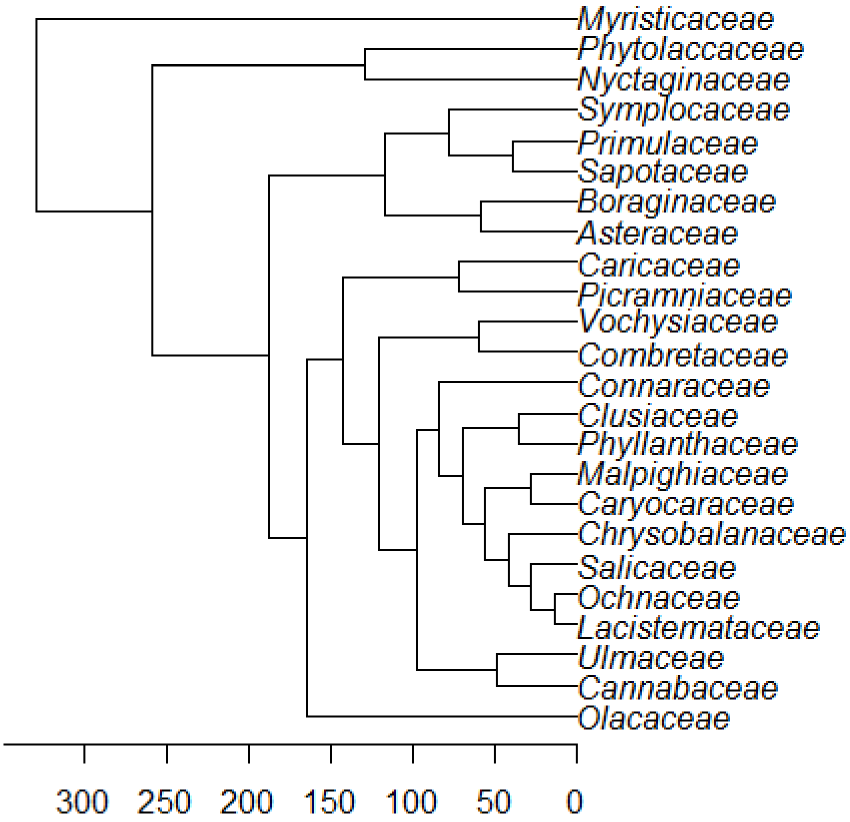


Figure 2. Phylogenetic tree constructed for the Phorophyte families in sampled forest sites in southeastern Brazil.



Chapter 2: Phylogenetic interactions among lianas in a southeastern Brazilian semideciduous tropical forest

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Abstract

Biotic interactions play an important role in structuring community spatial pattern, which is also influenced by species resource use and reproductive success. Since plants are sessile organisms, biotic interactions may be reflected in the pattern of species co-occurrence. The pattern of species co-occurrence may change with the predominance of positive or negative interactions among the species along evolutionary history and environmental gradients. Considering the relative influence of phylogeny and environmental gradients, we expected lianas co-occurring on the same host tree (phorophyte) to (1) be phylogenetically more related than expected by chance; and (2) respond to abiotic variation along a gradient. We sampled 1 ha with 100 plots of 10 x 10 m each in a tropical semideciduous forest in SE Brazil. We investigated the presence of phylogenetic signal in climbing traits of lianas co-occurring on the same phorophyte and tested for the co-occurrence of liana-phorophyte pairs across the space and environmental gradients. Closely related liana species co-occurred more frequently than expected by chance on the same phorophyte species. Climbing traits of liana species showed a significant phylogenetic signal. Space had a high influence on the co-occurrence of lianas. We assume that stochastic processes, such as dispersal limitation and phorophyte traits, are the main drivers of the spatial pattern of lianas co-occurrence on microscale.

Key Words: Seasonal forest, Climbing traits, Phylogenetic signal, Facilitation, Quantile regression.

Introduction

Woody climbers or lianas represent generally 15-45% of all species of a tropical forest, summing up 40% of the tropical forest leaf area and leaf productivity (Schnitzer 2005). They compete with trees above ground for light and below ground for nutrients, decreasing trees fecundity (Kainer et al. 2006) and growth rate (Campanello et al. 2007). Lianas use well developed specialized shoots to find a means of support, i.e., shoots with twining stems, tendrils, hooks, or adventitious roots, to reach the forest canopy and get suitable light conditions to grow (Putz 1984a; De Walt et al. 2000). Therefore, host tree (phorophyte) species may be assumed as a stable, important set of resources for liana species (Ollerton et al. 2007).

Tropical forests are nowadays attracting much attention of the ecologists for their heterogeneous habitat (Wright 2002; Leigh et al. 2004; Feeley et al. 2007). Heterogeneous habitat, such as those found in topographic gradients, affect local biological processes and support diverse communities (Collins and Klahr 1991; Enoki 2003). Some species compete for resources and tend to predominate and grow better than other species (Sammul et al. 2000), while some species may facilitate the establishment of other ones (Callaway 1995, Bruno et al. 2003). Facilitation is frequently found between seedlings of one species and adults of other species and may lead to species aggregation in space (Callaway and Walker 1997). Competition and facilitation are more apparent in small neighborhoods because plant species interact directly with nearest individuals (Stoll and Weiner 2000, Hubbell et al. 2001). Such ecological interactions may leave a signature on the community spatial pattern (Russo et al. 2005, Silva et al. 2010), because the species spatial pattern is the result of their use of resources and reproductive success (Condit et al. 2000; Gotzenberger et al. 2011). As competitively inferior species are unable to persist in the neighbourhood of competitively superior ones, a lower number of co-occurring species than expected at random may arise from competition. On the contrary, a higher number of co-occurring species may arise from facilitation (Lieberman and Lieberman 2007, Perry et al. 2009). Therefore, species spatial pattern may offer important clues of the predominant forces structuring community assembly (Hubbell et al. 2001; Hou et al. 2004, Silva et al. 2010).

Positive interactions have been repeatedly reported to be more important than interspecific competition for community assembly in systems subjected to environmental constraints (Callaway 1995, Bruno et al. 2003). Therefore, the predominance of facilitation or competition and the resulting pattern of species co-occurrence should change along an environmental gradient (Silva et al. 2010). If so, we expect that the pattern of co-occurrence of lianas on the same phorophyte may also vary along a topographic gradient. In this case, liana co-occurrence is predicted to be more frequent in tighter environments, such as sites with great slope and shallow, poor soils. Additionally, species co-occurrence patterns may be also influenced by species evolutionary history. Phylogenetically related plant species commonly present a high degree of evolutionary stasis (Qian & Ricklefs 2004) and trait conservatism related to environmental tolerances (i.e. light, soil moisture and pH; Prinzing et al. 2001). If so, closely related plant species are expected to have similar habitat uses (i.e. phylogenetic niche conservatism: Wiens and Graham, 2005; Losos 2008). As a result, we expect that closely related liana species may co-occur more frequently than expected at random on the same phorophyte. However, facilitation has been predominantly found among phylogenetically distant plant species (Valiente-Banuet et al. 2006) because competitive exclusion tends to be stronger among closely related species sharing a large number of traits (Webb et al. 2002). Therefore, the pattern of co-occurrence of related lianas on the same phorophyte may also offer clues of the role of evolutionary history of species in liana-phorophyte interaction (Webb et al. 2002).

In this study, we assessed the relative influence of phylogeny and environmental filters on the co-occurrence pattern of lianas on the same phorophyte. We tested (1) whether the co-occurring lianas on the same phorophyte species are more phylogenetically related than expected by chance and (2) whether they are associated with abiotic factors (i.e. soil chemical variables like organic matter, Al, P, Ca, Mg, K, pH, cation exchange capacity of soil, soil depth, slope and canopy openness). In summary, we tried to answer the following questions: (1) Do all liana species have the same chance to co-occur with other on a phorophyte? (2) How is the phylogenetic co-occurrence of lianas expected by chance on the phorophyte? (3) What is the role of abiotic variables in structuring the co-occurrence of lianas species? (4) How much variation of the frequency of co-occurrences of lianas is explained by the abiotic variables?

Methods

Study site and sampling

We surveyed a fragment of the Tropical Semideciduous Seasonal Forest of about 245 ha in Campinas municipality (22º50'S, 46º55'W), São Paulo state, southeastern Brazil. In the fragment some 20-50% of the canopy trees shed their leaves in the dry season (Veloso et al. 1991) of the regional climate, which is tropical with dry winter (Cwa; Koeppen 1948; Cielo-Filho et al. 2007), with a mean annual temperature of 24 ºC, and a mean annual rainfall of 1,409 mm. The rainy season usually longs from October to March, in which the average precipitation reaches

1,141.5 mm and the average temperature is 24 °C; the dry season usually occurs from April to September, when the average precipitation is 283 mm and the average temperature is 20 °C (CEPAGRI 2011, data for the period of june 1988 to October 2008). The altitude of the site varies between 630 to 760 m a.s.l., and the predominant soil is Acrisol (FAO nomenclature).

In the southern portion of the fragment, 100 plots of 10 m × 10 m each were randomly placed using the irrestricted randomization procedure (Cielo-Filho et al. 2007). In each plot we sampled lianas with DSH (stem diameter at soil height) $\geq$ 1 cm following Gerwing et al. (2006) and Schnitzer et al. (2008) protocols. In the center of each plot we extracted 500 g from the superficial soil, which was sent to Campinas Agronomic Institute to determine organic matter, Al, P, Ca, Mg, K, pH, and cation exchange capacity, potential acidity (H+Al), extractable bases (SB), base saturation (V) and soil texture (silt, sand and clay). We also estimated the percentage of canopy openness with a spherical convex densiometer at the breast height (Lemmon 1956). Using two plot sides as a coordinate system, we drew three random points at which we used a meter-scaled metal rod to measure soil depth and a clinometer to measure slope angle in degrees and used their average for data analysis.

Phylogenetic data

We constructed a phylogenetic tree for all sampled lianas with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic tree (Webb and Donoghue 2005) (Figure 1). The phylogenetic tree was based on the information from the current Phylomatic tree (R20080417), which is based on information from several published phylogenies (Webb and Donoghue 2005). Polytomies in family nodes (e.g. Bignoniaceae, Fabaceae, Apocynaceae) were resolved by spacing evenly the genus node above the family node following several published molecular phylogenies (e.g. Lohmann 2006; Simon et al. 2009; Livshultz et al. 2007). We assigned the branch length of the phylogenetic tree using BLADJ (branch length adjustment) averaging algorithm of the Phylocom software package (Webb et al. 2011). BLADJ sets the length of all branches by spacing the undated nodes evenly between the dated nodes and between dated nodes and terminal nodes and fixes the root node at specified age (Webb et al. 2011). The branch lengths were based on the minimum ages of nodes for higher orders, genera and families from fossils data (Wikström et al. 2001).

Data analyses

Do all liana species have the same chance to co-occur with other on a phorophyte? To answer this question, we generated a distribution of expected frequencies for each liana-liana potential pair of species. This approach was adopted because the occurrence of two liana species on the same phorophyte was observed in the field with the highest frequency. We followed Lieberman and Lieberman (2007) to generate a null model, in which combinations of pairs of species reflect a random sampling of the community: (1) we computed the observed number of liana-liana pairs; (2) we randomized the occurrence of each liana species in the pair and recorded the number of random pairs; (3) we repeated these steps 999 times and estimated a random mean and standard deviation (SD) for the null species assemblages; and (4) we compared the observed number of pairs to those expected by chance and computed *P* values. We ran the analysis in the R environment (R Development Core Team 2011) with the function available at http://www.cerradoecology.com /codes.html.

Is the co-occurrence of liana on the same phorophyte due to facilitation or niche conservatism among lianas? To answer this question we searched for a relationship between liana phylogenetic distances and the frequency with which pairs of lianas co-occurred on the same phorophyte. A negative relationship (i.e. increasing co-occurrence associated with decreasing phylogenetic distances) would indicate that closely related lianas occurred on the same phorophytes, whereas a positive relationship would indicate competition among lianas for the phorophyte through excluding closely related specie. We did quantile regressions (Cade et al. 1999) with those species pairs which co-occurred more often than expected by chance because it would give strong imprints of the interactions. If competition among lianas is greater between closely related species than between distantly related ones, a broad range of phylogenetic distances is expected to emerge between those liana species that co-occur on the same phorophytes more often than expected by chance. Therefore, the phylogenetic distance between lianas in each pair may have decreased variance with increasing number of co-occurrences; in such a way that a triangular relationship with a negatively sloping hypotenuse may arise. In these cases, quantile regressions are recommended (Cade et al. 1999). We used ‘quantreg’ package (Koenker 2008) for R environment (R Development Core Team 2011) to examine the nature of this upper bound with quantile regressions with data points in the 0.95 and 0.75 (upper 5 % and 25 %). We used bootstrapped standard errors (Koenker 2008) to assess the significance of the slopes of quantile regressions.

To understand the habitat use by lianas, we analyzed whether there was phylogenetic signal in their climbing mechanism, i.e. the closely related lianas share the same climbing mechanism (Losos 2008). We obtained the climbing mechanism of each lianas species from published articles (Santos et al. 2009; Tibiriçá et al. 2006), i.e. (1) tendril, a specialized stem, leaf or petiole with a thread-like structure that is used by lianas for support and attachment; (2) twining, the characteristic of the lianas twisting, curling and embracing around support and (3) scrambler, the lianas with long slender stem that help them to grip and hold the neighbouring stem. To analyze the presence of a phylogenetic signal we compared the minimum number of trait state changes across the phylogenetic tree to a null model (999 randomizations), in which the character states were randomized in the tips of the trees (Maddison and Slatkin 1991). The number of trait state changes is lower than expected by random will denote that closely related species have similar climbing mechanisms (Maddison and Slatkin 1991). Each climbing mechanism was considered as a state of the same character. We performed the analysis with'phylo.signal.disc' function in R environment (R development core team 2011) that was developed *ad hoc* by E.L. Rezende and corresponds to the 'fixed tree, character randomly reshuffled model' proposed by Maddison and Slatkin (1991).

In addition to evaluate the role of liana species abundance and the pairing frequency, we also did correlation test between the number of pairs a liana species establish and the abundance of liana species. We evaluated the significance of the test with Pearson coefficient.

Selection of environmental variables

What is the role of abiotic variables in structuring the co-occurrence of lianas species? To answer this question we first standardized the range of all abiotic variables (mean = 0, standard deviation = 1) to put different data units into the same scale. We used an equilibrium circle technique of Principal Components Analysis (PCA) for the selection of variables. We selected soil pH, potassium (K), extractable bases (SB), potential acidity (H+Al), silt and coarse sand that have vectors head outside the equilibrium circle (Figure 2), which showed significant contribution to the ordination (Legendre & Legendre 1998). We tested for multicollinearity with the variance inflation factor (VIF), which measures the proportion by which the variance of a regression coefficient is inflated in the presence of other explanatory variables (Borcard et al. 2011). Values of VIF greater than 10 indicate collinearity between variables (Borcard et al. 2011). We excluded soil pH which showed VIF values greater than 10 (Borcard et al. 2011).

Then, we tested if potassium (K), extractable bases (SB), potential acidity (H+Al), silt and coarse sand were spatially autocorrelated. The spatial autocorrelation of independent variables violates the assumption of independent data (Legendre 1993). Therefore, we calculated Moran's I coefficient for a series of eleven distance classes, being 293 m the limit class. Moran's I coefficient varies between -1 and +1, from which positive values indicate positive autocorrelation and spatial aggregation, whereas negative values indicate negative autocorrelation (Legendre & Legendre 1998). Negative autocorrelation may indicate either avoidance at short distance, i.e. variables are regularly spaced, or spatial gradient at long distance, if there is also a positive autocorrelation at short distance (Legendre & Legendre 1998). We estimated the significance of Moran's I coefficients with 999 randomizations.

Moreover, we also tested for spatial autocorrelation in the residuals of the regression of the frequency of liana pairs on the same phorophytes against abiotic variables since it may inflate Type 1 error. The presence of spatial autocorrelation in residuals indicates generally that there is a variable that was not sampled (varying in space) which is causing the autocorrelation (Diniz-Filho et al. 2003). In case of autocorrelation in residuals, the standard errors of the regression coefficients are usually underestimated (Diniz-Filho & Bini 2005). We also tested for spatial autocorrelation in residuals with Moran's I coefficient with 999 randomizations (Legendre & Legendre 1998).

Since we found spatial autocorrelation in some environmental variables, frequency of liana co-occurrences and residuals (Table 1 and 2), we incorporated the spatial structure of the data, in order to better estimate and test the minimum adequate model parameters. We used an approach that has been called eigenvector-based spatial filtering or the principal coordinate of neighbor matrices (PCNM), which extracts eigenvectors from a connectivity matrix expressing the spatial relationship among plots (Borcard & Legendre 2002, Diniz-Filho & Bini 2005). These eigenvectors (i.e. the spatial filters) express the relationships among plots at decreasing spatial scales, so that the first eigenvectors (those related to large eigenvalues) tend to describe broad-scale spatial patterns, whereas eigenvectors with small eigenvalues tend to describe local patterns (the spatial structure of the regression; Borcard & Legendre 2002, Diniz-Filho & Bini 2005). They were therefore used as additional predictors of the response variables in the MAM, in an attempt to reduce the autocorrelation in the residuals (Diniz-Filho & Bini 2005). Then, we selected five filters (i.e. the smallest number of eigenvectors) that ensured a minimum desirable level of spatial autocorrelation in the residuals. The selection of spatial filters did not reduce the level of autocorrelation in the last class of the residuals; therefore we did not use minimum adequate model (MAM : Diniz-Filho & Bini 2005) with ordinary least squares (OLS) sorted by Akaike information criterion (AIC; Diniz-Filho et al. 2008) to test whether those selected abiotic variables and spatial filters predict the co-occurrence of liana pairs.

Finally, to answer the last question, how much variation of the frequency of co-occurrences of lianas is explained by the abiotic variables? We needed to follow the procedures described by Legendre & Legendre (1998) because it quantifies the amount of variation related to the different sets of environmental or spatial correlates and provide observational proof on the relative importance of the different processes that determine community structure (Cottenie 2005). First we needed to perform multiple regressions of abiotic variables and spatial filters against the number of co-occurrences. The resulting value of R^2 would determine the portion of variation [a + b + c] related to abiotic variables [a], to spatial filters [c] selected by MAMs, and to the portion determined by the both variables [b]. Then, the portion [b] could be obtained by the equation [b] = [a + b] + [b + c] – [a + b + c] (Legendre & Legendre 1998). However we did not use MAM because the residuals could not be stabilized.

Results

We found 69 species of lianas of 24 different families in our sampling of the Tropical Seasonal Semideciduous Forest. Bignoniaceae was the richest family with 24 species, followed by Apocynaceae and Sapindaceae with 8 species each (Appendix 2). We observed 717 pairs of liana species co-occurring on phophytes, of which 249 pairs (34 % of the total pairs) had observed frequency greater than expected by chance ($P < 0.001$: hereafter positive co-occurrence) and 60 pairs (8 % of the total pairs) had observed frequency lower than expected by chance ($P < 0.001$: hereafter negative co-occurrence). The remaining 408 (58 % of the total pairs) did not have significance (Appendix 3).

We found significant negative slope at 0.95 and 0.75 quantiles, when we tested the relationship between phylogenetic distances and the number of positive co-occurring liana pairs (Table 3). The negative slope of the relationship (Figure. 3, 4) indicates that closely related liana species tend to co-occur more frequently on the same phorophytes. We also tested the relationship between the number of negative co-occurring pairs and their phylogentic distance, but we did not find any significant relationship (Table 4). We found a significant phylogenetic signal in climbing traits of liana species. The observed number of character state change was lower than expected by chance ($P < 0.001$). The random mean of trait state change was 16, whereas the observed number of character state change was 5. We observed significant correlation between frequency of pairs a liana species establish and the abundance of liana species. The Pearson co-effeicient was positive 0.97 at $P < 0.001$ (Figure 5). We could not construct a minimum adequate model, due to spatial autocorrelation in the residuals, even when spatial filters were applied. This indicated one or more non-collected variables, such as dispersal limitation, phorophyte traits, and the history of the fragment, which could have a much more important role in the co-occurrence of lianas than the variables that we analyzed.

Discussion

We found a strong phylogenetic signal in the co-occurrence pattern of lianas. Closely related liana pairs co-occurred more frequently on the same phorophyte species in the studied forest. It is probable that the occupation of the same phorophyte species by phylogenetically related lianas is an outcome of their sharing of similar climbing mechanisms, which would allow them to climb on phorohytes with similar traits. Since we could not adjust a multiple correlation model, our result suggested that stochastic processes, such as dispersal limitation, phorophyte traits, population dynamics, fragment history, might explain most of the spatial distribution of liana pairs in seasonal forests. Here, we argue that phorophyte traits and stochastic processes determining their spatial distribution may predominantly structure the co-occurrence of lianas.

Positive vs. negative co-occurrence of lianas

We observed positive and negative co-occurrence of lianas. Positive co-occurrence of lianas may be due to facilitation among liana species for a specific phorophyte. In general, slender trees are favourable sites for the establishment of tendril-bearing lianas, and trees with large-diameter trunk are favourable for twining lianas (Putz 1984a; De Walt et al. 2000). Therefore, a set of lianas with similar climbing mechanism tend to occur on phorophytes with similar traits, and once a liana has established on a phorophyte, the access of other liana species with similar climbing mechanism tends to be facilitated. Facilitation increases the observed frequency of liana co-occurrence higher than expected by chance and is usual in forest and shrublands (Lieberman and Lieberman 2007; Perry et al. 2009; Silva et al. 2010).

The negative co-occurrence may be due to richness of liana species. Increase in species richness is related to decrease in population density of individual species which reduce the probability of species combination as expected by chance (Lieberman and Lieberman 2007). It is because the number of potential *ij* species combination becomes so large with respect to the number of trees in the stand (Lieberman and Lieberman 2007). If there are many rare and few common species in the community, chance alone would make it unlikely that rare species would occur as neighbours (Lieberman and Lieberman 2007). The positive significant correlation between the number of pairs a liana species establishes and its abundance also showing that the more abundant a liana species is, the greater the number of other liana species with which it associates.

We observed that 58 % pairs have non-significant frequencies equal to expected by chance. Chance is an important event in structuring communities (see also Hubbell 2001), because it determines which species germinate and establish. When chance alone determine the growth or germination of tree species as the nearest neighbor of any other tree, then the frequencies of nearest-neighbor species pairs follow a simple model of random mixing (Lieberman and Lieberman 2007). If, however, observed frequencies do not depart from those expected with random mixing, the most parsimonious interpretation is that neither species interactions nor environmental factors are important in shaping tropical forest species composition at the scale under consideration (Lieberman and Lieberman 2007).

Phylogenetic signal

The presence of a significant phylogenetic signal in the liana climbing mechanism means that phylogenetically related lianas tended to have similar climbing mechanism. This phylogenetic signal can indicate a weak selective pressure for trait divergence among liana clades, considering that traits related to habitat use are usually conserved in plant lineages (Prinzing et al. 2001; Lossos 2008). Our results indicate that closely related liana species tend to co-occur more frequently on the same phorophyte species. Since phorophyte traits, such as trunk diameter, can determine liana climbing mechanism (Darwin 1876; Putz 1984a, b; De Walt et al. 2000), we observed that related liana species co-occurred more than expected by chance, reinforcing that related liana species facilitate one another on climbing the same phorophytes. The phylogenetic signal we observed in climbing mechanisms of lianas reinforce additionally our argument that closely related liana species may not compete with each other and co-occur on the same phorophyte species.

The spatial distribution of the co-occurring liana species

We observed spatial autocorrelation in the number of co-occurring lianas, and could not construct minimum adequate model due to the positive autocorrelation of the residuals of the regression, showing strong influence of space or non-sampled variable (Diniz-Filho et al. 2003). An important role of space may be the result of asexual reproduction and dispersal limitation (Hubbell 2005, Chave 2004). Dispersal limitation has been successful at predicting spatial autocorrelation pattern in tropical forests (Condit et al. 2000, Hubbell 2001), since it results in spatial aggregation of species (Legendre et al. 2009) because failure of wide seed distribution leads to clumping individuals (Terborgh et al. 2011). Lianas have the ability to sprout from falling shoots or stems (Nabe-Nielsen and Hall 2002), and clonal or vegetative propagation is associated with dispersal limitation of plant species due to the absence of pollen and seed production (Marin et al. 2010). Therefore, the spatial autocorrelation of liana co-occurrence that we observed may be a result of dispersal limitation, especially in case of the impossibility of constructing a model of multiple correlations between environmental variables and liana pairing frequency.

The predominance of wind-dispersed seed among lianas (Gentry 1991), which implies normally shorter dispersal distances than animal-dispersed seeds (Clark 2005), can also lead to dispersal limitation of lianas. Wind-dispersed seeds have high probability of landing in forest gaps (Augspurger & Franson 1988), which generally have high light intensity and favor the growth of light-demanding plants (Nabe-Nielsen 2002). Small, growing plants in forest gaps favor high density of lianas (Nabe-Nielsen 2002), leading to liana clumping in the space. Therefore, the history of the fragment is important for the lianas density because, in the early phase of succession or the forest gap the environmental conditions such as favorable light, small plants for the growth helps the survival and density of lianas (DeWalt et al. 2000). But as the forest or the forest gap gets older then the trees height increases, eventually decrease the canopy openness which prevents the light to the ground, making environment unfavorable for the lianas (Caballé 1986; Nabe-Nielsen 2002). This sequence of events would lead to a great influence of space on the co-occurrence of lianas, which could explain our results.

Nevertheless 58% of the liana pairs had an observed frequency statistically equal to the expected by chance, but our results support that niche conservatism and species interactions are also important in inducing co-occurrence of lianas on the same phorophytes. Our findings are in accordance with other studies (Silva et al. 2010; Cavender-Bares et al. 2006) that also showed similar results on fine scale. Since we observed very less negative co-occurrence in lianas as compare to positive which determine that lianas have more tendency of facilitation. Other studies (Putz 1984a; De Walt et al. 2000; Campanello et al. 2007) also support facilitation among lianas. Our results also support that species co-occurrence is determined by functional characteristics as well as the stochastic processes results in spatial distribution that tends to determines predominantly the co-occurrence of lianas pairs in the plots.

Acknowledgments

We are indebted to The Academy of Science for the Developing World (TWAS) and National Research Council (CNPq), for the scholarship granted to the first author and FAPESP for the scholarship granted to the second author.

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Figure 1. Phylogenetic supertree of sampled climbing plants species in the studied fragment Southeastern Brazil.

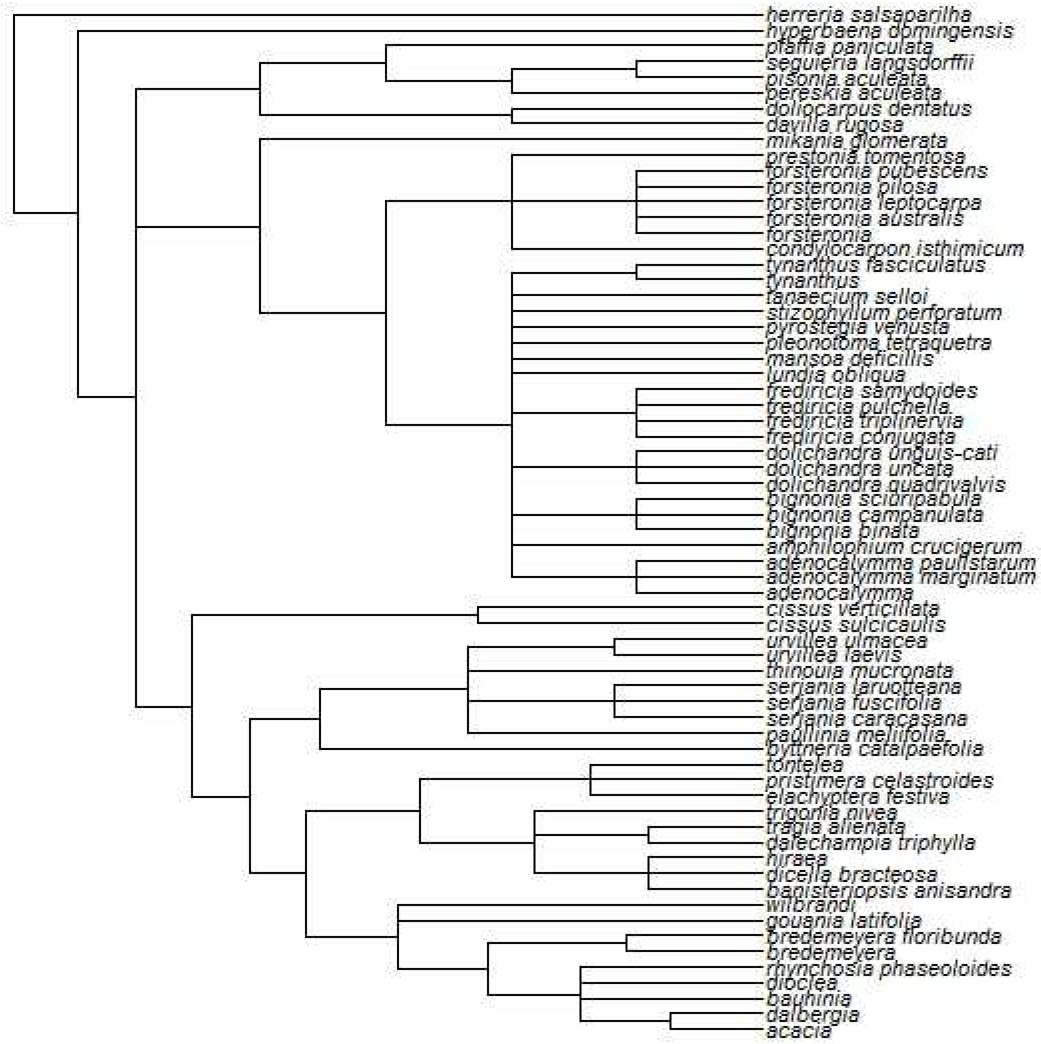

Figure 2. Selection of environmental variables with Principal component analysis circle equilibrium.

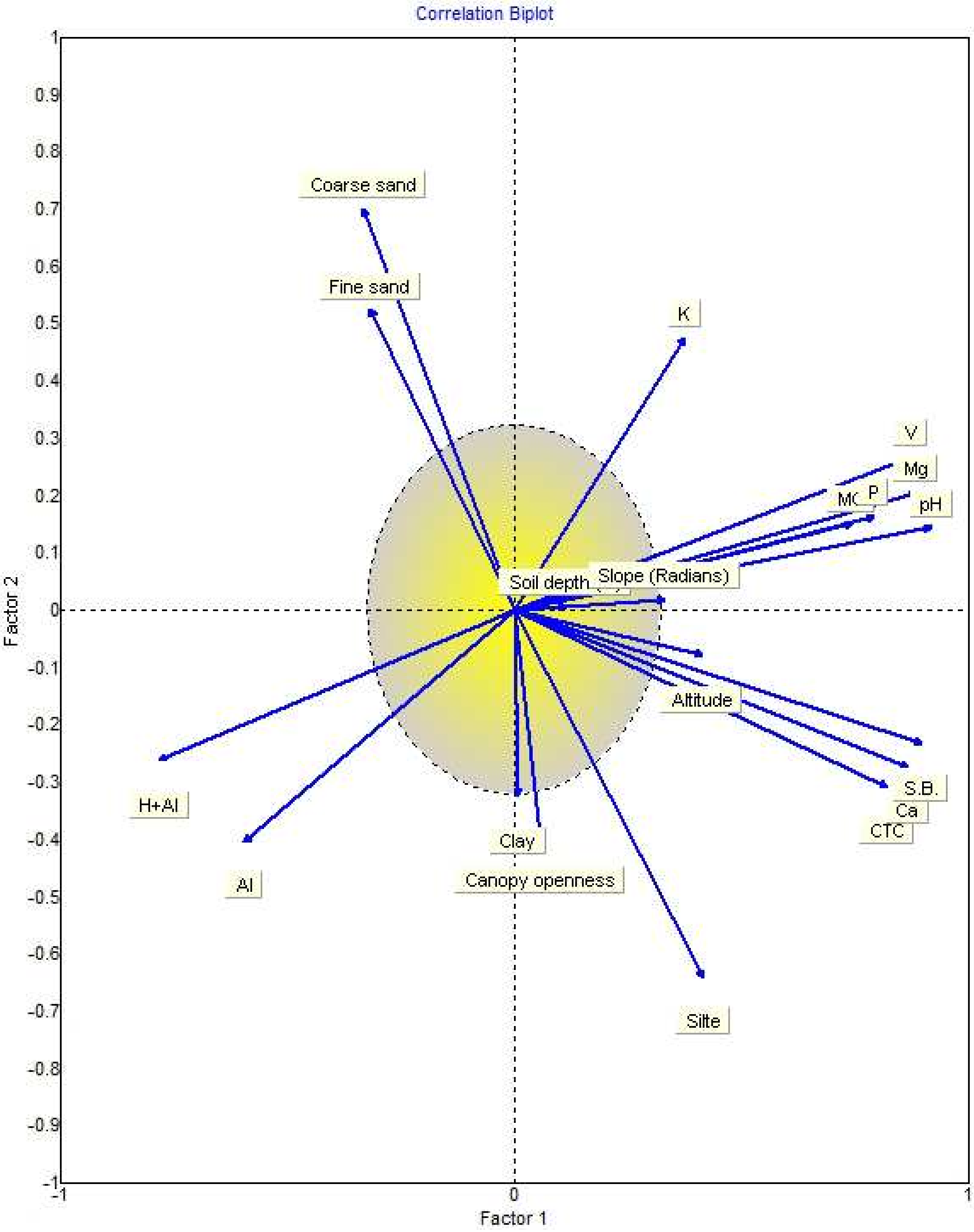

Figure 3. Relationship between phylogenetic distance of liana species and number of co-occurring liana pairs in a seasonal forest fragment, southeastern Brazil. The slope of the regression with data points 0.95; $P = 0.01$.

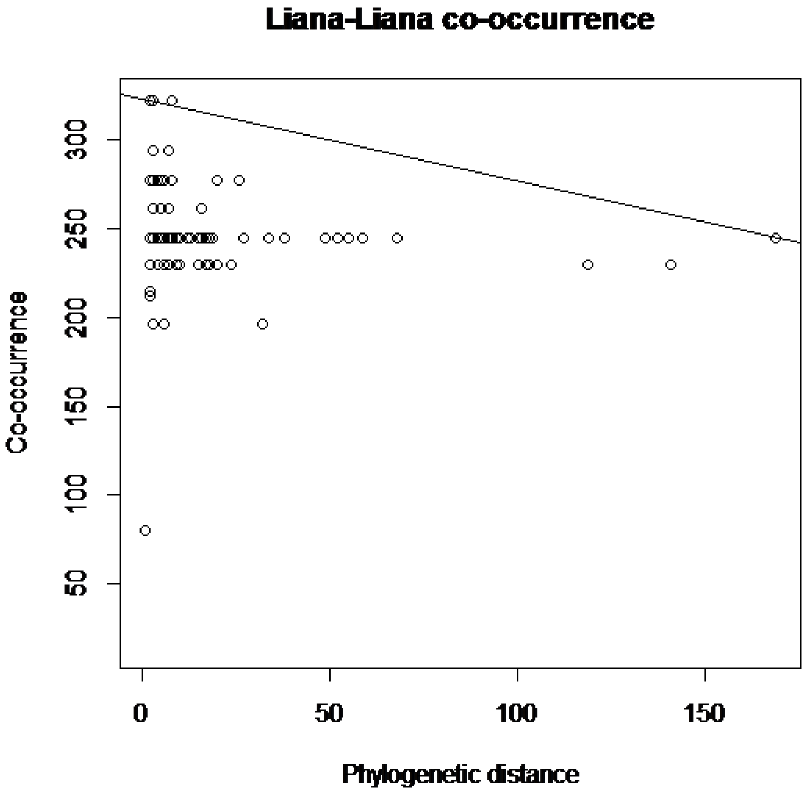

Figure 4. The slope of the regression with data points 0.75 between phylogenetic distance of liana species and number of co-occurring liana pairs in a seasonal forest fragment, southeastern Brazil; *P* = 0.01.

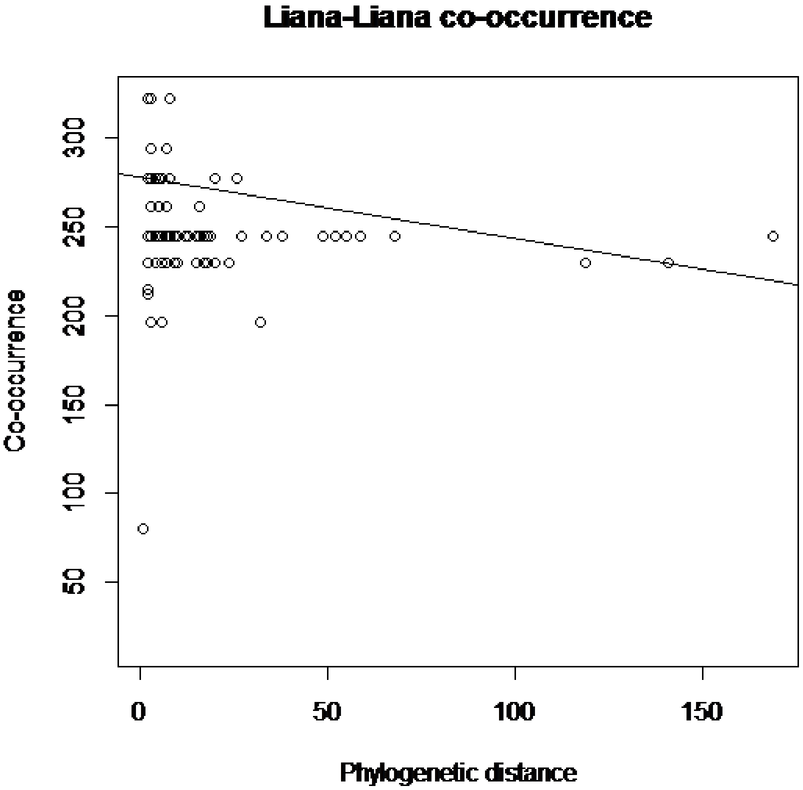

Figure 5. Correlation test between the abundance and the number of pairs liana species establishes with other liana species. The coefficient of the Pearson was 0.97 at *P = 0.001*.

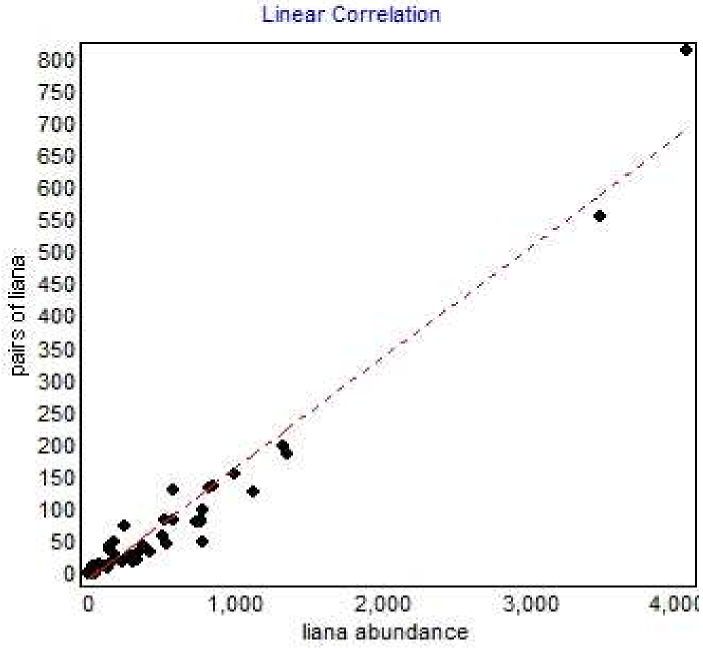

Table 1. Tests for spatial autocorrelation of environmental gradients and soil variables in sampled seasonal forest fragment, southeastern Brazil. The values of Moran's I coefficient are shown for each distance class of 293 m. Significant values at α = 0.05 are in bold. K % = percentage of organic carbon, H+Al % = Potential acidity, S.B% = Extractable bases, Sand and Silt.

Distance Classes	K%	H+Al%	S.B%	Coarse Sand%	Silt%
1	-0.035	**0.095**	**0.08**	**0.108**	0.023
2	-0.023	0.061	-0.044	0.075	0.007
3	0.03	0.056	-0.012	0.05	0.04
4	-0.026	0.057	-0.019	0.046	0.013
5	0.003	0.023	-0.023	0.028	-0.015
6	-0.033	-0.038	0.023	**-0.099**	0.045
7	-0.029	-0.019	0.019	**-0.106**	-0.073
8	-0.016	-0.047	-0.042	-0.067	-0.003
9	0.006	-0.068	-0.071	-0.047	-0.058
10	0.017	-0.062	0.001	-0.048	**-0.084**
11	-0.002	**-0.159**	-0.022	-0.015	-0.004

Table 2. Test for spatial autocorrelation of residuals of the regression of the number of co-occurring pairs of lianas against abiotic variables without spatial filters and with spatial filters and the number of co-occurring pairs of lianas in plots of seasonal forest fragment, southeastern Brazil. The values of Moran's I coefficient are shown for each distance class of 293 m. Significant values at α = 0.05 are in bold. S.F= Spatial filters.

Distance Classess	Residuals without S.F	Residuals with S.F	Number of liana pairs
1	**0.197**	-0.065	**0.244**
2	0.041	-0.007	0.011
3	-0.034	-0.043	-0.059
4	**-0.149**	0.039	**-0.148**
5	-0.044	0.006	-0.019
6	**-0.093**	-0.042	**-0.132**
7	-0.081	0.032	-0.027
8	0.013	0.008	-0.018
9	0.056	0.024	0.042
10	0.02	-0.062	0.044
11	-0.035	**-0.127**	-0.049

Table 3. Quantile regression between phylogenetic distance of liana species and number of co-occurring liana pairs in a seasonal forest fragment, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) are given. The *P* values for bootstrapped standard errors are also given. Significant values at $\alpha = 0.05$ are presented in bold face.

Slope	Value	Std. Error	T value	*P* value
0.95	-0.46108	0.17876	-2.57933	**0.01**
0.75	-0.34517	0.14484	-2.38315	**0.01**

Table 4. Quantile regression between the negative co-occurring pairs and phylogenetic distance of liana species in a seasonal forest fragment, southeastern Brazil. The slope of the regression with data points 0.95 and 0.75 (upper 5% and 25%) are given. The *P* values for bootstrapped standard errors are also given.

Slope	Value	Std. Error	T value	*P* value
0.95	-0.69504	0.62990	-1.10340	0.29
0.75	0	0.20819	0	1.00

Chapter 3: Role of stochastic processes in the co-occurrence pattern of liana-phorophyte in a southeastern Brazilian semideciduous tropical forest

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Abstract

Competition and facilitation are important processes driving community spatial pattern. The chance of species co-occurrence is respectively smaller or greater than expected by chance if competition or facilitation predominates. Across varying environmental gradients both processes occur and the predominance of one or other may be influenced by environmental variables. However, not only environment but host tree functional traits also affects liana-phorophyte co-occurrence because liana-phorophyte interactions are the result of of host functional traits. Therefore, considering the relative role of environmental gradients, we expected the frequency of liana-host tree co-occurrence 1) is related with trait variations among phorophyte 2) responding to environmental gradients. We sampled 1 ha with 100 plots of 10 x 10 m each in a tropical semi-deciduous forest in SE Brazil. We investigated frequency of lianas and host trees co-occurrence variation with the phylogenetic diversity measurements using as a proxy for functional diversity and variations along environmental gradient. We did not find direct role of trait variation in the number of co-occurrence. We observed very weak role of soil potassium and extractable bases but the space had high role in the frequency liana-phorophyte co-occurrence. We observed that phorophyte species assemble randomly but the few species have clumped distribution because of dispersal limitations in few plots of the sampled fragment. We argued that lianas have opportunistic behavior for climbing on the trees and dispersal limitation of lianas and host trees had high role in frequency of liana-phorophyte co-occurrence in micro scale.

Key words: Competition, Facilitation, Co-occurrence, Phylogenetic diversity, Dispersal limitation.

Introduction

Ecological interactions, such as competition and facilitation, have great influence on the long-term species dynamics in a community, but which interaction prevails among species remains an open ecological question (Dodds, 1997). Interactions are more easily assessed on fine scale because individuals are near to each other, and the plants, being sedentary, interact directly with one another (Stoll and Weiner 2000, Hubbell et al. 2001). Since competition and facilitation leave strong imprints, species spatial pattern can provide a hint to understand the prevailing interaction in the community (Perry et al. 2008), but interspecific interactions determine also species co-occurrence pattern in the community (Callaway 1995, Grime 2006, Bruno et al. 2003, Butterfield 2009). A number of co-occurring species smaller than expected by chance may arise from competition due to failure of inferior species in the neighbourhood of competitively superior ones. On the contrary, a number of co-occurring species greater than expected by chance may arise from facilitation (Lieberman and Lieberman 2007, Perry et al. 2009). An appropriate system to investigate these interactions is the liana-phorophyte (host tree) pair, which is ubiquitous in virtually all tropical forests.

On the one hand, lianas need support for climbing to get suitable light; and on the other hand, host trees facilitate lianas providing possible recruitment sites as “nurse”, but at the same time a great number of lianas on the same phorophyte results in tree fall (Campanello et al. 2007). Lianas compete with trees above ground for light and below ground for nutrients (Schnitzer et al. 2005, Toledo-Aceves & Swaine 2008), so that the prevailing interaction of trees with lianas is facilitation, but the prevailing interaction of lianas with trees is competition. Some trees have specific traits that can avoid lianas and reduce tree mortality, whereas other trees carry abundant lianas (Grogan & Landis 2009). However, not only the species co-occurrence pattern but also the species spatial pattern varies in a community.

Species co-occurrence pattern may vary according to changes in the balance between positive or negative interactions due to changes in environmental gradients (Silva et al. 2010) If so, we expect that the frequency of liana-phorophyte pairs may vary along a topographic gradient, in which soil conditions vary greatly. However, not only environment affects liana-phorophyte co-occurrence, but also the host tree functional traits, since liana-phorophyte interactions are the result of of host functional traits (De Walt et al. 2000). As the frequency and proportion of liana-attractive and liana-repulsive traits varies among tree species within a community, liana load on trees ranges from absent on some tree species to very heavy on others (Sfair et al. 2010), and the frequency of liana-phorophyte pairs can vary across an environmental gradient. The spectrum of functional traits of a community constitutes its functional diversity (Petchey and Gaston 2006). The functional diversity of a community may be assessed by phylogenetic diversity (Mouquet et al 2012), and, although acting more likely as a proxy to functional diversity, phylogenetic diversity means that evolutionary diversification leads to trait diversification and may result in greater niche complementarity (Flynn et al. 2011).

The expected number of features that species inherited from their common ancestors can be interpret from the branch length of phylogenetic trees (May 1990; Nee and May 1997). Therefore, the branch length of a single species may be used as a proxy for its number of features (Pavoine et al. 2005). Therefore the phylogenetic tree is use to incorporate phylogenetic diversity of the community (Faith 1992). Many studies have confirmed phylogenetic signals in plant traits (Srivastava et al. 2012) which show that phylogenetically closely related have little evolutionary changes (Qian & Ricklefs 2004). Therefore due to the presence of conservatisms in most of the traits in plants lineages, the phylogeny may be used as good proxies for habitat use and demographic niche (Best 2013).

Reasoning this way, if host trees have great phylogenetic diversity and hence great functional diversity, they might provide a wide range of potential niches whose suitability varies greatly for different liana species and can be modulated by environmental variables. On the one hand, considering the same environment stretch, species sharing a preference for some subset of the available conditions should occur more often than expected by chance, and those akin to a different subset of conditions should be found less often than expected at random (Lieberman and Lieberman 2007). If so, we expect to find a significant relation of environmental variables with the frequency of liana-phorophyte pairs along an environmental gradient. On the other hand, host tree functional diversity could also be associated with variation in the frequency of liana-phorophyte co-occurrence. Assuming that phylogenetic diversity is a proxy for functional diversity, a smaller phylogenetic diversity of host trees represents closely related species sharing similar traits (Prinzing et al. 2001; Webb et al. 2002), whereas a greater phylogenetic diversity denotes distant species with different functional traits. If closely related host trees (with smaller phylogenetic diversity) share a gradients stretch, we expect the frequency of liana-phorophyte pairs to be greater, since traits capable of avoiding specific lianas would be absent. Therefore, we expect the number of liana-phorophyte pairs to be related to the phylogenetic diversity of host trees.

In this study, we assessed the relative influence of environmental filters and the phylogenetic diversity of host tree species on the frequency of liana-phorophyte co-occurrence. We investigated whether the frequency of liana-phorophyte pairs is associated with (a) abiotic variables (position on slope, forest canopy openness, and soil depth, organic matter, Al, P, Ca, Mg, K, pH, and cation exchange capacity); and (b) phylogenetic and functional diversity of host tree species. We approached the role of these variables by constructing minimum adequate models (MAMs) with ordinary least squares model selection (OLS, Diniz-Filho et al. 2008). To guide our investigation, we proposed the following questions: (1) Is the frequency of liana-phorophyte pairs explained by some of the environmental variables? (2) How much variation of the frequency of liana-phorophyte pairs is explained by pure space (i.e. the spatial distribution of sampling units) instead of abiotic variables? (3) How much variation of the frequency of liana-phorophyte pairs is explained by the phylogenetic diversity of host tree species?

Methods

Study site and sampling

We surveyed a fragment of the Tropical Semideciduous Seasonal Forest of about 245 ha in Campinas municipality (22º50'S, 46º55'W), São Paulo state, southeastern Brazil. In the fragment some 20-50% of the canopy trees shed their leaves in the dry season (Veloso et al. 1991) of the regional climate, which is tropical with dry winter (Cwa; Koeppen 1948; Cielo-Filho et al. 2007), with a mean annual temperature of 24 ºC, and a mean annual rainfall of 1,409 mm. The rainy season usually longs from October to March, in which the average precipitation reaches 1,141.5 mm and the average temperature is 24 °C; the dry season usually occurs from April to September, when the average precipitation is 283 mm and the average temperature is 20 °C (CEPAGRI 2011, data for the period of june 1988 to October 2008). The altitude of the site varies between 630 to 760 m a.s.l., and the predominant soil is Acrisol (FAO nomenclature).

In the southern portion of the fragment, 100 plots of 10 m × 10 m each were randomly placed using the irrestricted randomization procedure (Cielo-Filho et al. 2007), and in each plot we sampled liana and phorophyte species. We sampled phorophytes with DBH (diameter at breast height) ≥ 5 cm and lianas with DSH (stem diameter at soil height) ≥ 1 cm. following Gerwing et al. (2006) and Schnitzer et al. (2008) protocols for sampling lianas. In the center of each plot we extracted 500 g from the superficial soil, which was sent to Campinas Agronomic Institute to determine organic matter, Al, P, Ca, Mg, K, pH, cation exchange capacity, potential acidity (H+Al), extractable bases (SB), base satuaration (V) and soil texture quantified percentage of (silt, sand and clay). We also estimated the percentage of canopy openness with a spherical convex densitometer at the breast height (Lemmon 1956). Using two plot sides as a coordinate system, we drew three random points at which we used a meter-scaled metal rod to measure soil depth and a clinometer to measure slope angle in degrees and used their average for data analysis.

Phylogenetic data

We constructed a phylogenetic tree for all sampled lianas with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic tree (Webb and Donoghue 2005) (Appendix 1). This tree was based on the information from current phylomatic tree (R20080417) which is based on information from several published phylogenies (Webb and Donoghue 2005). Polytomies in family nodes (e.g. Bignoniaceae, Fabaceae, Apocynaceae) were resolved by spacing evenly the genus node above family node following several published molecular phylogenies (e.g. Lohmann 2006; Simon et al. 2009; Livshultz et al. 2007). We assigned the branch length of the phylogenetic tree using BLADJ (branch length adjustment) averaging algorithm of the Phylocom software package (Webb et al. 2011). BLADJ set the length of all branches by spacing the undated nodes evenly between the dated nodes, and between dated nodes and terminal nodes, and fixes the root node at specified age (Webb et al. 2011). The branch lengths were based on the minimum ages of nodes for higher orders, genera and families from fossils data (Wikström et al. 2001).

Phylogenetic diversity measures

For the host tree species we calculated phylogenetic diversity (PD). Phylogenetic diversity is a measure of biodiversity which incorporates phylogenetic difference between species. It is defined and calculated as "the sum of the lengths of all those branches that are members of the corresponding minimum spanning path" (Faith, 1992). The MPD was calculated as the mean phylogenetic distance among all pairwise combinations of species (Webb 2000, Pavoine and Bonsall 2011). The MPD is slightly different from the PD function in that the former take a distance matrix as input rather than a phylogeny object. Each phylogenetic distance captures a different aspect of the species phylogenetic relatedness. MPD is a measure of tree-wide phylogenetic distance of species. In addition, we computed the standardized effect sizes of each diversity measure in order to compare values among different plots. Standardized effect sizes describe the difference between phylogenetic distances in the observed community and a null community generated by randomization. We computed the standardized effect size of PD and MPD ($\mathrm{SES}_{\mathrm{MPD}}$) as:

standardised effect size = (obs value – rnd value) / sd rnd.value, Where obs value is the observed value of the metric under analysis, rnd value is the mean metric value of null communities, and sd rnd.value is the standard deviation of the 1,000 random values of the measure. We generated random values by reshuffling taxa labels across the tips of the phylogenetic tree of all host tree species sampled in forest. Positive values of the standardized effect indicate that the site has a diversity value higher than expected by chance, i.e. a phylogenetic overdispersion of the local tree community; whereas negative values indicate that the site has a diversity value lower than expected by chance, i.e. a phylogenetic clustering (Webb et al. 2002, Pavoine & Bonsall 2011). We calculated all the metrics with the 'picante' package (Kembel et al. 2010) for R environment (R Development Core Team 2012).

Data analyses

Selection of environmental variables

To answer the third and fourth questions, what is the role of abiotic variables in structuring the co-occurrence of lianas species?, we first standardized the range of all abiotic variables (mean = 0, standard deviation = 1) to put different data units into same scale. We used an equilibrium circle technique of Principal Components Analysis (PCA) for the selection of variables. We selected soil pH, Potassium (K), extractable bases (SB), potential acidity (H+Al), silt and coarse sand that have vectors head outside the equilibrium circle (Figure.1), which showed significant contribution to the ordination (Legendre & Legendre 1998). We tested for multicollinearity with the variance inflation factor (VIF), which measures the proportion by which the variance of a regression coefficient is inflated in the presence of other explanatory variables (Borcard et al. 2011). We excluded soil pH content because they showed VIF values greater than 10, which indicate collinearity between variables (Borcard et al. 2011).

Then, we tested for spatial autocorrelation in Potassium (K), extratable bases (SB), potential acidity (H+Al), silt, coarse sand (hereafter abiotic variables) and phylogenetic diversity (PD) because spatial autocorrelation of independent variables violates the assumption of independent data (Legendre 1993). We calculated Moran's I coefficient for a series of eleven distance classes, being 293 m the limit class. Moran's I coefficient fluctuates between -1 and +1, where negative values indicate negative autocorrelation and positive values show positive autocorrelation and spatial aggregation (Legendre & Legendre 1998). Negative autocorrelation may show either avoidance at short distance, i.e. variables are regularly spaced, or spatial gradient at long distance, if there is also a positive autocorrelation at short distance (Legendre & Legendre 1998). We estimated the significance of Moran's I coefficients with 999 randomizations.

We also tested for spatial autocorrelation in the residuals of the regression of the frequency of liana-phorophyte pairs against the abiotic variables, since it may inflate Type 1 error. In general, the presence of spatial autocorrelation in residuals indicates that there is a variable that was not sampled (varying in space), but is causing the autocorrelation (Diniz-Filho et al. 2003). The spatial autocorrelation in residuals usually results in underestimation of standard error of regression coefficients (Diniz-Filho & Bini 2005). We used Moran's I coefficient with 999 randomizations to test for spatial autocorrelation in residuals (Legendre & Legendre 1998).

Selection of minimum adequate models

Since we found spatial autocorrelation in some environmental variables, phylogenetic diversity and residuals (Table 2 and 3), we incorporated the spatial structure of the data into our model, in order to better estimate and test the minimum adequate model (MEM) parameters. We used eigenvector-based spatial filtering, i.e., the principal coordinate of neighbour matrices (PCNM) approach, which extracts eigenvectors from a connectivity matrix expressing the spatial relationship among plots (Borcard and Legendre 2002, Diniz-Filho & Bini 2005). These eigenvectors (i.e. the spatial filters) express the relationships among plots at decreasing spatial scales, so that the first eigenvectors (those related to large eigenvalues) tend to describe broad-scale spatial patterns, whereas eigenvectors with small eigenvalues tend to describe local patterns (the spatial structure of the regression; Borcard and Legendre 2002, Diniz-Filho and Bini 2005). Therefore, in an attempt to reduce the autocorrelation in residuals, we used these eigenvectors as additional predictors of the response variables in the MAM (Diniz-Filho and Bini 2005). We selected seven filters (i.e. the smallest number of eigenvectors) for the number of liana-phorophyte co-occurrence that ensured a minimum desirable level of spatial autocorrelation in residuals.

Then, we used ordinary least square (OLS) sorted by Akaike information criterion (AIC; Diniz-Filho et al. 2008) to test whether those selected abiotic variables and spatial filters predict the frequency of liana-phorophyte co-occurrence in the studied fragment of tropical seasonal forest. In MAMs, the best model is that in which difference between minimum AIC values of all models and AIC value of the model considered (Δ_i) is lower than 2 (Diniz-Filho et al. 2008). Therefore, we selected a model with the lowest number of environmental variables and $\Delta_i < 2$.

Partitioning the variation of the liana-phorophyte co-occurrences

Finally, to answer our last question, we used multiple regression analyses to compute the relative contribution of the abiotic variables, phylogenetic diversity (PD) and spatial filters in the variation of the frequency of liana-phorophyte pairs. We followed the procedures described by Legendre & Legendre (1998). First, we performed multiple regressions of the explanatory variables and spatial filters against the number of co-occurrences. The resulting value of R^2 determined the fraction of the variation [a + b + c] related to abiotic variables [a], to spatial filters [c], and to the fraction determined by both sets [b]. We did a multiple regression of abiotic variables against the frequency of liana-phorophyte co-occurrences, from which the resulting value of R^2 determined [a + b]. We did another multiple regression of spatial filters against liana-phorophyte co-occurrences, from which the resulting value of R^2 determines [b + c]. Then, the portion [b] was obtained by the equation [b] = [a + b] + [b + c] – [a + b + c] (Legendre & Legendre 1998).

Since we observed spatial auto-correlation in the values of phylogenetic diversity (PD), therefore we also built a model to test the relationship between tree phylogenetic diversity per plot as the response variable and all the abiotic variables as factor variables to evaluate if this auto-correlation is due to niche conservatism or environmental filtering. We followed similar procedure for the analysis but in this case we extracted two spatial filters to reduce the level of spatial autocorrelation of the residuals. Similarly we also construct another model to test a relationship the abundance of trees per plot as the response variables and all the abiotic variables to evaluate whether stochastic, neutral processes are associated with tree abundance variation in the space or due to niche conservatism.

Finally to evaluate whether the frequency of liana-phorophyte pairs depends exclusively on the number of available trees, we performed a correlation test between the number of trees in the plot and number of phorophyte in the plot. We evaluated the significance of this correlation with the Pearson coefficient.

We did the selection of environmental variables and MAMs, multiple linear regressions, and spatial analysis using the software SAM version 4.0 (Rangel et al. 2010).

Results

We found 96 species of host trees in 36 families, and 75 species of lianas in 24 families. Among the host trees Fabaceae was the richest family with (15 species); and among the lianas Bignoniaceae was the richest family with 24 species. The comparisons between the observed PD and MPD values of each plot to null distributions showed non-significant values ($P > 0.05$) of phylogenetic diversity (PD) of host tree species in 83 plots and mean phylogenetic distance (MPD) in 77 plots. Thus 83 % and 77 % of observed $SE_{PD \text{ and } MPD}$ values showed random occurrence of phorophyte species respectively. However 17 plots showed significant values ($P < 0.05$) of phylogenetic diversity (PD) and 23 plots revealed significant values ($P < 0.05$) of mean phylogenetic distance (MPD) of host tree species. These results showed that 17% plots have less phylogenetic diversity and 23% plots have phylogenetically closely related phorophyte species.

Three abiotic variables (potential acidity, extractable bases and sand), phylogenetic diversity (PD) and the residuals of the regression also showed a positive autocorrelation in the first distance class (Table 1 and 2). For this reason, we extracted parsimoniously seven significant spatial filters with PCNM analysis to be used in our model selection. After that we reduced spatial autocorrelation of the residuals of the regression (Table 2).

Two environmental variables significantly related to the number of co-occurring pairs of liana and phorophyte species were the extractable bases (S.B) and potassium (K) content (Table 3). Liana-phorophyte species frequency showed no clear relationship with other variables (Table 3). Space and unexplained variables that were not collected showed influential role generating frequency of liana-phorophyte co-occurrence (Table 3 and 4). Abiotic vaiables (a) explained 8% of the variation and abiotic variable together with space (a+b) explained 5% of the variation. Space (c) alone explained 35 % of the frequency variation. Nevertheless, most of the variation in the number of co-occurring pairs (around 50 %) remained unexplained variable indicating hidden factor that we have not collected (Table 4).

In the model of phylogenetic diversity, we did not find any role of abiotic variables (Table 3). Abiotic variables (a) explained only 1 % but together with space (a+b) did not explain variation. Space alone (c) explained 24% of the variation and unexplained factor, which is the hidden variables, explained 74% of the variations in phylogenetic diversity of tree species (Table 4). In the model of the abundance of tree species, we did not observe the role of abiotic variables (Table 3). Abiotic variables (a) explained very less about 1% and abiotic variables in sharing with space (a+b) explained 1% of the variation in abundance of tree species. Space alone (c) explained 37% and the unexplained variable showed 61% of influential role in the variation tree species abundance (Table 4). We observed strong correlation between number of phorophyte per plot and number of trees (Figure 2). The co-efficient of the Pearson correlation was 0.97 at 98 degrees of freedom with significant value ($P < 0.001$).

Discussion

In general, we observed a weak influence of soil extractable bases and potassium content and no influence of other environmental variables on the liana-phorophyte frequency. Therefore, environmental conditions seem not to be important for the liana-phorophyte frequency. We observed random assembly of phorophyte species in most of the plots except few plots have phylogenetic clustering showing less phylogenetic diversity and phylogenetically closely related phorophyte species. There was no correlation between phylogenetic diversity and the frequency of liana-phorophyte pairs. It shows that phylogenetic diversity, meaning that trait variation among trees did not influence the variation of the frequency of the liana-phorophyte pairs. However, pure space explained 35% of the frequency variation, meaning that variables not considered in the analyses play an important role. Also, 50% of the frequency variation had no explanation, meaning that stochastic processes, such as dispersal limitation, herbivore and pathogen attacks, played the most important role in the variation of the frequency of the liana-phorophyte pairs.

Role of abiotic variables in the frequency of liana-phorophyte co-occurrence

We observed very less role of soil potassium and extractable bases on the frequency of liana-phorophyte co-occurrence. The relative small influence on the frequency of liana-phorophyte co-occurrence may be the outcome of stochastic processes. Environmental variables express weak role in the presence of dispersal limitation (Legendre et al. 2009). However lianas and phorophyte compete with one another for soil resources but we did not find this pattern in our study.

Phylogenetic diversity pattern

We observed the random occurrence of phorophyte species in most of the plots of studied fragment. The random co-occurrence may be due to chance which determines the germination and establishment of species (Sale 1977; Hubbell and Foster 1986; Fowler 1990). However the presence of time difference in germination is inevitable in species rich communities (Sale 1977; Hubbell and Foster 1986; Fowler 1990). Since we observed significant $\mathrm{SES}_{\mathrm{PD\ and\ MPD}}$ values in 17 and 23 plots respectively indicating that closely related tree species are occurring in these plots. The significant phylogenetic measurements may be due to dispersal limitation among the trees. According to neutral theory, stochastic population dynamics and limited dispersal could produce aggregated pattern in tropical forest (Hubbell 2005; Chave 2004). We have also observed the abundance of few species e.g *Almeidea lilacina* A. St. Hil. has 39 individuals, *Esenbeckia leiocarpa* Engl. has 48 individuals, *Metrodorea nigra* A. St. Hil. has 24 individuals in the all significant plots of phylogenetic diversity. *Esenbeckia leiocarpa* Engl. is usually found in clumped form because the seeds are dispersed by gravity at small distance (Crestana et al. 1983; Bawa and Hadley 1991). Similarly *Metrodorea nigra* A. St. Hil. also have clumped behavior in which seeds are not dispersed to long distance (Schwarcz et al. 2010). It shows that the seeds of these species germinated and established well in these plots. In addition we also did not find significant role between phylogenetic diversity and abiotic variables also explained that there is no environmental filtering acting of phylogenetic pattern, or there is no niche conservatism.

Liana-phorophyte co-occurrence frequency along phylogenetic diversity

We did not find the role of traits variation among trees in the frequency of liana-phorophyte co-occurrence. It implies that frequency of the liana-phorophyte pairs depends almost exclusively on the number of available trees. The strong and significant correlation between number of trees and the number of phorophyte per plot also support our arguments that frequency of the liana-phorophyte pairs depends heavily on the opportunistic behavior of the lianas: if trees are available, they can be climbed by lianas, no matter the traits the trees have or the environmental conditions. In general lianas germinate in the soil need support for climbing to reach the canopy. Soon after germination they search for the support and if they find any tree then they climb on that tree but if they do not find them they can`t establish theirself (Schnitzer and Bongers 2002, Gerwing et al. 2006).

Spatial distribution of co-occurring liana-phorophyte pairs

We have found a strong influential role of space and unexplained variables in the frequency of liana-phorophyte co-occurrence. The unexplained variables may be dispersal limitation of tree species and lianas species. Significant proportion of unexplained variations is mostly due to dispersal limitation (Jones et al. 2008). The presences of weak environmental variables in fine scale determine that dispersal limitation is the strong driver of generating species spatial pattern in tropical forests (Legendre et al. 2009). Dispersal limitation has been appointed as the prevalent process generating aggregated distribution in tropical forests (Condit et al. 2000, Hubbell 2001;

Jones et al. 2006; Terborgh et al. 2011). Similarly lianas also do vegetative propagation which result in aggregated distribution of lianas (Marin et al. 2010; Terborgh et al. 2011). The non-significant correlation between number of trees and the abiotic variables also support that tree species have not overpassed even the short distances in the community interior. The response of different species of the same community to one or more abiotic variables indicates that deterministic processes are acting on the species occurrence and abundance (Cielo Filho et al. 2007; Jones et al. 2008).

In conclusion the stochastic processes surpass the role of abiotic variables on the frequency of liana-phorophyte co-occurrence in our study. Trait variations among the trees have no effect on the frequency of co-occurrence indicating lianas opportunistic behavior to get support and reach the canopy. Stochasitic processes such as population dynamics and dispersal limitation are the major forces driving the frequency of liana-phorophyte co-occurrence pattern.

Acknowledgments

We are indebted to The Academy of Science for the Developing World (TWAS) and National Research Council (CNPq), for the scholarship granted to the first author and FAPESP for the scholarship granted to the second author.

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Figure 1. Phylogenetic supertree of sampled phorophyte species in the studied fragment Southeastern Brazil.

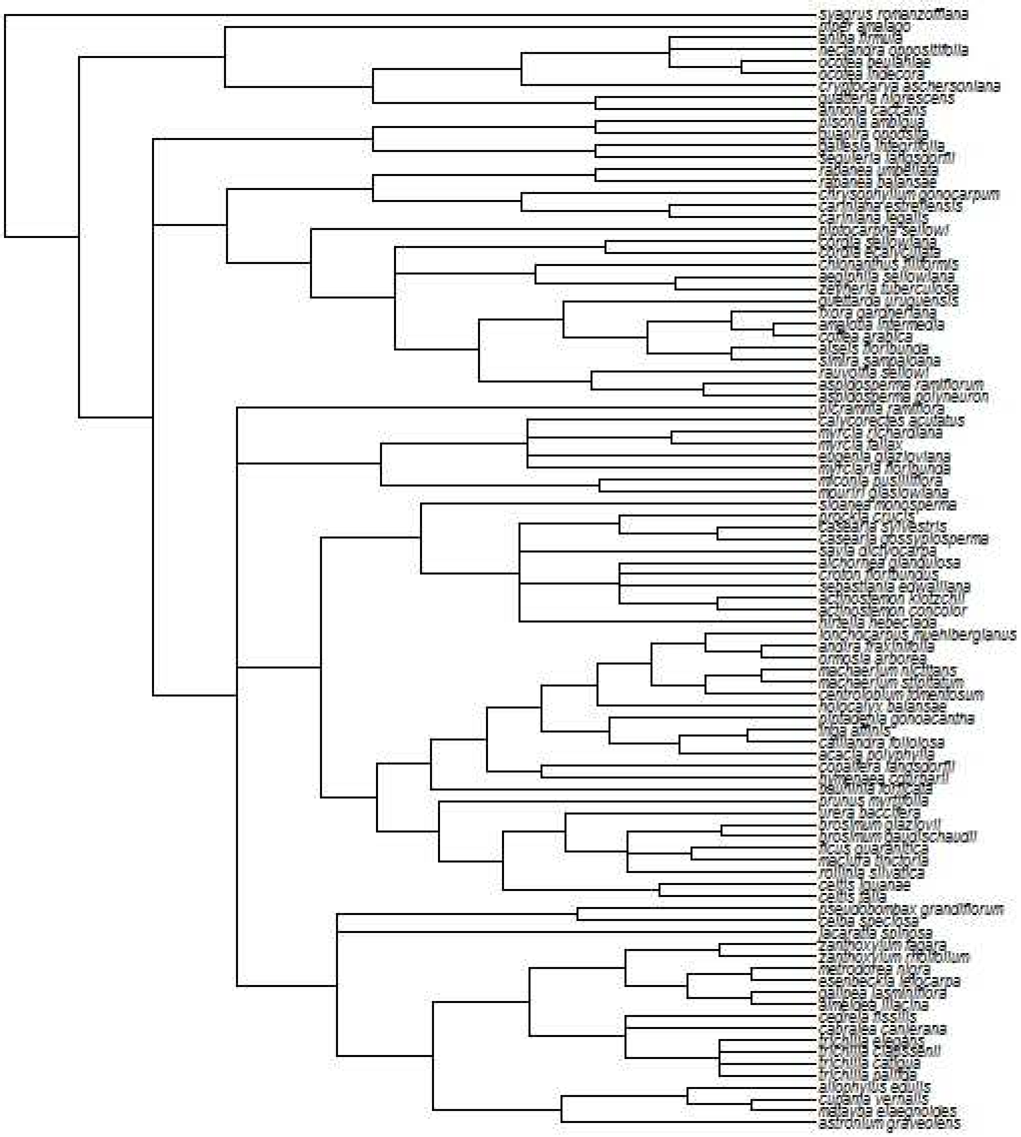

Figure 2. Selection of environmental variables with Principal component analysis circle equilibrium.

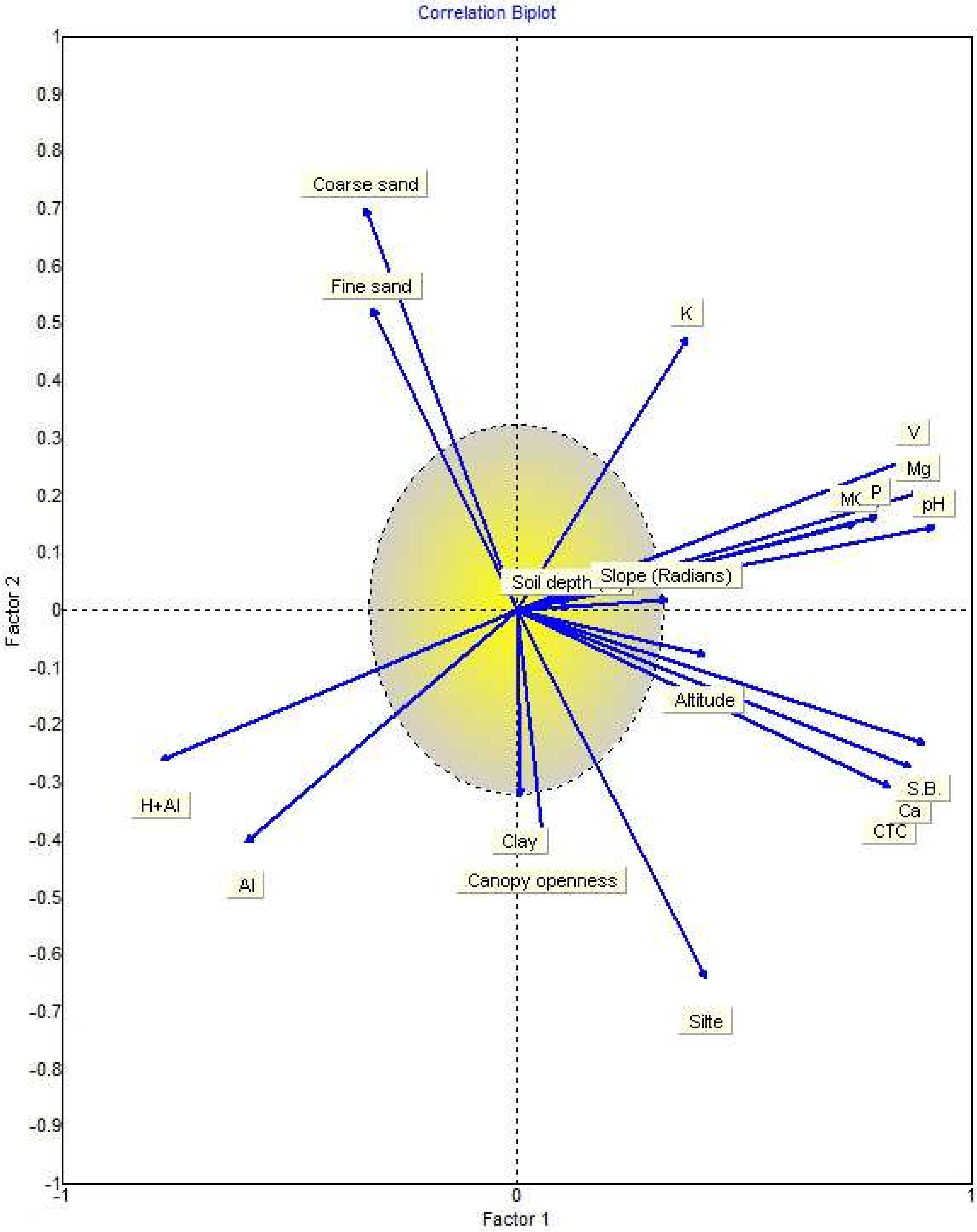

Figure 3. Relationship between number of phorophyte and number of trees per plot. The value of significant Pearson co-efficient was 0.97 and *P* < 0.001.

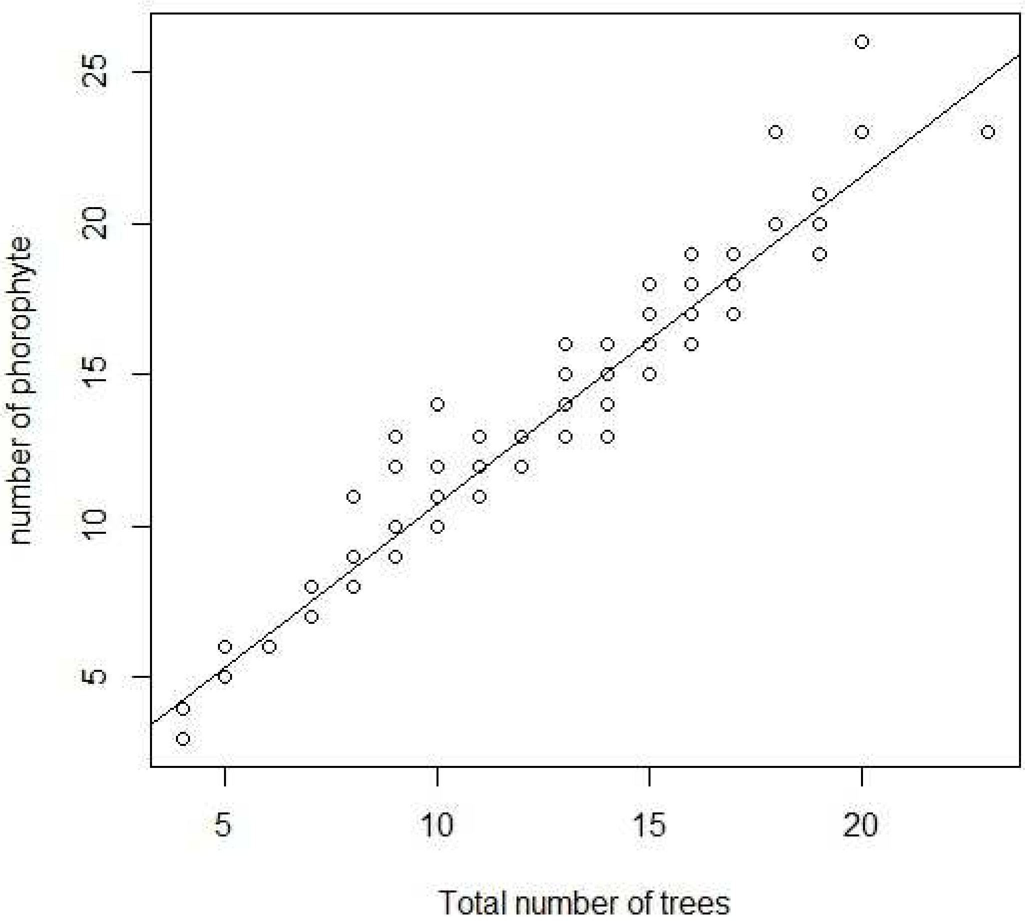

Table 1. Tests for spatial autocorrelation of environmental gradients and soil variables in sampled seasonal forest fragment, southeastern Brazil. The values of Moran's I coefficient are shown for each distance class of 293 m. Significant values at α = 0.05 are in bold. K % = potassium, H+Al % = Potential acidity, S.B% = Extractable bases, Coarse Sand, Silt, Phylogenetic diversity (PD) and Mean phylogenetic distance (MPD).

Distance Classess	K%	H+Al%	S.B%	Coarse Sand%	Silt%	PD	MPD
1	-0.035	**0.095**	**0.08**	**0.108**	0.023	**0.256**	0.076
2	-0.023	0.061	-0.044	0.075	0.007	**0.16**	-0.053
3	0.03	0.056	-0.012	0.05	0.04	0.026	-0.031
4	-0.026	0.057	-0.019	0.046	0.013	0.032	0.051
5	0.003	0.023	-0.023	0.028	-0.015	-0.026	-0.002
6	-0.033	-0.038	0.023	**-0.099**	0.045	**-0.121**	-0.042
7	-0.029	-0.019	0.019	**-0.106**	-0.073	**-0.106**	**-0.089**
8	-0.016	-0.047	-0.042	-0.067	-0.003	**-0.151**	-0.051
9	0.006	-0.068	-0.071	-0.047	-0.058	**-0.095**	0.021
10	0.017	-0.062	0.001	-0.048	**-0.084**	-0.017	0.005
11	-0.002	**-0.159**	-0.022	-0.015	-0.004	-0.065	0.008

Table 2. Test for spatial autocorrelation of residuals of the regression of the response variables against abiotic variables before and after the selection of spatial filter. The values of Moran's I coefficient are shown for each distance class of 293 m. Significant values at α = 0.05 are in bold. Residulas = Residulas without spatial filter, W.S.F= Residuals with Spatial filters.

Selected variables	Liana-phorophyte co-occurrence		Number of trees		Phylogenetic diversity of trees	
	Residuals	Residuals W.S.F	Residuals	Residulas W.S.F	Residulas	Residulas W.S.F
1	**0.209**	0.001	**0.259**	0.004	**0.225**	0.05
2	0.071	-0.049	**0.187**	-0.002	**0.132**	0.022
3	-0.004	-0.051	**0.099**	-0.021	0.01	-0.026
4	**-0.158**	0.025	**0.094**	0.055	0.026	0.017
5	-0.06	0.007	-0.088	-0.074	-0.057	-0.093
6	-0.086	-0.04	0.007	0.023	**-0.099**	-0.069
7	**-0.125**	-0.004	-0.049	0.051	-0.076	-0.005
8	-0.007	-0.002	-0.048	-0.028	**-0.133**	-0.053
9	0.049	0.02	-0.053	-0.038	-0.059	-0.021
10	0.045	0.024	**-0.219**	-0.021	-0.022	0.023
11	0.042	-0.033	**-0.301**	-0.056	-0.056	-0.011

Table 3. Parameters of multiple regressions of the response variables against abiotic variables. These abiotic variables were selected by building minimum adequate models, with ordinary least square and Akaike criterion. Empty cells indicate that the variables were not selected. Significant coefficient values at α = 0.05 are in bold. K % = potassium, H+Al % = Potential acidity, S.B% = Extractable bases, Coarse Sand, Silt, Phylogenetic diversity (PD) and Mean phylogenetic distance (MPD), Spt Filter = Spatial Filter.

Selected variables	Liana-phorophyte co-occurrence		Number of trees		Phylogenetic diversity of trees	
	Coeff	t	Coeff	t	Coeff	t
Constant	8.024	1.013	**12.168**	11.004	**717.462**	16.435
K%	**2.834**	2.451	0.101	0.42	-	-
H+Al%	-	-	**-**	-	1.566	1.25
S.B%	**0.049**	2.386	-	-	-	-
Coarse Sand%	-	-	-	-	-	-
Silt%	-	-	-	-	-	-
PD	**0.007**	0.955	-	-	-	-
MPD	-	-	-	-	-	-
Spt Filter 1	32.01	1.977	**-10.396**	-3.023	**-**370.06	-1.907
Spt Filter 2	**50.377**	3.088	**-10.863**	-3.166	**522.571**	2.694
Spt Filter 3	**-47.495**	-2.886	-13.49	-3.957	**670.086**	3.434
Spt Filter 4	**36.465**	2.196	11.137	3.268	**-550.528**	-2.836
Spt Filter 5	**-37.149**	-2.293	**-10.825**	-3.181	-	-
Spt Filter 6	**59.58**	3.655	-	-	-	-
Spt Filter 7	**-68.685**	-4.24	-	-	-	-

Table 4. Partitioning of the variation explained by those abiotic variables and spatial filters for the response variables. The variables were those selected by building minimum adequate models, with ordinary least square and Akaike criterion. The adjusted R^2 of the multiple regressions of the frequency of liana-phorophyte co-occurring pairs against environmental variables and spatial filters together and separate are shown. Spt Filter = Spatial Filter.

Responce Variables	Abiotic variables (a)	Abiotic variables +Spt Filter (a+b)	Spt Filter (b)	Unexplained (d)	r^2 adj
Liana-phorophyte co-occurrence	0.086	0.055	0.355	0.504	0.445
Number of trees	0.005	0.002	0.374	0.619	0.344
Phylogenetic diversity of trees	0.012	0.008	0.242	0.738	0.231

Considerações Finais

Nossos resultados indicam que os processos evolutivos que estruturam as interações liana-forófito foram diferentes em florestas e savanas. As condições ambientais nas savanas selecionam espécies de árvores com características funcionais comuns, tais como espessura da casca, que favorecem a ocorrência de espécies originais de liana. Nas florestas, ao contrário, esses traços são raros e associados a forófitos muito originais.

Observamos tendência de lianas com mecanismos de escalada semelhantes que facilita outra liana a escalar a árvore hospedeira. Essa tendência também pode ser relacionada com a abundância e distribuição agregada de espécies que possuem mecanismos de escalada semelhantes.

Nossa investigação mostrou que as características nutricionais do solo em uma escala fina apresentaram pouca importância na variação da co-ocorrência das espécies de lianas e na determinação da freqüência de co-ocorrência das lianas-forófitos.

Grande parte da variação (50%) da co-ocorrência de espécies não foi explicada pela variável estudada: fatores topoedáficos. Portanto, baseado nos fatores determinísticos que abordamos, as lianas são um grupo em que há a predominância do modelo neutro na montagem de sua comunidade, pois a variação da sua composição é decorrente de fatores estocásticos de suas populações e limitação por dispersão.

Grande parte da variação (50%) da freqüência de co-ocorrência das lianas- forófitos também não foi explicada pelas variáveis estudadas: fatores topoedáficos e atributos dos forófitos . Portanto, baseado nos fatores determinísticos que abordamos, predominância do modelo neutro na montagem de sua comunidade das lianas- forófitos, pois a variação da sua freqüência é decorrente de fatores estocásticos de suas populações e limitação por dispersão.

A freqüência dos pares de liana-forófito depende fortemente do comportamento oportunista das lianas: Se as árvores estão disponíveis, eles podem ser escalado por lianas, não importa as características das árvores e as condições ambientais. Mas lianas tem alguma preferência de diâmetro do tronco das árvores hospedeiras.

Appendix 1: List of liana species and climbing mechanisms from the four sampled forest sites in Southeastern Brazil.

FAMILY	SPECIES	CLIMBING MECHANISMS
ACANTHACEAE	*Mendoncia velloziana* Mart	Twining
AGAVACEAE	*Herreria salsaparilha* Mart	Twining
APOCYNACEAE	*Condylocarpon isthimicum* (Vell.) A.DC.	Twining
	Forsteronia australis Müll.Arg.	Twining
	Forsteroniag glabrescens Müll.Arg.	Twining
	Forsteronia leptocarpa (Hook. & Arn.) A.DC.	Twining
	Forsteronia pilosa (Vell.) Müll.Arg.	Twining
	Forsteronia pubescens A.DC.	Twining
	Forsteronia refracta Müll.Arg.	Twining
	Forsteronia velloziana (A.DC.) Woodson	Twining
	Prestonia coalita (Vell.) Woodson	Twining
	Prestonia riedelli (Müll.Arg.) Woodson	Twining
	Prestonia tomentosa R.Br.	Twining
	Secondatia densiflora A.DC.	Twining
ASTERACEAE	*Dasyphyllum flagellare* (Casar.) Cabrera	Scrambler
	Mikania glomerata Spreng.	Twining
	Mikania lundiana DC.	Twining
BIGNONIACEAE	*Adenocalymna bracteatum* (Cham.) DC.	Tendril
	Adenocalymma marginatum (Cham.) DC.	Tendril
	Adenocalymma paulistarum Bureau & K.Schum	Tendril
	Amphilophium paniculatum (L.) Kunth	Tendril
	Anemopaegma chamberlaynii (Sims) Buraeu & K.Schum.	Tendril
	Arrabidaea chica (Bonpl.) Verl.	Tendril
	Arrabidaea craterophora (DC.) Bureau	Tendril
	Arrabidaea leucopogon (Cham.) Sandwith	Tendril
	Arrabidaea pulchella (Cham.) Bureau	Tendril
	Arrabidaea pulchra (Cham.) Sandwith	Tendril
	Arrabidaea triplinervia (Mart. ex DC.) Baill.	Tendril
	Bignonia binata Thunb.	Tendril
	Bignonia campanulata Cham.	Tendril
	Lundia obliqua Sond.	Tendril
	Mansoa difficilis (Cham.) Bureau & K.Schum.	Tendril
	Pleonotoma tetraquetra (Cham.) Bureau	Tendril
	Pyrostegia venusta (Ker Gawl.) Miers	Tendril

	Stizophyllum perforatum (Cham.) Miers	Tendril
	Tynanthus elegans Miers	Tendril
	Tynanthus fasciculatus (Vell.) Miers	Tendril
CACTACEAE	*Pereskia aculeata* Mill.	Scrambler
CELASTRACEAE	*Anthodon decussatum* Ruiz & Pav.	Tendril
COMBRETACEAE	*Combretum discolor* Taub.	Twining
DILLENIACEAE	*Davilla rugosa* Poir.	Twining
	Doliocarpus dentatus (Aubl.) Standl.	Twining
EUPHORBIACEAE	*Dalechampia triphylla* Lam.	Twining
FABACEAE	*Bauhinia microstachya* (Raddi) J.F.Macbr.	Tendril
	Dalbergia frutescens (Vell.) Britton	Scrambler
	Dalbergia lateriflora Benth.	Twininig
	Machaerium dimorphandrum Hoehne	Scrambler
	Machaerium oblongifolium Vogel	Scrambler
	Machaerium uncinatum (Vell.) Benth.	Scrambler
	Rhynchosia phaseoloides (Sw.) DC.	Twininig
LOGANIACEAE	*Strychnos brasiliensis* (Spreng.) Mart.	Scrambler
MALPIGHIACEAE	*Banisteriopsis anisandra* (A.Juss.) B.Gates	Twining
	Banisteriopsis argyrophylla (A.Juss.) B.Gates.	Twining
	Banisteriopsis lutea (Griseb.) Cuatrec.	Twining
	Dicella bracteosa (A.Juss.) Griseb.	Twining
	Heteropterys argyrophaea A.Juss.	Twining
	Heteropterys dumetorum(Griseb.) Nied.	Twining
	Mascagnia cordifolia (A.Juss.) Griseb.	Twining
MALVACEAE	*Byttneria catalpaefolia* Jacq.	Scrambler
MARCGRAVIACEAE	*Marcgravia polyantha* Delpino	Scrambler
MENISPERMACEAE	*Cissampelos glaberrima* A.St.-Hil.	Twining
NYCTAGINACEAE	*Pisonia aculeata* L.	Scrambler
PASSIFLORACEAE	*Passiflora sidaefolia* M.Roem.	Tendril
	Passiflora suberosa L.	Tendril
RHAMNACEAE	*Gouania latifolia* Reissek	Tendril
RUBIACEAE	*Chiococca alba* (L.) Hitchc.	Scrambler
SAPINDACEAE	*Cardiospermum grandiflorum* Sw.	Tendril
	Paullinia meliifolia Juss.	Tendril
	Paullinia rhomboidea Radlk.	Tendril
	Paullinia seminuda Radlk.	Tendril
	Paullinia spicata Benth.	Tendril
	Paullinia trigonia Vell.	Tendril
	Serjania caracasana (Jacq.) Willd.	Tendril
	Serjania communis Cambess.	Tendril
	Serjania fuscifolia Radlk.	Tendril

	Serjania laruotteana Cambess.	Tendril
	Serjania lethalis A.St.-Hil.	Tendril
	Serjania reticulata Cambess.	Tendril
	Thinouia mucronata Radlk.	Tendril
	Urvillea laevis Radlk.	Tendril
	Urvillea ulmacea Kunth	Tendril
	Urvillea uniloba Radlk.	Tendril
SMILCACEAE	*Smilax campestris* Griseb.	Tendril
	Smilax fluminensis Steud.	Tendril
	Smilax polyantha Griseb.	Tendril
TRIGONIACEAE	*Trigonia nivea* Cambess.	Twining
VITACEAE	*Cissus campestris* (Baker) Planch.	Tendril
	Cissus erosa Rich.	Tendril
	Cissus sulcicaulis (Baker) Planch	Tendril
	Cissus verticillata (L.) Nicolson & C.E.Jarvis	Tendril

Appendix 2: List of liana species abundance and climbing mechanisms from the studied fragment in Southeastern Brazil.

Family	Species	Number of Individuals	Climbing mechanisms
Fabaceae	*Acacia nitidifolia* (Sw.) DC.	37	scrambler
Bignoniaceae	*Adenocalymma Sp*	2	tendril
Bignoniaceae	*Adenocalymma marginatum* (Cham.) DC.	186	tendril
Bignoniaceae	*Adenocalymma paulistarum* Bureau & K.Schum	86	tendril
Bignoniaceae	*Amphilophium crucigerum* (L.) L.G.Lohmann	2	tendril
Bignoniaceae	*Anemopaegma chamberlaynii* (Sims) Buraeu & K.Schum.	4	tendril
Apocynaceae	*Apocynaceae sp*	2	
Araceae	*Araceae Sp*	3	
Fabaceae	*Bauhinia Sp*	2	tendril
Mapighiaceae	*Banisteriopsis anisandra* (A.Juss.) B.Gates	83	twinning
Bignoniaceae	*Bignonia campanulata* Cham.	814	tendril
Bignoniaceae	*Bignonia binata* Thunb.	5	tendril
Bignoniaceae	*Bignonia sciuripabula* (K. Schum.) L.G. Lohmann	156	tendril
Polygalaceae	*Bredemeyera Sp*	1	
Polygalaceae	*Bredemeyera floribunda* Willd	14	scrambler
Malvaceae	*Byttneria catalpaefolia* Jacq.	4	scrambler
Celastraceae	*Celastraceae Sp*	10	
Vitaceae	*Cissus sulcicaulis* (Baker) Planch	2	tendril
Vitaceae	*Cissus verticillata* (L.) Nicolson & C.E.Jarvis	3	tendril
Apocynaceae	*Condylocarpon isthimicum* (Vell.) A.DC.	102	twinning
Fabaceae	*Dalbergia Sp*	4	twinning
Euphorbiaceae	*Dalechampia triphylla* Lam.	5	twinning
Dilleniaceae	*Davilla rugosa* Poir.	33	twinning
Malpighiaceae	*Dicella bracteosa* (A.Juss.) Griseb	44	twinning
Fabaceae	*Dioclea Sp*	4	twinning
Bignoniaceae	*Dolichandra quadrivalvis* (Jacq.) L.G.Lohmann	201	tendril
Bignoniaceae	*Dolichandra uncata* (Andrews) L.G. Lohmann	4	tendril
Bignoniaceae	*Dolichandra unguis-cati* (L.) L.G. Lohmann	23	tendril
Dilleniaceae	*Doliocarpus dentatus* (Aubl.) Standl.	18	twinning
Celastraceae	*Elachyptera festiva* (Miers) A.C. Sm.	134	twinning

Apocynaceae	*Forsteronia Sp*	86	twinning
Apocynaceae	*Forsteronia australis* Müll.Arg	15	twinning
Apocynaceae	*Forsteronia leptocarpa* (Hook. & Arn.) A.DC.	3	twinning
Apocynaceae	*Forsteronia pilosa* (Vell.) Müll.Arg.	52	twinning
Apocynaceae	*Forsteronia pubescens* A.DC.	130	twinning
Bignoniaceae	*Fridericia conjugata* (Vell.) L.G. Lohmann	127	tendril
Bignoniaceae	*Fridericia triplinervia* (Mart. ex DC.) L.G.Lohmann	137	tendril
Bignoniaceae	*Fridericia pulchella* (Cham.) L.G.Lohmann	2	tendril
Bignoniaceae	*Fridericia samydoides* (Cham.) L.G.Lohmmann	3	tendril
Rhamnaceae	*Gouania latifolia* Reissek	2	tendril
Asparagaceae	*Herreria salsaparilha* Mart.	1	tendril
Malpighiaceae	*Hiraea Sp*	5	
Menispermaceae	*Hyperbaena domingensis* (DC.) Benth.	2	
Bignoniaceae	*Lundia obliqua* Sond	30	tendril
Malpighiaceae	*Malpighiaceae*	5	
Bignoniaceae	*Mansoa difficilis* (Cham.) Bureau & K.Schum.	556	tendril
Asteraceae	*Mikania glomerata* Spreng.	31	twinning
Araceae	*Monstera Sp*	9	
Moraceae	*Paullinia meliifolia* Juss.	3	tendril
Cactaceae	*Pereskia aculeata* Mill.	51	scrambler
Amaranthaceae	*Pfaffia paniculata* (Mart.) Kuntze	9	
Nyctagenaceae	*Pisonia aculeata* L.	1	scrambler
Bignoniaceae	*Pleonotoma tetraquetra* (Cham.) Bureau	14	tendril
Apocynaceae	*Prestonia tomentosa* R. Br.	2	twinning
Celastraceae	*Pristimera celastroides* (Kunth) A.C. Sm.	75	
Bignoniaceae	*Pyrostegia venusta* (Ker Gawl.) Miers	36	tendril
Fabaceae	*Rhynchosia phaseoloides* (Sw.) DC.	19	twinning
Sapindaceae	*Sapindaceae Sp*	3	
Phytolaccaceae	*Seguieria langsdorffii* Moq.	6	
Sapindaceae	*Serjania caracasana* (Jacq.) Willd.	59	tendril
Sapindaceae	*Serjania fuscifolia* Radlk.	20	tendril
Sapindaceae	*Serjania laruotteana* Cambess.	34	tendril
Bignoniaceae	*Stizophyllum perforatum* (Cham.) Miers	86	tendril
Bignoniaceae	*Tanaecium selloi* (Spreng.) L.G. Lohmann	46	tendril
Sapindaceae	*Thinouia mucronata* Radlk.	23	tendril

Celastraceae	*Tontelea sp*	9	
Euphorbiaceae	*Tragia alienata* (Didr.) Múlgura & M.M. Gut.	2	
Trigoniaceae	*Trigonia nivea* Cambess.	12	twinning
Bignoniaceae	*Tynanthus Sp*	1	tendril
Bignoniaceae	*Tynanthus fasciculatus* (Vell.) Miers	49	tendril
Sapindaceae	*Urvillea laevis* Radlk.	81	tendril
Sapindaceae	*Urvillea ulmacea* Kunth.	3	tendril
Cucurbitaceae	*Wilbrandia Sp*	3	tendril

Appendix 3: Number of Liana-Liana co-occurring significant pairs in the studied fragment of Southeastern Brazil. f.obs = Number of observed pairs, f.exp = Number of expected pairs, g = Observed number greater than expected, l = Observed number less than expected.

spi	**spj**	**ni**	**nj**	**f.obs**	**f.exp**	**p**	**g/l**
Acacia sp1	Acacia sp1	150	150	4	0.414	0.001	g
Amphilophium crucigerum	Acacia sp1	25	150	4	0.152	0.001	g
Forsteronia sp	Acacia sp1	794	150	10	4.283	0.014	g
Serjania fuscifolia	Acacia sp1	230	150	5	1.282	0.001	g
Serjania laruotteana	Acacia sp1	163	150	3	0.918	0.022	g
Adenocalymma	Adenocalymma	47	47	1	0.04	0.002	g
Adenocalymma paulistarum	Adenocalymma	616	47	4	1.068	0.008	g
Bignonia campanulata	Adenocalymma	4263	47	14	7.314	0.022	g
Serjania caracasana	Adenocalymma	517	47	3	0.963	0.04	g
Wilbrandia	Adenocalymma	42	47	3	0.075	0.001	g
Adenocalymma marginatum	Adenocalymma marginatum	1407	1407	81	36.51	0.001	g
Banisteriopsis anisandra	Adenocalymma marginatum	778	1407	68	40.51	0.001	g
Bignonia campanulata	Adenocalymma marginatum	4263	1407	171	221.2	0.001	g
Bignonia sciuripabula	Adenocalymma marginatum	1023	1407	71	53.06	0.018	g
Cissus sulcicaulis	Adenocalymma marginatum	32	1407	7	1.649	0.001	g
Condylocarpon isthimicum	Adenocalymma marginatum	808	1407	29	42.08	0.03	g
Dalechampia triphylla	Adenocalymma marginatum	29	1407	4	1.558	0.048	g

Davilla rugosa	Adenocalymma marginatum	365	1407	8	18.9	0.001	g
Dicella bracteosa	Adenocalymma marginatum	153	1407	16	7.98	0.002	g
Dolichandra quadrivalvis	Adenocalymma marginatum	1376	1407	44	71.41	0.002	g
Dolichandra unguis-cati	Adenocalymma marginatum	171	1407	18	8.837	0.006	g
Elachyptera festiva	Adenocalymma marginatum	837	1407	17	43.43	0.001	l
Forsteronia pilosa	Adenocalymma marginatum	169	1407	2	8.827	0.002	l
Forsteronia pubescens	Adenocalymma marginatum	590	1407	14	30.38	0.001	l
Forsteronia sp	Adenocalymma marginatum	794	1407	27	41.04	0.018	l
Frediricia conjugata	Adenocalymma marginatum	1147	1407	81	59.08	0.002	g
Frediricia triplinervia	Adenocalymma marginatum	898	1407	21	46.49	0.001	l
Gouania latifolia	Adenocalymma marginatum	26	1407	7	1.365	0.001	g
Hyperbaea domingensis	Adenocalymma marginatum	34	1407	12	1.77	0.001	g
Lundia obliqua	Adenocalymma marginatum	295	1407	44	15.32	0.001	g
Mansoa deficillis	Adenocalymma marginatum	3617	1407	122	187.8	0.001	l
Pereskia aculeata	Adenocalymma marginatum	805	1407	53	41.6	0.048	g
Rhynchosia phaseoloides	Adenocalymma marginatum	300	1407	49	15.64	0.001	g
Serjania caracasana	Adenocalymma marginatum	517	1407	55	26.45	0.001	g
Thinouvia mucronata	Adenocalymma marginatum	339	1407	34	17.73	0.001	g
Tragia alienata	Adenocalymma marginatum	39	1407	8	1.928	0.001	g
Tynanthus faciculatus	Adenocalymma marginatum	536	1407	4	27.92	0.001	l
Araceae	Adenocalymma paulistarum	24	616	4	0.582	0.001	g
Byttneria catalpaefolia	Adenocalymma paulistarum	18	616	3	0.406	0.002	g
Condylocarpon isthimicum	Adenocalymma paulistarum	808	616	9	18.33	0.016	l

Davilla rugosa	Adenocalymma paulistarum	365	616	15	8.293	0.032	g
Forsteronia australis	Adenocalymma paulistarum	23	616	2	0.542	0.03	g
Fredíricia conjugata	Adenocalymma paulistarum	1147	616	10	25.94	0.001	l
Fredíricia triplinervia	Adenocalymma paulistarum	898	616	43	20.44	0.001	g
Tynanthus faciculatus	Adenocalymma paulistarum	536	616	21	12.26	0.016	g
Wilbrandia	Adenocalymma paulistarum	42	616	3	0.912	0.032	g
Dicella bracteosa	Amphilophium crucigerum	153	25	5	0.151	0.001	g
Lundia obliqua	Amphilophium crucigerum	295	25	3	0.281	0.001	g
Stizophyllum perforatum	Amphilophium crucigerum	538	25	3	0.464	0.001	g
Bignonia campanulata	Anemopaegma chamberlaynii	4263	28	10	4.434	0.001	g
Forsteronia pubescens	Anemopaegma chamberlaynii	590	28	2	0.598	0.048	g
Fredíricia conjugata	Anemopaegma chamberlaynii	1147	28	4	1.215	0.012	g
Hiraea	Anemopaegma chamberlaynii	17	28	4	0.011	0.001	g
Tragia alienata	Anemopaegma chamberlaynii	39	28	2	0.038	0.001	g
Araceae	Araceae	24	24	1	0.011	0.001	g
Bredemeyera floribunda	Araceae	103	24	2	0.099	0.001	g
Elachyptera festiva	Araceae	837	24	3	0.751	0.008	g
Urvillea laevis	Araceae	731	24	2	0.657	0.038	g
Bignonia sciuripabula	Banisteriopsis anisandra	1023	778	19	29.05	0.038	l
Dalechampia triphylla	Banisteriopsis anisandra	29	778	3	0.83	0.018	g
Dolichandra quadrivalvis	Banisteriopsis anisandra	1376	778	28	39.63	0.05	l
Dolichandra unguis-cati	Banisteriopsis anisandra	171	778	10	4.798	0.032	g
Doliocarpus dentatus	Banisteriopsis anisandra	77	778	6	2.233	0.008	g
Elachyptera festiva	Banisteriopsis anisandra	837	778	12	23.92	0.002	l
Forsteronia pubescens	Banisteriopsis anisandra	590	778	8	16.97	0.008	l

Forsteronia sp	Banisteriopsis anisandra	794	778	12	22.75	0.014	l
Frediricia triplinervia	Banisteriopsis anisandra	898	778	13	25.95	0.002	l
Lundia obliqua	Banisteriopsis anisandra	295	778	16	8.338	0.016	g
Mansoa deficillis	Banisteriopsis anisandra	3617	778	75	103.1	0.004	l
Rhynchosia phaseoloides	Banisteriopsis anisandra	300	778	32	8.583	0.001	g
Thinouvia mucronata	Banisteriopsis anisandra	339	778	21	9.783	0.002	g
Tragia alienata	Banisteriopsis anisandra	39	778	7	1.118	0.001	g
Trigonia nivea	Banisteriopsis anisandra	130	778	9	3.694	0.001	g
Tynanthus faciculatus	Banisteriopsis anisandra	536	778	8	15.62	0.042	g
Urvillea ulmacea	Banisteriopsis anisandra	13	778	2	0.354	0.012	g
Bignonia campanulata	Bauhinia sp	4263	6	3	0.947	0.022	g
Mansoa deficillis	Bauhinia sp	3617	6	3	0.814	0.016	g
Bignonia campanulata	Bignonia binata	4263	13	5	2.11	0.036	g
Forsteronia sp	Bignonia binata	794	13	2	0.415	0.028	g
Stizophyllum perforatum	Bignonia binata	538	13	2	0.26	0.002	g
Bredemeyera	Bignonia campanulata	10	4263	6	1.599	0.001	g
Cissus verticillata	Bignonia campanulata	2	4263	2	0.33	0.006	g
Dolichandra uncata	Bignonia campanulata	16	4263	6	2.508	0.024	g
Elachyptera festiva	Bignonia campanulata	837	4263	169	131.6	0.002	g
Forsteronia pubescens	Bignonia campanulata	590	4263	74	92.57	0.04	l
Forsteronia sp	Bignonia campanulata	794	4263	155	124.9	0.008	g
Fredericia pulchella	Bignonia campanulata	3	4263	3	0.481	0.001	g
Frediricia triplinervia	Bignonia campanulata	898	4263	95	140.7	0.001	l
Hiraea	Bignonia campanulata	17	4263	9	2.666	0.002	g
Monstera	Bignonia campanulata	66	4263	5	10.24	0.036	l

Pfaffia paniculata	Bignonia campanulata	36	4263	12	5.714	0.001	g
Pleonotoma tetraquetra	Bignonia campanulata	112	4263	27	17.37	0.016	g
Pristimera celastroides	Bignonia campanulata	247	4263	59	38.89	0.002	g
Rhynchosia phaseoloides	Bignonia campanulata	300	4263	27	46.95	0.002	g
Seguieria langsdorfii	Bignonia campanulata	67	4263	4	10.55	0.012	l
Stizophyllum perforatum	Bignonia campanulata	538	4263	64	84.21	0.012	l
Thinouvia mucronata	Bignonia campanulata	339	4263	38	53.43	0.022	l
Tragia alienata	Bignonia campanulata	39	4263	2	6.017	0.03	l
Trigonia nivea	Bignonia campanulata	130	4263	8	20.56	0.001	l
Wilbrandia	Bignonia campanulata	42	4263	13	6.449	0.018	g
Bignonia sciuripabula	Bignonia sciuripabula	1023	1023	35	19.16	0.001	g
Condylocarpon isthimicum	Bignonia sciuripabula	808	1023	19	30.49	0.014	l
Dalbergia sp1	Bignonia sciuripabula	25	1023	6	0.972	0.002	g
Davilla rugosa	Bignonia sciuripabula	365	1023	4	13.87	0.002	l
Forsteronia australis	Bignonia sciuripabula	23	1023	3	0.874	0.02	g
Mansoa deficillis	Bignonia sciuripabula	3617	1023	112	136.2	0.016	l
Pristimera celastroides	Bignonia sciuripabula	247	1023	16	9.273	0.022	g
Pyrostegia venusta	Bignonia sciuripabula	421	1023	26	15.94	0.001	g
Stizophyllum perforatum	Bignonia sciuripabula	538	1023	6	20.15	0.001	l
Tanaecium selloi	Bignonia sciuripabula	380	1023	23	14.22	0.028	g
Urvillea ulmacea	Bignonia sciuripabula	13	1023	2	0.496	0.032	g
Forsteronia sp	Bredemeyera	794	10	2	0.319	0.014	g
Forsteronia sp	Bredemeyera floribunda	794	103	9	2.999	0.002	g
Pleonotoma tetraquetra	Bredemeyera	112	103	2	0.467	0.024	g

	floribunda						
Frediricia triplinervia	Byttneria catalpaefolia	898	18	3	0.576	0.006	g
Tanaecium selloi	Byttneria catalpaefolia	380	18	4	0.286	0.001	g
Cissus sulcicaulis	Cissus sulcicaulis	32	32	1	0.023	0.001	g
Frediricia conjugata	Cissus sulcicaulis	1147	32	7	1.405	0.001	g
Mikania glomerata	Cissus sulcicaulis	169	32	4	0.203	0.001	g
Pyrostegia venusta	Cissus sulcicaulis	421	32	2	0.525	0.032	g
Condylocarpon isthimicum	Condylocarpon isthimicum	808	808	23	11.88	0.001	g
Diocela sp	Condylocarpon isthimicum	18	808	2	0.556	0.028	g
Dolichandra unguis-cati	Condylocarpon isthimicum	171	808	10	5.139	0.038	g
Forsteronia pubescens	Condylocarpon isthimicum	590	808	31	17.37	0.001	g
Forsteronia sp	Condylocarpon isthimicum	794	808	11	23.57	0.004	g
Frediricia conjugata	Condylocarpon isthimicum	1147	808	20	34.22	0.002	g
Frediricia triplinervia	Condylocarpon isthimicum	898	808	17	26.59	0.05	l
Mansoa deficillis	Condylocarpon isthimicum	3617	808	141	107.6	0.002	g
Paulinia melifolia	Condylocarpon isthimicum	22	808	4	0.654	0.001	g
Pyrostegia venusta	Condylocarpon isthimicum	421	808	2	12.47	0.001	l
Rhynchosia phaseoloides	Condylocarpon isthimicum	300	808	3	9.084	0.014	l
Seguieria langsdorfii	Condylocarpon isthimicum	67	808	6	2.013	0.006	g
Serjania laruotteana	Condylocarpon isthimicum	163	808	10	4.873	0.034	g
Elachyptera festiva	Dalbergia sp1	837	25	4	0.752	0.001	g
Pristimera celastroides	Dalbergia sp1	247	25	2	0.199	0.002	g
Urvillea laevis	Dalbergia sp1	731	25	2	0.678	0.046	g
Frediricia conjugata	Dalechampia triphylla	1147	29	6	1.238	0.001	g
Pereskia aculeata	Dalechampia triphylla	805	29	3	0.84	0.018	g

Rhynchosia phaseoloides	Dalechampia triphylla	300	29	3	0.334	0.002	g
Serjania laruotteana	Dalechampia triphylla	163	29	2	0.187	0.004	g
Trigonia nivea	Dalechampia triphylla	130	29	3	0.135	0.001	g
Davilla rugosa	Davilla rugosa	365	365	10	2.492	0.002	g
Elachyptera festiva	Davilla rugosa	837	365	2	11.26	0.001	l
Forsteronia australis	Davilla rugosa	23	365	2	0.323	0.008	g
Forsteronia sp	Davilla rugosa	794	365	26	10.7	0.001	g
Paulinia melifolia	Davilla rugosa	22	365	3	0.267	0.001	g
Pristimera celastroides	Davilla rugosa	247	365	8	3.316	0.012	g
Seguieria langsdorfii	Davilla rugosa	67	365	4	0.913	0.004	g
Tontelea sp1	Davilla rugosa	44	365	4	0.561	0.001	g
Dicella bracteosa	Dicella bracteosa	153	153	7	0.444	0.001	g
Fredиricia conjugata	Dicella bracteosa	1147	153	2	6.364	0.03	l
Lundia obliqua	Dicella bracteosa	295	153	13	1.531	0.001	g
Mikania glomerata	Dicella bracteosa	169	153	3	1.017	0.036	g
Pfaffia paniculata	Dicella bracteosa	36	153	2	0.22	0.004	g
Pleonotoma tetraquetra	Dicella bracteosa	112	153	5	0.616	0.001	g
Prestonia tomentosa	Dicella bracteosa	11	153	2	0.071	0.001	g
Stizophyllum perforatum	Dicella bracteosa	538	153	8	2.999	0.014	g
Serjania caracasana	Diocela sp	517	18	2	0.329	0.022	g
Urvillea laevis	Diocela sp	731	18	2	0.501	0.022	g
Dolichandra uncata	Dolichandra quadrivalvis	16	1376	3	0.805	0.012	g
Elachyptera festiva	Dolichandra quadrivalvis	837	1376	60	42.12	0.012	g
Forsteronia pubescens	Dolichandra quadrivalvis	590	1376	43	29.57	0.014	g
Gouania latifolia	Dolichandra quadrivalvis	26	1376	5	1.391	0.002	g
Mansoa deficillis	Dolichandra quadrivalvis	3617	1376	254	183.8	0.001	g
Monstera	Dolichandra quadrivalvis	66	1376	9	3.363	0.002	g
Pereskia aculeata	Dolichandra	805	1376	29	41.02	0.046	l

	quadrivalvis						
Pfaffia paniculata	Dolichandra quadrivalvis	36	1376	5	1.854	0.012	g
Pyrostegia venusta	Dolichandra quadrivalvis	421	1376	13	21.41	0.032	l
Serjania caracasana	Dolichandra quadrivalvis	517	1376	15	26.05	0.012	l
Thinouvia mucronata	Dolichandra quadrivalvis	339	1376	7	17.19	0.006	l
Urvillea laevis	Dolichandra quadrivalvis	731	1376	52	37.26	0.018	g
Elachyptera festiva	Dolichandra uncata	837	16	2	0.493	0.032	g
Frediricia triplinervia	Dolichandra uncata	898	16	2	0.517	0.028	g
Pristimera celastroides	Dolichandra uncata	247	16	3	0.152	0.001	g
Dolichandra unguis-cati	Dolichandra unguis-cati	171	171	4	0.557	0.001	g
Doliocarpus dentatus	Dolichandra unguis-cati	77	171	5	0.473	0.001	g
Frediricia conjugata	Dolichandra unguis-cati	1147	171	3	7.241	0.048	g
Herreria salsaparilha	Dolichandra unguis-cati	31	171	3	0.21	0.001	g
Monstera	Dolichandra unguis-cati	66	171	3	0.439	0.001	g
Thinouvia mucronata	Dolichandra unguis-cati	339	171	9	2.171	0.001	g
Tontelea sp1	Dolichandra unguis-cati	44	171	2	0.271	0.002	g
Trigonia nivea	Dolichandra unguis-cati	130	171	4	0.794	0.001	g
Doliocarpus dentatus	Doliocarpus dentatus	77	77	4	0.128	0.001	g
Herreria salsaparilha	Doliocarpus dentatus	31	77	4	0.092	0.001	g
Monstera	Doliocarpus dentatus	66	77	4	0.201	0.001	g
Thinouvia mucronata	Doliocarpus dentatus	339	77	4	0.934	0.008	g
Trigonia nivea	Doliocarpus dentatus	130	77	5	0.352	0.001	g
Urvillea laevis	Doliocarpus dentatus	731	77	5	2.063	0.028	g
Elachyptera festiva	Elachyptera	837	837	39	12.77	0.001	g

	festiva						
Forsteronia pubescens	Elachyptera festiva	590	837	29	18.08	0.022	g
Forsteronia sp	Elachyptera festiva	794	837	13	24.37	0.012	l
Mansoa deficillis	Elachyptera festiva	3617	837	151	111.6	0.001	g
Pyrostegia venusta	Elachyptera festiva	421	837	6	12.91	0.028	l
Serjania fuscifolia	Elachyptera festiva	230	837	2	7.016	0.014	l
Stizophyllum perforatum	Elachyptera festiva	538	837	5	16.78	0.002	l
Tanaecium selloi	Elachyptera festiva	380	837	3	11.63	0.002	l
Tontelea sp1	Elachyptera festiva	44	837	5	1.389	0.002	g
Stizophyllum perforatum	Forsteronia australis	538	23	4	0.438	0.001	g
Urvillea laevis	Forsteronia australis	731	23	4	0.608	0.001	g
Forsteronia pilosa	Forsteronia pilosa	169	169	5	0.537	0.001	g
Frediricia triplinervia	Forsteronia pilosa	898	169	15	5.672	0.001	g
Serjania laruotteana	Forsteronia pilosa	163	169	4	1.049	0.001	g
Tanaecium selloi	Forsteronia pilosa	380	169	6	2.326	0.02	g
Tynanthus faciculatus	Forsteronia pilosa	536	169	15	3.325	0.001	g
Forsteronia pubescens	Forsteronia pubescens	590	590	28	6.353	0.001	g
Frediricia conjugata	Forsteronia pubescens	1147	590	7	25.23	0.001	l
Mansoa deficillis	Forsteronia pubescens	3617	590	119	78.61	0.001	g
Pereskia aculeata	Forsteronia pubescens	805	590	9	17.42	0.026	l
Seguieria langsdorfii	Forsteronia pubescens	67	590	5	1.461	0.006	g
Tynanthus faciculatus	Forsteronia pubescens	536	590	24	11.78	0.001	g
Forsteronia sp	Forsteronia sp	794	794	25	11.72	0.002	g
Frediricia conjugata	Forsteronia sp	1147	794	47	33.51	0.022	g
Pereskia aculeata	Forsteronia sp	805	794	36	23.64	0.012	g

Serjania caracasana	Forsteronia sp	517	794	7	15.13	0.008	l
Tanaecium selloi	Forsteronia sp	380	794	2	11.16	0.001	l
Tynanthus	Forsteronia sp	4	794	2	0.149	0.001	g
Tynanthus faciculatus	Forsteronia sp	536	794	8	15.75	0.024	l
Frediricia conjugata	Frediricia conjugata	1147	1147	34	24.15	0.034	g
Gouania latifolia	Frediricia conjugata	26	1147	6	1.067	0.001	g
Lundia obliqua	Frediricia conjugata	295	1147	5	12.48	0.022	l
Mikania glomerata	Frediricia conjugata	169	1147	17	7.008	0.001	g
Paulinia melifolia	Frediricia conjugata	22	1147	3	0.91	0.03	g
Pereskia aculeata	Frediricia conjugata	805	1147	45	34.14	0.05	g
Pristimera celastroides	Frediricia conjugata	247	1147	4	10.49	0.018	l
Serjania fuscifolia	Frediricia conjugata	230	1147	19	9.898	0.008	g
Stizophyllum perforatum	Frediricia conjugata	538	1147	12	22.94	0.004	l
Tanaecium selloi	Frediricia conjugata	380	1147	25	16.19	0.03	g
Frediricia samydoides	Frediricia samydoides	5	5	2	0	0.001	g
Frediricia triplinervia	Frediricia samydoides	898	5	1	0.142	0.012	g
Frediricia triplinervia	Frediricia triplinervia	898	898	24	14.91	0.012	g
Mikania glomerata	Frediricia triplinervia	169	898	1	5.718	0.004	l
Pereskia aculeata	Frediricia triplinervia	805	898	37	26.4	0.03	g
Pyrostegia venusta	Frediricia triplinervia	421	898	22	13.77	0.018	g
Rhynchosia phaseoloides	Frediricia triplinervia	300	898	2	10.05	0.001	l
Stizophyllum perforatum	Frediricia triplinervia	538	898	34	17.61	0.001	g
Tanaecium selloi	Frediricia triplinervia	380	898	25	12.68	0.001	g
Tynanthus faciculatus	Frediricia triplinervia	536	898	26	17.72	0.044	g
Monstera	Herreria salsaparilha	66	31	2	0.061	0.001	g

Thinouvia mucronata	Herreria salsaparilha	339	31	2	0.391	0.016	g
Trigonia nivea	Herreria salsaparilha	130	31	3	0.164	0.001	g
Urvillea laevis	Herreria salsaparilha	731	31	3	0.882	0.032	g
Hiraea	Hiraea	17	17	2	0.003	0.001	g
Lundia obliqua	Hyperbaea domingensis	295	34	7	0.345	0.001	g
Serjania caracasana	Hyperbaea domingensis	517	34	3	0.671	0.008	g
Lundia obliqua	Lundia obliqua	295	295	7	1.581	0.002	g
Mansoa deficillis	Lundia obliqua	3617	295	26	39.09	0.03	l
Pleonotoma tetraquetra	Lundia obliqua	112	295	6	1.241	0.001	g
Pyrostegia venusta	Lundia obliqua	421	295	13	4.616	0.004	g
Rhynchosia phaseoloides	Lundia obliqua	300	295	7	3.335	0.032	g
Tragia alienata	Lundia obliqua	39	295	3	0.427	0.002	g
Urvillea laevis	Lundia obliqua	731	295	3	7.886	0.03	l
Mikania glomerata	Mansoa deficillis	169	3617	12	22.68	0.008	l
Rhynchosia phaseoloides	Mansoa deficillis	300	3617	18	39.85	0.001	l
Serjania caracasana	Mansoa deficillis	517	3617	49	69.45	0.008	l
Tynanthus faciculatus	Mansoa deficillis	536	3617	93	71.57	0.016	g
Mikania glomerata	Mikania glomerata	169	169	6	0.506	0.001	g
Pfaffia paniculata	Mikania glomerata	36	169	3	0.227	0.001	g
Prestonia tomentosa	Mikania glomerata	11	169	3	0.064	0.001	g
Pristimera celastroides	Mikania glomerata	247	169	5	1.522	0.008	g
Rhynchosia phaseoloides	Mikania glomerata	300	169	5	1.938	0.022	g
Seguieria langsdorfii	Mikania glomerata	67	169	6	0.439	0.001	g
Serjania caracasana	Mikania glomerata	517	169	7	3.222	0.04	g
Urvillea laevis	Mikania glomerata	731	169	16	4.508	0.001	g
Monstera	Monstera	66	66	1	0.08	0.006	g
Trigonia nivea	Monstera	130	66	3	0.324	0.001	g
Urvillea laevis	Monstera	731	66	8	1.749	0.001	g

Pereskia aculeata	Pereskia aculeata	805	805	4	12.1	0.004	l
Rhynchosia phaseoloides	Pereskia aculeata	300	805	20	8.955	0.001	g
Tynanthus faciculatus	Pereskia aculeata	536	805	26	15.98	0.012	g
Prestonia tomentosa	Pfaffia paniculata	11	36	2	0.014	0.001	g
Serjania fuscifolia	Pfaffia paniculata	230	36	2	0.305	0.008	g
Thinouvia mucronata	Pfaffia paniculata	339	36	2	0.441	0.032	g
Urvillea laevis	Pfaffia paniculata	731	36	3	0.963	0.028	g
Stizophyllum perforatum	Pisonia aculeata	538	6	2	0.112	0.001	g
Tanaecium selloi	Pisonia aculeata	380	6	2	0.105	0.001	g
Pleonotoma tetraquetra	Pleonotoma tetraquetra	112	112	1	0.219	0.042	g
Thinouvia mucronata	Prestonia tomentosa	339	11	2	0.121	0.001	g
Pristimera celastroides	Pristimera celastroides	247	247	5	1.105	0.002	g
Thinouvia mucronata	Pristimera celastroides	339	247	7	3.096	0.03	g
Tontelea sp1	Pristimera celastroides	44	247	7	0.394	0.001	g
Rhynchosia phaseoloides	Pyrostegia venusta	300	421	12	4.694	0.002	g
Urvillea ulmacea	Pyrostegia venusta	13	421	2	0.198	0.001	g
Wilbrandia	Pyrostegia venusta	42	421	2	0.609	0.044	g
Rhynchosia phaseoloides	Rhynchosia phaseoloides	300	300	11	1.619	0.001	g
Serjania caracasana	Rhynchosia phaseoloides	517	300	13	5.672	0.006	g
Thinouvia mucronata	Rhynchosia phaseoloides	339	300	20	3.681	0.001	g
Tragia alienata	Rhynchosia phaseoloides	39	300	6	0.43	0.001	g
Trigonia nivea	Rhynchosia phaseoloides	130	300	4	1.437	0.026	g
Urvillea laevis	Rhynchosia phaseoloides	731	300	14	8.113	0.036	g

Seguieria langsdorfii	Seguieria langsdorfii	67	67	1	0.09	0.008	g
Tynanthus faciculatus	Serjania caracasana	536	517	2	10.24	0.001	l
Serjania fuscifolia	Serjania fuscifolia	230	230	4	0.975	0.002	g
Tynanthus faciculatus	Serjania fuscifolia	536	230	11	4.568	0.006	g
Urvillea ulmacea	Serjania fuscifolia	13	230	2	0.103	0.001	g
Stizophyllum perforatum	Serjania laruotteana	538	163	8	3.262	0.018	g
Tynanthus	Serjania laruotteana	4	163	2	0.024	0.001	g
Tynanthus faciculatus	Serjania laruotteana	536	163	8	3.223	0.008	g
Urvillea ulmacea	Serjania laruotteana	13	163	2	0.076	0.001	g
Stizophyllum perforatum	Stizophyllum perforatum	538	538	14	5.383	0.001	g
Tanaecium selloi	Stizophyllum perforatum	380	538	15	7.55	0.014	g
Trigonia nivea	Stizophyllum perforatum	130	538	6	2.687	0.042	g
Urvillea ulmacea	Stizophyllum perforatum	13	538	3	0.25	0.001	g
Tanaecium selloi	Tanaecium selloi	380	380	9	2.637	0.002	g
Tragia alienata	Thinouvia mucronata	39	339	2	0.488	0.03	g
Tontelea sp1	Tontelea sp1	44	44	1	0.046	0.002	g
Trigonia nivea	Trigonia nivea	130	130	4	0.315	0.001	g
Urvillea laevis	Trigonia nivea	731	130	7	3.439	0.034	g
Tynanthus faciculatus	Tynanthus faciculatus	536	536	14	5.445	0.001	g
Urvillea laevis	Tynanthus faciculatus	731	536	6	14.12	0.014	l

Appendix 4: Standardized phylogenetic diversity “a”(PD) and Mean phylogenetic distance “b” (MPD) of phorophyte species in the plots of studied fragment in Southeastern Brazil. Obs = Observed value, rnd = Mean metric value, sd rnd = Standard deviation random values. Significant values at *P* < 0.001are in bold.

(a)

Plot	ntaxa	pd.obs	pd.rand.mean	pd.rand.sd	pd.obs.rank	pd.obs.z	pd.obs.p	runs
1	9	826.6	908.8108371	87.061262	162	-0.9443	0.162	999
2	**7**	**602.3**	**737.9347746**	**77.590716**	**40**	**-1.7481**	**0.04**	**999**
3	**8**	**649.476**	**824.6965326**	**81.430606**	**21**	**-2.1518**	**0.021**	**999**
4	8	799.944	828.7611879	85.356733	336	-0.3376	0.336	999
5	7	751.611	739.3216144	77.991505	544	0.15757	0.544	999
6	8	712.286	825.4576369	83.439328	93	-1.3563	0.093	999
7	11	981.038	1069.911538	92.791673	182	-0.9578	0.182	999
8	6	696.333	655.1574195	69.332408	726	0.59389	0.726	999
9	6	658.333	653.5042772	70.842971	499	0.06817	0.499	999
10	10	999.792	989.5543888	95.262109	512	0.10746	0.512	999
11	7	714.133	745.5507162	76.738787	340	-0.4094	0.34	999
12	8	775.619	827.5076553	81.932231	270	-0.6333	0.27	999
13	**9**	**680.7**	**910.3487661**	**82.825112**	**4**	**-2.7727**	**0.004**	**999**
14	9	860.786	910.1356259	85.996833	287	-0.5739	0.287	999
15	11	1119.02	1071.611103	91.442613	695	0.51841	0.695	999
16	7	648.778	737.8497013	77.063399	123	-1.1558	0.123	999
17	7	770.167	738.9606207	79.336721	637	0.39334	0.637	999
18	8	782.033	827.5826949	80.382037	280	-0.5667	0.28	999
19	6	725.667	651.6495543	71.38745	851	1.03684	0.851	999
20	9	822.957	905.7624389	89.704282	174	-0.9231	0.174	999
21	13	1157.44	1210.139796	101.35193	288	-0.52	0.288	999
22	6	635.367	650.6292365	73.259335	411	-0.2083	0.411	999
23	9	837.133	907.5649791	86.7778	193	-0.8116	0.193	999
24	10	939.44	988.7443742	94.388115	299	-0.5224	0.299	999
25	**10**	**777.667**	**989.7968939**	**88.513134**	**11**	**-2.3966**	**0.011**	**999**
26	3	424.333	357.704381	52.203829	975	1.27632	0.975	999
27	8	760.7	824.0841084	83.104247	213	-0.7627	0.213	999
28	7	614.367	740.2306499	77.687216	58	-1.6201	0.058	999
29	4	380.022	462.2905612	61.081846	87	-1.3469	0.087	999
30	12	1029.87	1144.471586	92.230214	104	-1.2426	0.104	999
31	12	1046.47	1143.022959	96.745302	160	-0.998	0.16	999
32	**13**	**1033.74**	**1213.249015**	**103.26879**	**48**	**-1.7382**	**0.048**	**999**
33	10	1063.24	991.2609416	88.740085	777	0.8111	0.777	999
34	**7**	**578.722**	**739.4294857**	**77.07711**	**25**	**-2.085**	**0.025**	**999**

35	8	790.056	828.6925493	87.024993	334	-0.444	0.334	999
36	8	753.333	827.9962721	82.053014	178	-0.9099	0.178	999
37	6	593.167	651.8586069	67.210653	195	-0.8733	0.195	999
38	**8**	**655.333**	**826.4371549**	**79.435793**	**20**	**-2.154**	**0.02**	**999**
39	12	1116.33	1143.893699	99.146357	378	-0.278	0.378	999
40	9	935.5	913.2236023	87.730001	595	0.25392	0.595	999
41	5	453.167	558.4371404	65.744295	67	-1.6012	0.067	999
42	9	887.252	914.8929125	91.269447	363	-0.3028	0.363	999
43	3	407.5	358.6208051	50.860402	869	0.96105	0.869	999
44	11	1026.06	1066.142916	94.342025	338	-0.4248	0.338	999
45	10	1020.28	989.2086252	87.843815	630	0.35375	0.63	999
46	8	746.833	825.0069416	82.375276	170	-0.949	0.17	999
47	8	772.69	830.4096031	78.3062	224	-0.7371	0.224	999
48	8	726.25	827.3767538	79.537406	108	-1.2714	0.108	999
49	**6**	**496.167**	**648.3994991**	**73.821142**	**29**	**-2.0622**	**0.029**	**999**
50	11	1121.79	1064.99232	94.837449	711	0.59891	0.711	999
51	4	539.167	462.2534428	59.645149	950	1.28951	0.95	999
52	13	1274.94	1217.309675	101.97386	693	0.56518	0.693	999
53	5	456.167	557.6361486	67.2725	75	-1.5083	0.075	999
54	**4**	**358.167**	**460.7648645**	**58.113791**	**47**	**-1.7655**	**0.047**	**999**
55	10	879.833	990.0224708	90.383614	109	-1.2191	0.109	999
56	8	814.633	825.1634921	85.558143	430	-0.1231	0.43	999
57	**4**	**359.967**	**462.5735906**	**55.975143**	**42**	**-1.8331**	**0.042**	**999**
58	8	724.833	824.5801045	77.606293	107	-1.2853	0.107	999
59	10	1008.69	988.4331901	93.418455	577	0.21684	0.577	999
60	5	492.524	559.8386237	63.964397	147	-1.0524	0.147	999
61	5	600.5	559.1154085	67.20397	732	0.61581	0.732	999
62	6	668.583	651.4574727	71.276577	592	0.24027	0.592	999
63	8	803.633	827.7963838	80.980462	380	-0.2984	0.38	999
64	6	587.833	652.108274	72.727382	189	-0.8838	0.189	999
65	**8**	**677.911**	**824.8986001**	**83.080016**	**44**	**-1.7692**	**0.044**	**999**
66	11	1069.33	1067.884272	91.512557	503	0.01583	0.503	999
67	**8**	**620.467**	**823.7290102**	**81.916929**	**6**	**-2.4813**	**0.006**	**999**
68	7	809	740.5505223	76.190409	813	0.8984	0.813	999
69	9	917.833	906.4610224	87.783422	532	0.12955	0.532	999
70	10	849.744	984.8089742	89.377759	79	-1.5112	0.079	999
71	5	564.3	560.3499573	64.920712	515	0.06084	0.515	999
72	10	987.357	995.6900793	91.857648	459	-0.0907	0.459	999
73	4	383.333	461.178897	56.276661	96	-1.3833	0.096	999
74	**7**	**515.167**	**744.3798411**	**75.592331**	**5**	**-3.0322**	**0.005**	**999**
75	**8**	**577.7**	**823.074457**	**82.531665**	**4**	**-2.9731**	**0.004**	**999**

76	4	483.5	459.952664	57.40475	653	0.4102	0.653	999
77	**11**	**838.363**	**1065.527087**	**95.998417**	**15**	**-2.3663**	**0.015**	**999**
78	3	368.667	357.9933839	52.663948	477	0.20267	0.477	999
79	**9**	**726.633**	**911.5473004**	**83.478693**	**17**	**-2.2151**	**0.017**	**999**
80	8	736.538	831.4113061	78.557253	118	-1.2077	0.118	999
81	12	1045.14	1149.00911	97.730171	149	-1.0628	0.149	999
82	7	691.8	736.6272823	78.57831	271	-0.5705	0.271	999
83	8	854.5	828.1082115	81.403903	614	0.32421	0.614	999
84	7	722.083	743.7908887	74.570169	365	-0.2911	0.365	999
85	7	637.722	738.7442806	74.674627	98	-1.3528	0.098	999
86	6	623.467	654.2609172	69.247449	315	-0.4447	0.315	999
87	14	1307.91	1283.736492	102.77977	583	0.23521	0.583	999
88	7	688.8	739.7052632	75.317308	243	-0.6759	0.243	999
89	9	1004.17	912.0686123	86.383263	861	1.06616	0.861	999
90	10	909.571	988.5948776	88.97951	204	-0.8881	0.204	999
91	4	553.833	460.1699043	59.414264	966	1.57645	0.966	999
92	13	1298.86	1219.071616	103.27346	770	0.77263	0.77	999
93	12	1007.28	1146.437874	95.757745	81	-1.4533	0.081	999
94	9	895.278	911.4989399	87.093804	399	-0.1862	0.399	999
95	7	730.25	739.5046776	76.385332	429	-0.1212	0.429	999
96	**5**	**384.7**	**557.8574896**	**64.67305**	**9**	**-2.6774**	**0.009**	**999**
97	10	857.578	994.0773056	90.133958	73	-1.5144	0.073	999
98	7	651.167	739.1443337	74.934591	129	-1.1741	0.129	999
99	7	674.7	743.8001807	76.144781	194	-0.9075	0.194	999
100	12	1042.27	1144.031513	99.850195	162	-1.0191	0.162	999

(b)

Plot	ntaxa	mpd.ob	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p	runs
1	9	215.013	237.5643116	15.5526244	82	-1.45	0.082	999
2	**7**	**203.965**	**238.4346366**	**17.721911**	**45**	**-1.94502**	**0.045**	**999**
3	8	214.155	238.0972921	15.6445837	70	-1.5304	0.07	999
4	8	225.175	238.3139966	16.2871179	181	-0.80673	0.181	999
5	7	240.106	239.0282306	17.6505598	495	0.061051	0.495	999
6	8	220.723	238.6569633	16.545657	136	-1.08392	0.136	999
7	11	226.5	237.8822625	12.8371613	188	-0.8867	0.188	999
8	6	233.467	237.5030287	19.5148522	401.5	-0.20684	0.4015	999
9	6	235.133	238.3128273	19.8810068	422	-0.15993	0.422	999
10	10	222.761	238.5342652	14.3148383	129	-1.10187	0.129	999
11	7	221.044	238.2499663	17.7793757	173	-0.96772	0.173	999
12	8	226.604	237.5634058	15.9830026	239	-0.68571	0.239	999
13	**9**	**195.843**	**237.7177537**	**14.8327243**	**10**	**-2.82316**	**0.01**	**999**
14	9	239.757	238.4133862	15.9592826	499	0.084166	0.499	999
15	11	233.97	238.0017728	13.3690204	369	-0.30155	0.369	999
16	**7**	**197.598**	**237.4072828**	**17.892017**	**24**	**-2.22498**	**0.024**	**999**
17	7	232.794	237.7903732	17.9765645	364	-0.27796	0.364	999
18	8	227.217	238.3187684	16.0684078	225	-0.69093	0.225	999
19	6	251.933	237.8648899	19.752214	756	0.712246	0.756	999
20	9	220.422	237.5749372	14.9618436	130	-1.14647	0.13	999
21	13	226.903	238.5598233	11.8082906	163	-0.98717	0.163	999
22	6	232.071	237.9365869	19.5984224	360	-0.29928	0.36	999
23	9	222.227	237.792494	15.0740817	138	-1.03263	0.138	999
24	10	236.605	237.883503	14.1060184	457	-0.09065	0.457	999
25	10	227.867	237.5353962	13.5147487	234	-0.71542	0.234	999
26	3	263.333	236.6517829	35.4920242	786.5	0.751762	0.7865	999
27	8	229.264	238.9408752	16.2825375	252	-0.59429	0.252	999
28	7	208.13	237.9894807	18.5131193	61	-1.61287	0.061	999
29	**4**	**171.007**	**237.4651175**	**26.9071504**	**20**	**-2.46989**	**0.02**	**999**
30	12	218.299	238.6331283	12.3629645	54	-1.64476	0.054	999
31	12	232.368	237.8946773	12.6018296	320	-0.43859	0.32	999
32	13	222.514	238.1150753	11.4221035	85	-1.36587	0.085	999
33	10	247.499	237.7095973	14.6173542	731	0.669743	0.731	999
34	**7**	**185.259**	**238.4436012**	**17.6641525**	**10**	**-3.01086**	**0.01**	**999**
35	8	223.524	238.1083618	15.7454617	170	-0.92627	0.17	999
36	8	209.381	237.6813449	16.4911868	62	-1.71609	0.062	999
37	6	214.533	238.9483523	19.7531768	112	-1.236	0.112	999
38	**8**	**185.012**	**238.7332069**	**16.2178568**	**4**	**-3.31248**	**0.004**	**999**
39	12	226.318	238.1798887	12.1182125	163	-0.97883	0.163	999

40	9	236.667	237.8499351	14.6922926	436	-0.08054	0.436	999
41	**5**	**176.733**	**239.290793**	**22.2205229**	**12**	**-2.8153**	**0.012**	**999**
42	9	241.634	238.6821253	15.0013274	548	0.196801	0.548	999
43	3	252.111	237.8554151	36.1940532	534	0.393869	0.534	999
44	11	232.282	237.6521637	12.9342836	325	-0.41519	0.325	999
45	10	242.101	238.1987681	13.5027336	591	0.289032	0.591	999
46	8	218.952	238.2278207	16.1667297	122	-1.19229	0.122	999
47	8	230.585	237.9871943	15.9663321	323	-0.46361	0.323	999
48	8	217.673	238.4646498	16.2660829	107	-1.27824	0.107	999
49	**6**	**183.644**	**238.2352556**	**20.8573181**	**11**	**-2.61735**	**0.011**	**999**
50	11	233.912	238.1683208	12.8732595	365	-0.33066	0.365	999
51	4	257.722	238.7131668	26.0796704	764	0.728884	0.764	999
52	13	252.615	238.1761018	11.9190005	895	1.211379	0.895	999
53	**5**	**185.267**	**237.5198991**	**22.5874506**	**21**	**-2.31337**	**0.021**	**999**
54	**4**	**161.278**	**237.4344868**	**28.0242407**	**11**	**-2.71753**	**0.011**	**999**
55	**10**	**212.326**	**237.9266036**	**14.282596**	**46**	**-1.79244**	**0.046**	**999**
56	8	239.303	237.5628231	16.443494	521	0.105838	0.521	999
57	**4**	**181.156**	**237.9994862**	**27.7944828**	**41**	**-2.04515**	**0.041**	**999**
58	**8**	**208.607**	**238.7712808**	**15.7651502**	**43**	**-1.91334**	**0.043**	**999**
59	10	244.616	237.5157208	14.2275524	669	0.499043	0.669	999
60	5	213.171	237.6430757	23.0820265	140	-1.0602	0.14	999
61	5	235.8	238.6969175	22.8347323	410	-0.12686	0.41	999
62	6	239.033	237.6984893	20.6507326	499	0.064639	0.499	999
63	8	228.76	239.0121782	15.7639018	240	-0.65039	0.24	999
64	6	211.289	237.5125383	19.7530518	104	-1.32757	0.104	999
65	**8**	**201.434**	**237.6833024**	**16.4435405**	**27**	**-2.20446**	**0.027**	**999**
66	11	228.733	237.8822641	13.1246854	241	-0.69708	0.241	999
67	**8**	**182.093**	**238.1816876**	**16.5472386**	**3**	**-3.38962**	**0.003**	**999**
68	7	240.19	238.0918188	17.5271123	520	0.119738	0.52	999
69	9	224.864	238.1313265	15.436206	186	-0.85948	0.186	999
70	**10**	**212.944**	**238.6920758**	**13.9180979**	**39**	**-1.84996**	**0.039**	**999**
71	5	225.193	238.3364776	22.6176828	250	-0.5811	0.25	999
72	10	245.906	237.4283409	14.1114336	694	0.600798	0.694	999
73	**4**	**190.667**	**237.9640028**	**27.2103197**	**48**	**-1.73821**	**0.048**	**999**
74	**7**	**169.127**	**238.6483663**	**17.8320022**	**1**	**-3.89869**	**0.001**	**999**
75	**8**	**180.098**	**238.1880552**	**15.9802141**	**4**	**-3.63515**	**0.004**	**999**
76	4	233.556	238.2506804	26.5740215	359.5	-0.17668	0.3595	999
77	**11**	**210.565**	**237.9660527**	**13.6647785**	**39**	**-2.00525**	**0.039**	**999**
78	3	226.222	238.5156299	32.516484	323	-0.37807	0.323	999
79	**9**	**206.878**	**237.8424424**	**15.2358516**	**26**	**-2.03236**	**0.026**	**999**
80	8	222.61	238.2488396	16.3237671	171	-0.95805	0.171	999

81	12	239.145	238.1618328	12.1480167	513	0.080899	0.513	999
82	7	221.013	238.8998847	17.0690772	146	-1.04793	0.146	999
83	8	240.5	238.1222563	16.7691762	525	0.141793	0.525	999
84	7	231.913	238.3542835	17.4287495	328	-0.3696	0.328	999
85	7	211.127	238.092199	18.1775936	76	-1.48343	0.076	999
86	6	212.529	238.22421	19.3012411	92	-1.33128	0.092	999
87	14	227.909	237.5452104	11.1774748	181	-0.86212	0.181	999
88	7	220.441	238.3983304	18.0240878	148	-0.99628	0.148	999
89	9	251.176	238.1640751	15.2290211	804	0.854412	0.804	999
90	10	227.846	237.8213789	14.5890709	226	-0.68375	0.226	999
91	4	272.389	237.2154355	27.9387848	880	1.258947	0.88	999
92	13	235.253	238.4102296	11.6412123	365	-0.27122	0.365	999
93	**12**	**207.412**	**238.354748**	**12.3409424**	**12**	**-2.50729**	**0.012**	**999**
94	9	223.117	237.5293068	15.181514	176	-0.94931	0.176	999
95	7	240.786	237.8832119	18.7159955	535	0.155081	0.535	999
96	**5**	**170.973**	**238.419554**	**23.5994091**	**13**	**-2.85796**	**0.013**	**999**
97	10	216.218	237.9892742	14.0298363	72	-1.55176	0.072	999
98	7	205.841	238.2035926	18.2799348	51	-1.77037	0.051	999
99	7	213.511	238.0845854	18.294627	104	-1.34321	0.104	999
100	12	230.731	237.6138172	11.942574	270	-0.57633	0.27	999