JULIANO VAN MELIS

“ESTRUTURAÇÃO DA COMUNIDADE DE TREPADEIRAS EM UMA FLORESTA ESTACIONAL SEMIDECÍDUA”

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> *"There is a theory which states that if ever anyone discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarrely inexplicable.*
>
> *There is another theory which states that this has already happened."*
>
> Douglas Adams (1952-2001)

Resumo

Apesar da importância que as trepadeiras apresentam em florestas tropicais, estudos sobre a montagem da comunidade de lianas (trepadeiras lenhosas e sublenhosas) que investiguem desde a contribuição dos fatores abióticos e bióticos até fatores intrínsecos (coexistência entre indivíduos) são escassos. O objetivo geral desta tese é pesquisar a estruturação da comunidade das espécies de lianas em uma Floresta Estacional Semidecídua (FES), investigando (1) a importância relativa dos fatores ambientais e espaciais para diferentes espécies de lianas, (2) a estruturação filogenética da comunidade de trepadeiras em diferentes ambientes, e (3) os efeitos diretos ou mediados das árvores e arbustos para o número de espécies e indivíduos de trepadeiras. Mostramos que (1) grande parte da variação na composição de espécies de lianas em uma FES é devido a fatores não investigados (fatores estocásticos) e o espaço (autocorrelação espacial). Portanto, concluímos que os maiores determinantes na variação da composição de espécies de lianas em uma FES é a aleatoriedade (sendo reflexo da variação estocástica das populações) e a limitação por dispersão (demonstrada pela alta autocorrelação espacial). No segundo capítulo (2), encontramos que uma maioria discreta das parcelas apresentou maior aproximação filogenética do que o esperado ao acaso na comunidade de trepadeiras amostrada. Houve pouca influência de variáveis relacionadas à dinâmica florestal na variação da aproximação filogenética, sendo que áreas com árvores mais altas e maior proporção de árvores do presente apresentavam maior aproximação filogenética que outras áreas. Concluímos que em áreas de dossel mais baixo e menor proporção de árvores do presente (clareiras) não apresentam menor sinal filogenético, pois todas as espécies de lianas apresentariam potencial de existirem nestas áreas, enquanto que nas áreas de floresta madura haveria a existência de filtros ambientais para a existência de poucos ramos filogenéticos. Por último (3), encontramos que os atributos da comunidade de árvores e arbustos são fatores importantes na variação dos atributos da comunidade de lianas, sendo parte dele decorrente do distúrbio no dossel. Mas o distúrbio no dossel como fator direto é mais importante na variação da abundância e número de espécies de lianas em uma Floresta Estacional Semidecídua.

Palavras-chave: trepadeiras, lianas, vinhas, partição de variância, estrutura filogenética, modelos generalizados aditivos, modelo de equações estruturais.

Abstract

Despite the fact that climbing plants present in tropical forests, studies which investigate the contribution of abiotic and biotic factors or intrinsic factors (coexistence between individuals) on community assembly of lianas (woody and sub-woody climbers) are scarce. The overall objective of this thesis is to research the community structure of liana species in a Seasonal Semideciduous Forest (SSF), investigating (1) the relative importance of environmental and spatial factors on community assembly of lianas, (2) the phylogenetic structure of climbing plants community along the forest development (treefall gaps to old-growth forest), and (3) the direct or indirect effects of trees and shrubs for the number of species and individuals of climbing plants. We show that (1) much of the variation in species composition of lianas in a SSF is due to stochastic factors and space. Therefore, we conclude that the major determinants of variation in lianas' species composition in a TSF are stochastic variance of populations, shown by the unexplained factors, and dispersion limitation, shown by spatial autocorrelation. In the second chapter (2), we found that a slight majority of the sample plots showed cluster phylogenetic structure in the climbing plants community. There was a slight influence of variables related to forest dynamics in the variation of the phylogenetic structure, and areas with tall trees and higher proportion of present trees had higher values of clustering in phylogenetic structure than other areas. We conclude that in areas of lower canopy and smaller proportion of present trees (treefall gaps) showed few phylogenetic branches, since all species of climbing plants would be existing in these areas, while areas of old-growth forest would demonstrate environmental filters for the climbing plants. Finally, we also found (3) that the community of trees and shrubs' attributes (abundance and species richness) are important factors in the variation of attributes liana community (species richness and abundance), being part of it due to the canopy disturbance. But canopy disturbance was the more important direct factor in variance of abundance and species richness of lianas in a Seasonal Semideciduous Forest.

Keywords: climbing plants, lianas, vines, Neotropical forest, variation partitioning, phylogenetic structure, Mean pairwise distance (MPD), Net relatedness index (NRI, Generalized Additive Model (GAM), Structural equation modeling (SEM)

SUMÁRIO

Introdução Geral

Apesar das lianas representarem mais de 40% dos caules lenhosos e mais de 20% da diversidade de espécies lenhosas das florestas tropicais (Putz & Mooney 1991), estudos abordando a estruturação das comunidades de lianas são raros (por exemplo: DeWalt et al. 2000, 2006, Dalling et al. 2012). Para árvores e arbustos, independente da formação florestal, o levantamento amostral é mais fácil, não necessitando de protocolos, como construídos recentemente para lianas (por exemplo: Gerwing et al. 2006, Schnitzer *et al.* 2008). O próprio termo "liana" para esta sinúsia de plantas é controvertido (para discussões em português, veja Martins & Batalha 2011, Villagra 2012). Este trabalho adotou o termo "lianas" para plantas lenhosas ou sublenhosas que mantem-se enraizadas no solo por toda a sua vida e que necessitam de suporte externo para manterem-se eretas, usando métodos preênseis (gavinha, caule volúvel, etc) para isso. O termo generalista "trepadeira" (em inglês: *climbing plants*) também foi utilizado quando não há exclusão de espécies herbáceas (não lignificadas e ausência de periderme).

Em florestas tropicais, são muitos os estudos que abordam a montagem da comunidade e a coexistência entre espécies de árvores (por exemplo: Harms et al. 2001; Potts et al. 2004; John et al. 2007, Kraft et al. 2008), sendo esparsos os estudos abordando as lianas. A montagem de uma comunidade local é entendida como o processo onde espécies provenientes de um pool regional colonizam e interagem para formar estas comunidades locais (HilleRisLambers et al. 2012). Entender o papel de fatores determinísticos e aleatórios na montagem das comunidades tem gerado importantes resultados e debates para que o objetivo de predizer e entender como as espécies se distribuem nas comunidades seja alcançado (Weiher et al. 1998).

As lianas podem ter vantagem competitiva sobre as árvores devido a suas características ecofisiológicas (ver Granados & Korner 2002, Schnitzer et al. 2005, Schnitzer & Bongers 2011), podendo intensificar a perda de biomassa arbórea (Laurance et al. 2001, Phillips et al. 2002), pois as lianas, ao necessitarem de árvores-suportes (forófitos), ocasionam redução do crescimento e maiores taxas de mortalidade, além da diminuição da fertilidade destas árvores (Putz 1984a, Stevens 1987, van der Heijden & Phillips 2009a). Portanto, entender como as comunidades de lianas são organizadas e quais variáveis estão mais diretamente associadas com sua estrutura podem fornecer importantes conhecimentos para fundamentar seu manejo se necessário.

Normalmente, fatores ambientais originam padrões biogeográficos em largas escalas (Wiens & Donoghue 2004), enquanto interações interespecíficas atuam na escala fina das comunidades contribuindo para a coexistência das espécies (Chesson 2000). Para lianas, a importância de variáveis topoedáficas (altitude e nutrientes do solo) mostraram resultados modestos na influência nos valores de abundância e densidade em escalas grandes, desde em uma escala fina de 50 ha (Dalling et al. 2012) até em uma escala de região biogeográfica (van der Heijden & Phillips 2008, 2009b). Contudo, desde as escalas mais finas até as maiores escalas de estudo, o distúrbio no dossel é indicado como o maior determinante para a abundância, número de espécies e existência de algumas espécies (Laurance et al. 2001, van der Heijden & Phillips 2008, 2009b, Malizia et al. 2010, Dalling et al. 2012). Com isso, o aumento observado na abundância, biomassa e produtividade de lianas nas florestas neotropicais seria consequência do aumento de distúrbios destas florestas (Schnitzer & Bongers 2011), além do aumento do carbono atmosférico, que provoca maiores taxas de morte e crescimento (*turnover*, na forma mais simplificada em inglês) dos indivíduos arbóreos (Lewis et al. 2004).

Mas os fatores ambientais são considerados somente um dos filtros na montagem das comunidades locais. Antes de passarem pelo filtro abiótico, as espécies capazes de se estabelecerem em um local são oriundas de um subconjunto influenciado pela sorte/acaso (*chance*, em inglês) e pela dispersão (Belyea & Lancaster 1999, HilleRisLambers et al. 2012). As teorias sobre montagem de comunidades atualmente existentes podem ser divididas em duas categorias: aquelas que asseguram que estratégias distintas (nicho) permitem a coexistência das espécies e aquelas em que processos demográficos estocásticos e a dispersão são mais importantes para a coexistência das espécies, sendo denominada de “neutra”, pois o papel da limitação da dispersão e de fatores demográficos estocásticos são tão importantes que se pode assumir a equivalência do *fitness per capita* das espécies (Hubbell 2001, Wright 2002, Kraft et a. 2008, McGill 2010).

Um método chave para entender a importância relativa desses fatores na montagem das comunidades é a utilização das características morfofisiológicas (*traits,* em inglês) das espécies que influenciem a dinâmica populacional e a colonização das espécies nos ambientes (Hardy et al. 2012). Esse método torna-se difícil de ser executado com lianas, pois são poucos os estudos que contemplem características morfofisiológicas de trepadeiras (ver Asner & Martin 2012) e pela possibilidade de características foliares das trepadeiras não estarem correlacionadas com a área amostrada, pois elas podem esparramar os seus galhos em áreas mais afastadas do dossel. Pela possibilidade de se enraizarem em um lugar e disponibilizar as folhas em lugares mais afastados, as lianas podem ser responsáveis pela homogeneização de nutrientes edáficos na floresta, pois elas adquirem nutrientes em um local pelas raízes e depositam suas folhas mortas na serapilheira em um local mais afastado de onde foi adquirido o nutriente (Powers et al. 2004). Uma alternativa para o método baseado em características morfofisiológicas é a utilização de dados filogenéticos como substituto (*surrogate*, em inglês), onde a conservação filogenética do nicho é assumida. Esta conservação é a tendência do nicho de um táxon manter-se estável dentro do clado (Wiens et al. 2010). Portanto, a presença de um sinal filogenético positivo em um ambiente (maior aproximação dos clados, do que o esperado ao acaso) seria o reflexo de um forte filtro ambiental para a montagem de comunidades (Webb 2000) ou diferenças nas aptidões (*fitness* em inglês) e exclusão competitiva das espécies (Mayfield & Levine 2010).

Porém, a competição por recursos que ocorre em espécies que utilizam o mesmo nicho em táxons com conservação filogenética do nicho, resulta em padrões filogenéticos randômicos, principalmente em florestas maduras e primárias (Verdú et al. 2009, Letcher 2010, Letcher et al. 2012, Norden et al. 2012, Whitfield et al. 2012). Por isso, além dos processos de limitação por dispersão e filtro ambiental, o último processo/filtro para a existência de uma espécie em um ambiente é relacionado às relações interespecíficas. Lianas dependem de um suporte externo, em geral uma árvore (forófito), para o seu estabelecimento (Nesheim & Økland 2007). Assim, as relações liana-forófito exercem papel importante na organização da comunidade de lianas.

Algumas características morfológicas e fisiológicas das espécies de árvores e arbustos podem favorecer a escalada de lianas em seus galhos, enquanto outras características impedem ou diminuem a infestação por lianas (Putz 1984a, 1984b, Malizia & Grau 2006). Dentre essas características que dificultam ou impedem a infestação por lianas estão principalmente uma taxa de crescimento alta, troncos flexíveis, folhas grandes caducas (por exemplo: espécies de Arecaceae e *Cecropia*), casca lisa e elevada altura da primeira ramificação (Putz 1984b, Campbell & Newberry 1993, Muthuramkumar & Parthasarathy 2001, Carsten et al. 2002, Campanello et al. 2007). A diversidade de árvores representaria heterogeneidade ambiental, possibilitando a maior diversidade de trepadeiras (Sfair & Martins 2011). Portanto, a relação das espécies de trepadeiras com as espécies de árvores e arbustos seria o último filtro para a montagem da comunidade de trepadeiras, influenciando a sua diversidade.

Objetivo geral da tese

Esta tese tem como objetivo geral pesquisar a estruturação da comunidade das espécies de lianas em uma Floresta Estacional Semidecídua, investigando (1) a importância relativa dos fatores ambientais e espaciais para diferentes espécies de lianas, (2) a estruturação filogenética da comunidade de trepadeiras em diferentes ambientes, e (3) os efeitos diretos ou mediados das árvores e arbustos para o número de espécies e indivíduos de trepadeiras.

Organização da tese

O **Capítulo 1** desta tese foca na contribuição proporcional de fatores ambientais e espaciais para a variação da diversidade de lianas (maiores que 1.0 cm de Diâmetro a Altura do Peito) em um fragmento de Floresta Estacional Semidecídua. Os nossos resultados mostraram que grande parte da variação (82%) na composição das espécies de lianas é explicada por fatores não determinísticos, pois não são relacionados com os fatores edáficos, características das árvores coocorrentes (florestais) ou a autocorrelação espacial. Dentre estes fatores, o espaço sozinho foi responsável por cerca de 10% da variação na composição das espécies. Cerca de 6% da variação foi explicada em parte pelos fatores edáficos e florestais, mas sendo grande parte redundantes com o espaço. A alta autocorrelação espacial refletiria a limitação por dispersão na variação da composição das espécies de lianas. Portanto, concluímos que a variação da composição de espécies de lianas em uma Floresta Estacional Semidecídua é determinada pela limitação por dispersão dentre os fatores estudados, mas grande parte não é explicada pelos fatores analisados.

O **Capítulo 2** desta tese investiga a estruturação filogenética da comunidade de trepadeiras (maiores que 1.0 cm de Diâmetro a Altura do Peito) em uma Floresta Estacional Semidecídua relacionando com características da comunidade florestal, buscando indícios de exclusão competitiva ou filtro de habitat entre os ramos filogenéticos ao longo da sucessão florestal (mosaico florestal). Encontramos que 60% dos quadrantes amostrados mostraram significativa aproximação na estruturação filogenética, enquanto no restante, as espécies existentes apresentaram estruturação filogenética igual ao esperado ao acaso (aleatório). Houve pequena influência de fatores relacionados à dinâmica florestal no padrão filogenético das amostras, onde áreas com árvores mais altas e com maior proporção de árvores do presente apresentam maior aproximação dos ramos filogenéticos.

O **Capítulo 3** teve como objetivo investigar por modelos de equações estruturais, os efeitos diretos e indiretos dos parâmetros (abundância e riqueza) da comunidade de árvores e arbustos (maiores que 15 cm de perímetro a altura do peito), distúrbio do dossel e fatores edáficos na determinação da variação dos parâmetros (abundância e riqueza) da comunidade de trepadeiras (maiores que 1 cm de Diâmetro a Altura do Peito) em uma Floresta Estacional Semidecídua. Encontramos que os atributos da comunidade de árvores e arbustos são fatores importantes na variação dos atributos da comunidade de trepadeiras, mas o distúrbio no dossel é o fator direto mais importante na variação da abundância e número de espécies de trepadeiras em uma Floresta Estacional Semidecídua.

Esta tese possui dois anexos. No **anexo 1** são disponibilizados os scripts utilizados nas análises estatísticas realizadas pela linguagem R, na versão 2.12 para Windows 7. No **anexo 2** é disponibilizada a tabela fitossociológica das trepadeiras inventariadas neste estudo, caracterizando-as como lenhosas, sublenhosas e herbáceas e com dados sobre densidade, frequência, número de ramos e ordenadas pelo Índice de Valor de Importância.

Referências bibliográficas

ASNER, G.P.; MARTIN, R.E. 2012. Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition. Ecology Letters 15(9):1001-1007.

BELYEA, L.R.; LANCASTER, J. 1999. Assembly rules within a contingent ecology. Oikos 86: 402–416.

CAMPANELLO, P.I.; GARIBALDI, J.F.; GATTI, M.G.; GOLDSTEIN, G. 2007. Lianas in a subtropical Atlantic Forest: host preference and tree growth. Forest Ecology and Management 242(2-3): 250-259.

CAMPBELL, E.J.F.; NEWBERY, D.M. 1993. Ecological relationship between lianas and trees in lowland rain forest in Sabah, East Malaysia. Journal of Tropical Ecology 9:469-490

CARSTEN, L.D.; JUOLA, F.A.; MALE, T.D.; CHERRY, S. 2002. Host associations of lianas in the south-east Queesland rain forest. Journal of Tropical Ecology 18:107-120.

CHESSON, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–66

DALLING, J.W.; SCHNITZER, S.A.; BALDECK, C.; HARMS, K.E.; JOHN, R.; MANGAN, S.A.; LOBO, E.; YAVITT, J.B.; HUBBELL, S.P. 2012. Resource-based habitat associations in a neotropical liana community. Journal of Ecology 100:1174-1182.

DEWALT, S.J.; SCHNITZER, S.A.; DENSLOW, J.S. 2000. Density and diversity of lianas along a seasonal tropical forest chronosequence in central Panama. Journal of Tropical Ecology 16: 1–19.

DEWALT, S.J.; ICKES, K.; NILUS, R.; HARMS, K.E.; BURSLEM, D.F.R.P. (2006) Liana habitat associations and community structure in a Bornean lowland tropical forest. Plant Ecology 186: 203–216.

GERWING, J.J.; SCHNITZER, S.A.; BURNHAM, R.J.; BONGERS, F.; CHAVE, J.; DEWALT, S.J.; EWANGO, C.E.N.; FOSTER, R.; KENFACK, D.; MARTÍNEZ-RAMOS, M.; PARREN, M.; PARTHASARATHY, M.; PÉREZ-SALICRUP, D.R.; PUTZ, E.F.; THOMAS, D.W. 2006. A standard protocol of liana censuses. Biotropica 38: 256-261.

GRANADOS, J.; KÖRNER, C. 2002. In deep shade, elevated CO2 increases the vigor of tropical climbing plants. Global Change Ecology 8(11): 1109-1117

HARDY, O.J.; COUTERON, P.; MUNOZ, F.; RAMESH, B.R.; PÉLISSIER, R. 2012. Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. Global Ecology and Biogeography 21: 1007–1016

HARMS, K.E.; CONDIT, R.; HUBBELL, S.P.; FOSTER, R.B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. Journal of Ecology 89: 947–959.

HILLERISLAMBERS, J.; ADLER, P.B.; HARPOLE, W.S.; LEVINE, J.M.; MAYFIELD, M.M. 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics 43:227–48

HUBBELL, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton. 448p

JOHN, R.; DALLING, J.W.; HARMS, K.E.; YAVITT, J.B.; STALLARD, R.F.; MIRABELLO, M.; HUBBELL, S.P.; VALENCIA, R.; NAVARRETE, H.; VALLEJO, M.; FOSTER, R.B. 2007. Soil nutrients Influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences of the United States of America, 104, 864–869.

KRAFT, N.J.B.; VALENCIA, R.; ACKERLY, D.D. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. Science 322: 580-582.

LAURANCE, W.F.; PÉREZ-SALICRUP, D.; DELAMÔNICA, P.; FEARNSIDE, P.M.; D'ANGELO, S.; JEROZOLINSKI, A.; POHL, L.; LOVEJOY, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82: 105–116.

LETCHER, S.G. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. Proceedings of the Royal Society B 277:97–104.

LETCHER, S.A.; CHAZDON, R.J.; ANDRADE, A.C.S.; BONGERS, F.; VAN BREUGEL, M.; FINEGAN, B.; LAURANCE, S.G.; MESQUITA, R.C.G.; MARTÍNEZ-RAMOS, M.; WILLIAMSON, G.B. 2012 Phylogenetic community structure during succession: Evidence from three Neotropical forest sites. Perspectives in Plant Ecology, Evolution and Systematics 14 (2012) 79–87

LEWIS, S.L.; PHILLIPS, O.L.; BAKER, T.R.; LLOYD, J.;MALHI, Y.; ALMEIDA, S.; HIGUCHI, N.; LAURANCE, W.F.; NEILL, D.A.; SILVA, J.N.M; TERBORGH, J.; TORRES-LEZAMA, A.; VÁSQUEZ-MARTINEZ, R.; BROWN, S.; CHAVE, J.; KUEBLER, C.; NÚÑEZ-VARGAS,P.; VINCETI, B. 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. Philosophical Transactions of the Royal Society of London Series B 35: 421–436.

MALIZIA, A.; GRAU, H. R. 2006. Liana-host tree associations in a subtropical montane forest of north-western Argentina. Journal of Tropical Ecology 22:331-339.

MALIZIA, A.; GRAU, H.R.; LICHSTEIN, J.W. 2010. Soil phosphorus and disturbance influence liana communities in a subtropical montane forest. Journal of Vegetation Science 21(3): 551-560.

MARTINS, F.R.; BATALHA, M.A. 2011. Formas de vida, espectro biológico de Raunkiaer e fisionomia da vegetação. In: FELFILI, J. M.; EISENLOHR, P.V.; MELO, M.M.R.F.; ANDRADE, L.A.; MEIRA NETO, J.A.A. (Eds). Fitossociologia no Brasil, métodos e estudo de casos: v.1. Editora UFV, Viçosa.

MAYFIELD, M.M.; LEVINE, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093

MCGILL, B.J. 2010. Towards a unification of unified theories of biodiversity. Ecology Letters 13: 627-642.

MUTHURAMKUMAR, S.; PARTHASARATHY, N. 2001. Tree-liana relationships in a tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. Journal of Tropical Ecology 17:395-409.

NESHEIM, I.; ØKLAND, R.H. 2007. Do vines in neotropical forests see the forest or the trees? Journal of vegetation Science 18:395-404.

NORDEN, N.; LETCHER, S.G.; BOUKILI, V.; SWENSON, N.G.; CHAZDON, R. 2012. Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. Ecology 93(8): S70–S82

PHILLIPS, O.L.; MARTINEZ, R.V.; ARROYO, L.; BAKER, T R.; KILLEEN, T.; LEWIS, S. L.; MALHI, Y.; MENDOZA, A.M.; NEILL, D.; VARGAS, P.N.; ALEXIADES, M. CERÓN, C.; DI FIORE, A.; ERWIN, T.; JARDIM, A.; PALACIOS, W.; SALDIAS, M.; VINCENTI, B. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418: 770-774.

POTTS,M.D.; DAVIES, S.J.; BOSSERT, W.H.; TAN, S.; NUR SUPARDI,M.N. 2004. Habitat heterogeneity and niche structure of trees in two tropical rain forests. Oecologia, 139: 446–453.

POWERS, J.S.; KALICIN, M.; NEWMAN, M. 2004. Tree species do not influence local soil chemistry in a species-rich Costa Rican rain forest. Journal of Tropical Ecology 20: 587-590.

PUTZ, F. E. 1984a.The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713–1724.

PUTZ, F. E. 1984b. How trees avoid and shed lianas. Biotropica 16: 19-23.

PUTZ, F.E.; MOONEY, H.A. (Eds.) 1991. The biology of vines. Cambridge: Cambridge University Press. 544p

SCHNITZER, S.A.; KUZEE, M.; BONGERS, F. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. Journal of Ecology 93: 1115-1125.

SCHNITZER, S.A.; BONGERS, F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecology Letters 14(4): 397-406.

SCHNITZER, S.A.; RUTISHAUSER, S.; AGUILAR, S. 2008. Supplemental protocol for liana censuses. Forest Ecology and Management 255: 1044-1049.

SFAIR, J.C.; MARTINS, F.R. 2011. The role of heterogeneity on climber diversity: is liana diversity related to tree diversity? Global Journal of Biodiversity Science and Management, 1(1): 1-10.

STEVENS, G.C. 1987. Lianas as structural parasites: the Bursera simaruba example. Ecology 68: 77–81.

VAN DER HEIJDEN, G.M.F.; PHILLIPS, O.L. 2008. What controls liana success in Neotropical forests? Global Ecology and Biogeography 17: 372–383.

VAN DER HEIJDEN, G.M.F.; PHILLIPS, O.L. 2009a. Liana infestation impacts tree growth in a lowland tropical moist forest. Biogeosciences Discussions 6: 3133-3158.

VAN DER HEIJDEN, G.M.F.; PHILLIPS, O.L. 2009b. Environmental effects on Neotropical liana species richness. Journal of Biogeography 36(8): 1561-1572.

VERDÚ, M.; REY, P.J.; ALCÁNTARA, J.M.; SILES, G.; VALIENTE-BANUET, A. 2009. Phylogenetic signatures of facilitation and competition in successional communities. Journal of Ecology 97(6): 1171-1180.

VILLAGRA, B.L.P. 2012. Estrutura da comunidade de trepadeiras em Mata Atlântica, Santo André, SP, Brasil. Tese (Doutorado) - Instituto de Botânica da Secretaria do Meio Ambiente do Estado de São Paulo.

WEIHER, E.; CLARKE, G.D.P.; KEDDY, P.A. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos 81(2): 309-322.

WHITFIELD, T.J.S.; KRESS, W.J.; ERICKSON, D.L.; WEIBLEN, G.D. 2012. Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. Ecography 35(9): 821-830.

WIENS, J.; DONOGHUE, M. 2004.Historical biogeography, ecology and species richness. Trends in Ecology and Evolution 19:639–644

WIENS, J.J.; ACKERLY, D.D.; ALLEN, A.P.; ANACKER, B.L.; BUCKLEY, L.B.; CORNELL, H.V.; DAMSCHEN, E.I.; DAVIES, T.J.; GRYTNES, J.A.; HARRISON, S.P.; HAWKINS, B.A.; HOLT, R.D.; MCCAIN, C.M.; STEPHENS, P.R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13: 1310–1324

WRIGHT, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1-14

Capítulo 1: Liana community assembly on fine scale in a Neotropical Seasonal Forest.[1]

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Title: Liana community assembly on fine scale in a Neotropical Seasonal Forest

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Abstract: A great proportion of the vascular flora of tropical seasonal forests is represented by lianas, and the local community assembly of lianas is believed to be submitted to the same limitations imposed by dispersal, environment, and community internal dynamics of other growth forms. Our aim was to investigate how much each of these filters contributes to liana community assembly in a Neotropical Seasonal forest on a fine spatial scale. The internal dynamics was expressed through ecounity type, and tree wood density, crown illumination index, median and maximum height and deciduousness, which were used to characterize each plot. As environmental variables we considered plot altitude and soil pH, texture and nutrients (topo-edaphic variables). Applying PCNM (principal coordinates neighbor matrices) to the coordinates of each plot, we admitted that liana dispersal limitation was indicated by a positive spatial autocorrelation explained only by space. We calculated the variation partitioning among topo-edaphic, forest tree dynamics, and spatial variables (PCNM) to explain the spatial distribution of liana species per plot in a well-conserved forest fragment in SE Brazil. We found a large amount (82.05%) of unexplained variation in the liana data. Among the isolated explaining variables, space (representing dispersal limitation) contributed 9.88%, internal dynamics 1.16%, and topo-edaphic variables 0.88%. The rest 6.03% was due to interaction among these three sets of variables, most being redundant with space. Applying redundancy analyses to the species with the greatest scores, we observed that some liana species occurred most frequently in shaded plots with tall trees, denoting variation of liana composition among ecounits. Moreover, liana species distribution responded to the same predictors of tree community that had been found by other authors in the same plots. Dispersal limitation was the main filter assembling liana community on fine scale, whereas filters associated with tree community internal dynamics and topo-edaphic variables played a reduced role.

Keywords: internal dynamics, spatial autocorrelation, vines, climbers, Atlantic forest

Introduction

Dispersal limitation, environmental limitations and internal dynamics (interspecific relationships) are considered to be groups of factors or agents capable of assembling ecological communities at local scale (Belyea and Lancaster 1999). Dispersal and environment would respectively limit the arrival and establishment of species in a given site, whereas interspecific relationships would determine which species can persist and constitute a community (Booth and Swanton 2002). Initially, dispersal filters act on regional species pool through dispersal barriers, such as distance or landscape arrangement, reducing the number of species that can arrive at a site (Belyea and Lancaster 1999). Then, community assembly is modeled by a series of environmental filters (Keddy 1992, Weiher and Keddy 1995), such as soil humidity and fertility, which affects species demographic responses (Russo et al. 2005), implying that not all species that arrived can establish in that site. Finally, the biotic filter acts, because once the species survived the environmental filter and established, the individuals grow and interact and only those with strong competitive ability persist (Keddy 1992). However, a pervasive issue in investigating ecological communities is how to disentangle the operation of each one of these filters.

Lianas (woody climber plants) are an important growth-form in tropical forests, and we believe that like other growth-forms the assembly of liana communities is submitted to the same filters imposed by dispersal, environment, and internal dynamics. Indeed, on large spatial scale, liana, tree, and shrub diversity shows congruent patterns (van der Heijden and Phillips 2009, Sfair and Martins 2011), which may indicate similar evolutionary and ecological processes assembling the communities of these growth-forms. Soil and climate are among the most important limiting environmental variables of liana distribution. For instance, Schnitzer and Bongers (2002), DeWalt et al. (2006) and Malizia et al. (2010) found that soil fertility and moisture can limit liana establishment on a local scale; Gentry (1991), Schnitzer (2005), and van der Heijden and Phillips (2009) observed greater abundance and richness of lianas in tropical seasonal climates. These findings denote a likely influence of local constrains on the biogeography of lianas. Concerning the internal dynamics, Sfair and Martins (2011) found a relationship between liana richness and Shannon heterogeneity index of trees; and Malizia et al. (2010) concluded that liana communities seem to be strongly influenced by canopy disturbance rather than by the abundance or species composition of canopy trees. In addition, most liana species are dispersed by wind and present clonal reproduction generating aggregated spatial patterns (Gentry 1991; Nabe-Nielsen and Hall 2002), which indicates a strong influence of dispersal limitation.

A sequence of random events is considered a stochastic process, such as pure dispersal limitation, since predicting which species will in fact arrive at a site is not possible (Hubbell 2001, Ozinga et al. 2005). In a model in which the community composition is controlled by dispersal limitation, floristic similarity among sites would decrease with increasing geographical distance and would be independent of any environmental difference among sites (Hubbell 2001, Jones et al. 2006). As different authors have tried to explain the variation of the spatial structure of ecological communities, they have noticed that a significant proportion of the variation remains always unexplained due mainly to non-environmental variance (Borcard et al. 1992; Legendre 1993). Faced with these results, Jones et al. (2008) concluded that pure dispersal limitation could explain at least part of this unexplained variation. In the absence of strong environmental gradients, pure dispersal limitation generates species spatial patterns on fine scales (Legendre et al. 2009). On the other hand, coordinated responses of different species of the same community to one or more biotic or abiotic variables are considered to indicate the predominance of deterministic processes, because these variables can significantly be correlated with species occurrence and abundance and so predict their variation (Cielo Filho et al. 2007; Jones et al. 2008).

Since climbers constitute a great proportion of the diversity of tropical forests (Gentry 1991), we find it worthwhile to understand how much environment (represented by both abiotic and biotic filters) and space (understood as the dispersal filter) are important to assemble liana communities. Here we considered a fragment of the Neotropical Seasonal Semideciduous Forest to investigate the relative importance of space, topo-edaphic variables, and internal forest dynamics to explain the spatial variation of a liana community. We adopted a fine-scale approach to investigate how much of the liana community variation relies on space. If most of the variation of the liana community could be explained by space only, the community assembly would be presided by pure dispersal limitation. For this purpose we investigated: (1) which environmental variables were important to explain variation of liana species abundance among plots; (2) how different environmental variables and space contributed to an overall explanation of this variation; and (3) what are the patterns of the spatial and environmental variables structuring the liana community. We hypothesized that environmental and internal dynamics variables are important to liana community assembly, but considering their reproductive biology (clonality and wind-dispersed seeds), dispersal limitation is of paramount importance.

Material and Methods

To distinguish between niche and neutral processes, respectively considered as purely deterministic and purely stochastic models (Hubbel 2005), ecologists have applied variation partitioning and spatial modeling on different spatial scales to detect dispersal and/or environmental limitation processes in the community assembly (Gilbert and Lechowicz 2004; Smith and Lundholm 2010). Therefore, we used this approach to detect how much of the variation is due to deterministic factors (environmental filters) or due dispersal limitation (purely spatial autocorrelation).

Study Site

The sampled area is located in a highly fragmented area in the municipality of Campinas, São Paulo state, SE Brazil (Figure 1-2). The forest fragment (total area: 24.5 km²) is located in the Sousas-Joaquim Egídio Environmental Protection Area. The vegetation is seasonal semideciduous forest with an accentuated rainfall seasonality and deciduousness observed in up to 50% of the canopy trees during the dry season (IBGE 1992). Altitude varies between 630 and 760 m above sea level. The predominant soil is Acrisol (FAO nomenclature) with sandy texture and many rock fragments (Embrapa 1999). According to Koeppen's classification, the climate is Cwa, with hot, rainy summer and mild, dry winter, temperatures between -3°C and 18°C in the coolest months (June-July), summer with unless four months (November-March) with temperature mean warmer than 10°C and 22°C in the warmest months, and summer precipitation in the moist month (January) not higher than ten-fold of the driest month in the winter (CIIAGRO/IAC).

The stand (22°49'S and 46°55'W) we studied has 6.5 ha in the south portion of the fragment and was selected by Cielo-Filho et al. (2007) with the aid of a 1:25,000 aerial photograph and examination in the field, avoiding great edge effects resulting from fragmentation processes. There are no signs of recent anthropogenic disturbances in the area, such as coal on the ground surface, soot on the tree trunks or recent logging evidences, however, this forest could not be classified as a primary vegetation. The sampling area is located on a slope, approximately 270 m in length, with average steepness of 15%, and 40 m of difference between the up and low ends (Figure 1c). We sampled 100 square plots with 100 m² each, separated with each other from 2m (nearest distance) to 270m (farther distance), which were settled down through simple randomization, totaling a sampled area of 10,000 m² (Figure 1c).

Sampling

From August to October 2008 we resampled all the living trees with DBH ≥ 5.0 cm in the plots that were sampled in 2001 by Cielo-Filho et al. (2007). Following Gerwing et al. (2006), from October 2008 to April 2009 we sampled all the liana stems with DBH ≥ 1.0 cm that were rooted in each plot. We considered as a single individual each stem with no evident connection with other stem at the soil surface. Vouchers were lodged in the UEC herbarium.

Internal Forest Dynamics

Since tropical forests are described as mosaics of ecologically uniform ecounits or mosaics of dynamic forest patches (Torquebiau 1986, Wu and Loucks 1995), we classified each tree as belonging to the past, present or future sets, according to Torquebiau (1986). Past trees are those with visible signs of senescence or death, such as branches and parts of the tree or even the main trunk broken or dead, and/or presence of parasites and pathogens. Present trees are sustainable adults presenting a bole with morphological inversion point and having potential for extension and expansion, and even though their size is maximum, they can restore lost parts. Future trees have not reached their maximum height yet, have no bole with morphological inversion point, and the growth of the major orthotropic axis is led by an apical meristem. We used the proportion of past trees as an indicative of treefall gap, since the presence of dead-wood structures (ie, standing dead trees and fallen logs) is a key characteristic of an area considered as a treefall gap. In the same way we used the proportion of present trees as an indicative of old-growth forest (Oldeman 1990).

For each plot, we estimated the forest canopy cover index using a spherical convex densitometer at the breast height (Lemmon 1956). We used the crown illumination index CII (Clark and Clark 1992) to assess light exposition of each tree. Keeling and Phillips (2007) found a strong positive correlation between average CII and gap openness; so, we used average CII per plot as a measure of gap openness.

Forest disturbance is correlated with low tree height and small basal area and wood density (Laurance et al. 2001; Baker et al. 2004). We searched the literature to obtain wood density (WD) for each tree species we sampled. When data were absent for species, we used genus-level approximation for WD values, since WD is highly correlated with genus level (Chave et al. 2006).

Considering that we studied a seasonal semideciduous forest, we classified leaf phenodynamics of each species as evergreen, semideciduous or deciduous, following the literature. Scattered in every tropical seasonal semideciduous forest there are gaps of deciduousness, which correspond to momentary sunny places that appear during the dry season under deciduous canopy trees when they are leafless (Gandolfi et al. 2009). As these deciduousness gaps can affect survival and development of seeds, seedlings, sapling and poles (Gandolfi et al. 2009), we assumed that they could also influence liana establishment and persistence.

The number of past trees (PT), present trees (PR), and semi-deciduous and deciduous trees (SDT) was standardized by Wisconsin method, which is a common double standardization where "species" (in these cases, category of tree) are first standardized by its maxima (highest abundance per plot), and then sites (each plot of 100 m²) are standardized by site totals (function "wisconsin" in the R software vegan package, Oksanen et al. 2011). This standardization is necessary in order to compare variables expressed in incompatible units. Therefore, for each plot we considered the following surrogates of the community internal dynamics: mean CII, median WD, median of log values of tree basal area (BAmed), median tree height (Hmed), height of the tallest tree (Hmax), PT, PR and SDT.

Topo-Edaphic data

Superficial soil samples (0-20 cm in depth) were collected in the center of each plot for physico-chemical analyses, which were performed by the Instituto Agronômico de Campinas. Chemical analyses determined total cation exchange capacity (CEC), extractable bases (SB), base saturation (V), organic matter (OM), potential acidity (H+Al), pH, exchangeable cations (Ca, Mg, K) and extractable phosphorus (P). Texture analysis quantified percentages of clay, silt and sand.

The relative elevation of each plot was obtained with the aid of a transparent hose almost completely filled with water, as described by Cielo-Filho et al. (2007). They started from the lowest plot on the slope and measured the differences of the water column height in each end of the hose, which was positioned in the center of two nearest plots. Therefore, our topo-edaphic variables were represented by plot altitude and soil pH, texture and nutrients.

Spatial data

Spatial autocorrelation is known to inflate type I error and render species-environment relationships significance invalid (Peres-Neto and Legendre 2010). For the adequate modeling of space, a sufficiently flexible model is needed (Jones et al. 2008). Taking these limitations into account, we generated a set of continuous spatial variables from the *x* and *y* coordinates of each plot, using principal coordinates of neighbor matrices (PCNM), which generate variables that model the spatial relationships among sampling sites (Borcard et al. 2004). A total of 65 PCNMs was generated, with threshold distance of 27.313 m.

Data analysis

We excluded one plot from our analyses because its outlier values of edaphic variables (organic matter, SB, CEC) due to the massive presence of rocks and its shallow soil. To reduce the impact of rare species, we excluded species sampled with less than 10 stems. We transformed the species matrix data using Hellinger transformation, in which abundance is expressed as the square-root of the species relative abundance in each plot, thus reducing the weight of the most abundant species in the analysis (Legendre and Gallagher 2001, Borcard et al. 2011).

First we performed a redundancy analysis (RDA) for each variable representing the filters of internal forest dynamics, topo-edaphic and spatial data. Then, we applied a multiple regression analysis with a forward procedure to select the variables that most contributed to the variation of species abundance among plots for each determinant filter by adopting a significance level of 5% and running 999 random permutations, following the procedures described by Blanchet et al. (2008) and Borcard et al. (2011). Such procedure can reduce the number of explanatory variables and find a parsimonious redundancy analysis (RDA) model. As the variables could be significantly correlated with themselves, first we performed a partitioning of variation in the partial RDA (Blanchet et al. 2008; Borcard et al. 2011). Second, we calculated the proportion of variation explained in RDA by each spatial, topo-edaphic, or internal dynamics variable separately, or by all them concurrently. Third, we tested for the significance of each fraction of variation partitioning by means of 999 random permutations under the reduced model, recording the proportion of variation explained (R^2_{adj}). Finally, we performed an RDA with all selected variables, checked which variables most contributed to the ordination axes, and assessed which species were best modeled by the first three ordination axes. Following Jones et al. (2008), we recorded the eight species with the highest scores (positive or negative) on each axis and interpreted their distribution patterns based on the selected explanatory variables. We mapped the first three major axes of RDA with the selected variables and the abundance of the four species that were best modeled by RDA.

All analyses were performed in the R language version 2.12 (R Developmental Core Team 2010). We used vegan (Oksanen et al. 2011) and packfor (Dray et al. 2009) packages for analysis.

Results

We sampled 3,806 living liana stems of 90 species in 25 families, of which 20 were identified to genus only, three to family, and two (each with one individual) are still undetermined (Online Resource 1). Each plot contained two to 25 species (median of 11) and five to 150 living stems (median of 31). With 815 individuals sampled, *Bignonia campanulata* was almost ubiquitous in the study area, occurring in 96 out of the 100 plots. The other three most abundant species were *Mansoa difficilis* (556 individuals), *Dolichandra quadrivalvis* (200 individuals) and *Adenocalymma marginatum* (186 individuals), all belonging to the Bignoniaceae family. In order to reduce biased results due to rare species, a total of 40 species in 3586 living stems were analyzed, belonging to non-rare species (at least 10 stems per hectare, Online Resource 1).

The simple RDA of the topo-edaphic variables had a poor explanation power ($R^2_{adj} = 0.0391$) with a total proportion of eigenvalues in the constrained axes of 16.66%. The internal dynamic variables (hereafter *forest* variables) in simple RDA showed only 13.06% of the total proportion of eigenvalues in the constrained axes ($R^2_{adj} = 0.0427$). When we considered both forest and topo-edaphic variables together, the proportion of eigenvalues in the constrained axes raised to 28.09%, but the model had still a low explanation power ($R^2_{adj} = 0.0727$) in RDA. In contrast, simple RDA with all PCNMs contributed 73.19% to eigenvalues in the constrained axes ($R^2_{adj} = 0.204$). All permutation tests for RDAs under reduced models were significant ($p < 0.005$).

In the forward selection procedure, all the topo-edaphic variables reduced to relative elevation, which contributed only 5.94% to eigenvalues in the constrained axes of the RDA ($R^2_{adj} = 0.0497$). Selected forest variables in the forward procedure reduced variables to Hmax, Hmed and CII, which contributed 6.57% to the eigenvalues of the constrained axes of the RDA ($R^2_{adj} = 0.036$). The total 65 PCNM matrices reduced to 20 PCNMs, which explained 30.12% of the eigenvalues in the constrained axes ($R^2_{adj} = 0.155$).

Variation partitioning showed that the selected variables explaining liana variation were partially intercorrelated (Table 1). In our fine scale study, a great amount of data remained unexplained (residuals R^2_{adj} = 82.04%) by our analyzed variables. Considering the explained variation, space was the major explanation variable, contributing 9.88% to the total variance when alone and 15.94% when together with other variables (Table 1). In the RDA with all selected variables, relative elevation (ρ = 0.511), Hmax (ρ = -0.517), and CII (ρ = 0.389) had the three highest correlations with RDA axis 1 (Table 2). Relative elevation (ρ = -0.72), CII (ρ = 0.463) and PCNM 5 (ρ = 0.429) were highly correlated with RDA axis 2. The third axis of the RDA model was highly correlated with PCNM 2 and 8 (ρ = -0.322 and 0.347, respectively). The first RDA axis seemed to be associated with an ecounit gradient (treefall gap to old-growth forest) because the most strongly correlated variables belonged to forest variables (CII and Hmax). Positive association with this first axis was linked to sites with trees presenting higher CII (higher proportion of trees directly lighted by the sun) and negatively with maximum height values (lower canopy height). Negative association with the first axis was related to shadier trees (smaller mean CII) and with the presence of taller trees. Two out of the top eight species scores were negatively correlated and six were positively correlated with RDA axis 1 (Table 3). Therefore, *Elachyptera festiva* (a twiner liana) was associated with areas with shaded trees in a higher canopy forest (old-growth forest), and *Adenocalymma marginatum* (a tendril liana) with the higher presence of emergent trees (higher CII) in a lower canopy forest (treefall gap).

Positive correlation with RDA axis 2 denoted association with plots having lower relative elevation, i.e., plots on the slope inferior portion. The high association between this axis and relative elevation indicated that the altitudinal gradient was represented in RDA axis 2, which was also correlated with PCNM 5. Also, CII was positively correlated with RDA axis 2, which denoted some association between higher relative elevation and open sites. Therefore, *Mansoa difficilis*, *Fridericia triplinervia* and *Forsteronia pubescens* occurred nearby the Ribeirão Cachoeira stream, and *Banisteriopsis anisandra*, *Mikania glomerata*, *Urvillea laevis*, *Pristimera celastroides* and *Bredemeyera floribunda* preferably occurred in the superior portion of the slope.

Discussion

In tropical forests, variation partitioning of environmental and spatial variables has been used to investigate variation in plant species composition, with the total proportion of variation explained ranging from 16 to 86% (Cottenie 2005; Jones et al. 2008). We found a large amount (81.24%) of unexplained variation in the liana data. The relative small proportions of variation explained by the internal dynamics, spatial and topo-edaphic variables are the outcome of stochastic processes and non-included variables in our analyses. Different results among studies concerning the influence of environmental constraints on the variation of species composition could reflect differences between focal plant groups or geographic areas (Jones et al. 2008), but general conclusions could be generated from studies on fine scale, revealing the characteristic scale of species' response to environment (de Knegt et al 2010). Our results indicated that the liana community we investigated in the seasonal semideciduous forest fragment on a fine spatial scale is mainly affected by hided factors (unexplained variation), denoting a stochastic process of community assembly, but dispersal limitation, indicated by the great amount of variation associated to space, is the best explanation variable between the studied factors.

Distinguishing between neutral and non-neutral processes is a challenge in ecological studies (Ruokolainen et al. 2009), and our analyses could not separate neutral from non-neutral dispersal limitation. Aggregated spatial patterns are observed for almost every plant species in the tropics (e.g. Condit et al. 2000) and are usually attributed to strong dispersal limitation acting in the community assembling processes (e.g. Terborgh et al. 2011). However, although Houchmandzadeh (2008) demonstrated with robust mathematical modeling how neutral dispersal limitation results in clumping existence, reliable models representing non-neutral dispersal and environment constrains are still lacking (McGill 2010). Also, dispersal limitation does not imply merely neutral processes in the community assembly (see Clark 2009). For lianas, non-neutral dispersal limitation is thought to derive mainly from their clonal reproduction (Nabe-Nielsen and Hall 2002) and from the predominance of wind-dispersed seeds among their species (Gentry 1991), which implies shorter mean dispersal distances than for animal-dispersed (zoochorous) species, as demonstrated for trees (Clark et al. 2005).

Edaphic data has not been considered in most beta-diversity studies in which space explained more variation than environment (Jones et al. 2008), and although Malizia et al. (2010) found a significant positive relationship between soil phosphorus and liana distribution in a Subtropical Montane Forest, edaphic variables were not important in our study. Forward selection of all topo-edaphic variables reduced them to only relative elevation, probably due to robust spatial autocorrelation of topographic data over the not so robust spatial autocorrelation of the other soil variables. Our study did not include soil water content, what could be an important driver to the sampled area, since altitude is correlated with soil moisture in riverside semideciduous forests (Oliveira-Filho et al. 1997). We found that great part of topo-edaphic determination was redundant with spatial data, avoiding the separation between purely spatial autocorrelation and topo-edaphic factors.

Our finding agrees with Legendre et al. (2009), who stated that on fine scales pure dispersal limitation is more important to generate species spatial patterns when there are weak environmental drivers. However, we detected some trends of internal dynamics limitation due to the topo-edaphic drivers and to the ecounit gradient (gap to old-growth forest) influence on the variation of liana composition. Many authors have stated that liana is a growth-form that is disturbance-adapted (Putz 1984; Hegarty and Caballé 1991; Gerwing and Farias 2000), because most lianas are light-demanding and have the ability to sprout roots and shoots from fallen and cut stems. More than light, gap edges provide small-diameter supports that benefit lianas climbing to the canopy (Putz 1984; DeWalt et al. 2000; Laurance et al. 2001). Chazdon (2008) described a model of forest succession in three phases – stand initiation, stem exclusion and understory reinitiation – where each phase has a characteristic species composition (Letcher 2010). During the stem exclusion phase of forest succession there is a decrease of liana density (DeWalt et al. 2000; Chazdon 2008; Letcher and Chazdon 2009; Madeira et al. 2009; Letcher 2010), leading to consider lianas as a unique specialized functional group, although there is considerable variation among species (Gerwing 2004). Moreover, our study contemplated stabilished individuals with a broad variation of stem sizes, what denotes hierarchically responses to ecological filters (Nogueira et al. 2011). Current community could reflects past disturbances, showing species which persist throught the succession (Donato et al. 2012) and a fine analysis could reflect estabilishment differences of lianas species.

A massive literature supports the dissimilarity between pioneer and shade-tolerant tree species in tropical forests, which is important to species coexistence (Brokaw 1985; Pacala and Rees 1998; Wright 2002). However, there is no specific information on the pioneer-non pioneer gradient for lianas. There are evidences that gaps present more liana species than non-gap sites as expressed on both per area and per stem (Schnitzer and Carson 2001), and some liana species are more frequent in environments with some characteristics (Ibarra-Manríquez and Martínez-Ramos 2002). DeWalt et al. (2000) found that tendril lianas have preference for young forest stages whereas twiner lianas have preference for old-growth forest stages. To some extent, our results agree with this observation. For instance, *Elachyptera festiva* (a twiner liana) was associated with old-growth forest ecounits, and

Adenocalymma marginatum (a tendril liana) was much more frequent in treefall gaps. On the other hand, *Mansoa difficils* (a tendril liana) was associated with old-growth forest ecounits, which could be explained by the fact that even tendril climbers have different life history strategies (Gerwing 2004).

Nonetheless, our data did not explain a large amount of variation of the studied liana community composition. Relationships between host trees and lianas are biased and present non-random characteristics: some host trees would have more lianas than expected and some others would never have lianas in their crowns (Nesheim and Økland 2007, Sfair et al. 2010). Generally environment is more important for climbers during their earlier developmental stages, whereas host-tree properties become more important once the plant starts to climb (Nesheim and Økland 2007). Therefore, we propose that part of the unexplained variation of the liana community composition would be due to species-specific host tree-liana interactions, which are nested in neotropical forests (Sfair et al. 2010). Possibly, the presence of key tree species is important on the plant-to-plant (individual) scale to explain liana community structure, since some characteristics of the host trees can alter their chances of having lianas (Carse et al. 2000).

In the same plots we surveyed, Cielo-Filho et al. (2007) had found that the tree community composition could be explained by the same predictors: position on slope, maximum tree height as a surrogate of disturbance, and space. This fact is a background to infer that lianas and trees, at least in this forest, would respond to the same community assembly rules. In addition, climber species richness and the Shannon heterogeneity index of trees in SE Brazilian forests are correlated on large spatial scale, indicating that the heterogeneity of tree traits would be associated with the number of potential niches for climbers (Sfair and Martins 2011). Although adopting different techniques of numerical analyses, both our study on lianas and the one by Cielo-Filho et al. (2007) on trees in the same plots revealed similar responses of liana and tree species to the same drivers on fine scale, where they founded that the first axes of a Principal Component Analysis, correlated with relative plot elevation and height of tallest trees, explained 22% of the total variance. In spite of this, we have a background to conclude that position on slope, tree height and crown illumination index can have some role in driving small differences in liana species and abundance distribution, and an important filter controlling the assembly of the liana community on fine scale in a seasonal semideciduous forest is the dispersal limitation, but the greatest amount of liana composition variation is unexplained, due to stochastic variation of .populations.

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References

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen T, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill D, Patiño S, Pitman N, Silva JNM, Vásquez-Martinez R (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545–562.

Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. Oikos 86:402–416.

Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. Ecology 89:2623–2632

Booth BD, Swanton CJ (2002) Assembly theory applied to weed communities. Weed Science 50: 2–13.

Borcard D, Legendre P, Drapeau P (1992) Partialling out the Spatial component of Ecological Variation. Ecology 73(3):1045-1055.

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:1826-1832.

Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer. New York.

Brokaw NVL (1985) Gap-phase regeneration in a Tropical forest. Ecology 66(3): 682-687

Chazdon RL (2008) Chance and determinism in tropical forest succession. In Carson WP, Schnitzer SA (Eds.), Tropical Forest Community Ecology. Blackwell, Malden, MA, pp. 384–408.

Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006) Regional and Phylogenetic variation of wood density across 2456 Neotropical tree species. Ecological Applications 16: 2356-2367.

Cielo-Filho R, Gneri MA, Martins FR (2007) Position on slope, disturbance, and tree species coexistence in a Seasonal Semideciduous Forest in SE Brazil. Plant Ecology 190:189-203.

CIIAGRO/IAC 2012 (Centro Integrado de Informações Agrometereológicas – Instituto Agronômico de Campinas). http://www.ciiagro.sp.gov.br/

Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86(10):2684-2694.

Clark DB, Clark DA (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62(3): 315-344.

Clark JS (2009) Beyond neutral science. Trends in Ecology and Evolution 24(1):8-15.

Condit R, Ahston PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbel SP, Foster RB, Itoh A, LaFrankie JV, Lee HS, Losos E, Manokaran N, Sukumar R, Yamakura T (2000) Spatial patterns in the Distribution of tropical tree species. Science 288:1414-1418.

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175-1182.

De Knegt HJ, van Langevelde F, Coughenour MB, Skidmore AK, de Boer WF, Heitkönig IMA, Knox NM, Slotow R, van der Wall C, Prins HHT (2010) Spatial autocorrelation and the scaling of species-environment relationships. Ecology 91(8): 2455-2465.

DeWalt SJ, Schnitzer SA, Denslow JS (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. Journal of Tropical Ecology 16:1-19.

DeWalt SJ, Ickes K, Nilus R, Harms KE, Burslem DFRP (2006) Liana habitat associations and community structure in a Bornean lowland tropical forest. Plant Ecology 186(2): 203-216.

Donato, D.C., Campbell, J.L., Franklin, J.F. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? Journal of Vegetation Science 23 576-584

Dray S, Legendre P, Blanchet G (2009) packfor: Forward Selection with permutation (Canoco p.46). R package version 0.0-7/r58. http://R-Forge.R-project.org/projects/sedar/

EMBRAPA (1999) Sistema brasileiro de classificação de solos. Empresa Brasileira de Pesquisa Agropecuária - Centro Nacional de Pesquisa de Solos, Brasília

Gandolfi S, Joly CA, Leitão-Filho HF (2009) “Gaps of Deciduousness”: Cyclical gaps in tropical forests. Scientia Agricola 66(2): 280-284.

Gerwing J.J. (2004) Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. Forest Ecology and Management 190: 57–72

Gerwing JJ, Schnitzer SA, Burnham RJ, Bongers F, Chave J, DeWalt SJ, Ewango CEN, Foster R, Kenfack D, Martínez-Ramos M, Parren M, Parthasarathy M, Pérez-Salicrup DR, Putz EF, Thomas DW(2006) A standard protocol of liana censuses. Biotropica 38(2): 256-261.

Gilbert B, Lechowicz MJ (2004) Neutrality, niches, and dispersal in a temperate forest understory. Proc. Nat. Acad. Sci. USA 101:7651-7656.

Hernandez-Stefanoni JL (2005) Relationships between landscape patterns and species richness of trees, shrubs and vines in a tropical forest. Plant Ecology 179(1): 53-65.

Houchmandzadeh B (2008) Neutral clustering in a simple experimental ecological community. Phys. Rev. Lett., 101(7):078103(1-4).

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.

Hubbell SP (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. Functional Ecology 19(1): 166-172.

Ibarra Manríquez G, Martínez-Ramos M (2002) Landscape variation of liana communities in a Neotropical rain forest. Plant Ecology 160(1):91-112.

IBGE (1992) Manual técnico da vegetação brasileira. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Jones MM, Tuomisto H, Clark DB, Olivas P (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. Journal of Ecology 94:181-195.

Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB, Olivas PC (2008) Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155:593-604.

Keddy PA (1992) Assembly and Response Rules: Two Goals for Predictive Community Ecology. Journal of Vegetatio Science 3 (2): 157-164.

Keeling HC, Phillips OL (2007) A calibration method for the crown illumination index for assessing forest light environments. Forest Ecology and Management 242:431-437.

Laurance WF, Pérez-Salicrup D, Delamônica P, Fearnside PM, DÁngelo S, Jerozolinski A, Pohl L, Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82: 105–116

Legendre P (1993) Spatial autocorrelation: Trouble or new paradigm? Ecology 74(6): 1659-1673.

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun, I-F, He, F (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90:663-674.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314-320.

Letcher SG, Chazdon RL (2009) Lianas and self-supporting plants during tropical forest succession. Forest Ecology and Management 257: 2150–2156.

Letcher SG (2010) Phylogenetic structure of angiosperm communities during tropical forest succession. Proc. R. Soc. B 277: 97-104.

Madeira BG, Espírito-Santo MM, D'Ângelo Neto S, Nunes YRF, Azofeifa GAS, Fernandes GW, Quesada M (2009) Changes in tree and liana communities along a successional gradiente in a tropical dry forest in South-eastern Brazil. Plant Ecol 201:291-304.

Malizia A, Grau HR, Lichstein JW (2010) Soil phosphorus and disturbance influence liana communities in a subtropical montane forest. Journal of Vegetation Science 21(3): 551-560.

McGill BJ (2010) Towards a unification of unified theories of biodiversity. Ecology Letters 13:627-642.

Nabe-Nielsen J, Hall P (2002) Environmentally induced clonal reproduction and life history traits of the liana *Machaerium cuspidatum* in an Amazonian rain forest, Ecuador. Plant Ecology 162 (2): 215-226.

Nesheim I, Økland RH (2007) Do vines in neotropical forests see the forest or the trees? Journal of vegetation Science 18:395-404.

Nogueira A, Costa FRC, Castilho CV (2011) Liana abundance patterns: the role of ecological filters during development. Biotropica 43: 442–449.

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2011) vegan: Community Ecology Package. R package version 1.17-6. http://CRAN.R-project.org/package=vegan

Oldeman RAA (1990) Forests: elements of silvology. Springer-Verlag, Berlin, 624p

Oliveira-Filho AT, Curi N, Vilela EA, Carvalho DA (1997) Tree species distribution along soil catenas in a Riverside semideciduous forest in southeastern Brazil. Flora 192: 47-64.

Ozinga WA, Schaminée JHJ, Bekker RM, Bonn S, Poschlod P, Tackenberg O, Bakker J, Groenendael JM (2005) Predictability of plant species composition form environmental conditions is constrained by dispersal limitation. Oikos 108: 555-561.

Pacala SW, Rees M (1998) Models suggesting field experiments to test towo hyphotesis explaining successional diversity. American Naturalist 152(5):729-737.

Pérez-Salicrup DR, Sork VL, Putz FE (2001) Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33: 34-47

Putz FE (1984) The natural history of lianas on Barro Colorado Islando, Panama. Ecology 65:1713-1724.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ruokolainen L, Santa E, Kaitala V, FOWLER MS (2009) When can we distinguish between neutral and non-neutral processes in community dynamics under ecological drift? Ecology Letters 12: 909-919.

Russo SE, Davies SJ, King DA, Tan S (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. Journal of Ecology 93:879-889.

Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82: 913–919.

Schnitzer SA, Bongers FA (2002) The ecology of lianas and their role in forests. Trends in Ecology & Evolution, 17 (5): 223-230.

Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. The American Naturalist 166 (2): 262-276.

Sfair JC, Martins FR (2011) The role of heterogeneity on climber diversity: is liana diversity related to tree diversity? Global Journal of Biodiversity Science and Management 1(1):1-10.

Sfair JC, Rochelle ALC, Rezende AA, van Melis J, Weiser VL, Martins FR (2010) Nested liana-tree netword in three distinct neotropical vegetation formations. Perspectives in Plant Ecology, Evolution and Systematics 12:277-281.

Smith TW, Lundholm JT (2010) Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography 33: 648-655.

Terborgh J, Alvarez-Loayza P, Dexter K, Cornejo F, Carrasco C (2011) Decomposing dispersal limitation: limits on fecundity or seed distribution? Journal of Ecology 99(4):935-944.

Torquebiau EF (1986) Mosaics patterns in dipterocarp rain forest in Indonesia, and their implications for practical forestry. Journal of Tropical Ecology 2: 301-325.

van der Heijden GMF, Phillips OL (2008) What controls liana success in Neotropical forests? Global Ecology and Biogeography 17: 372-383.

van der Heijden GMF, Phillips OL (2009) Environmental effects on Neotropical liana species richness. Journal of Biogeography 36(8): 1561-1572.

Weiher E, Keddy PA (1995) The assembly of experimental wetland plant communities. Oikos 73:323-335.

Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1-14.

Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. The Quarterly Review of Biology 70(4): 439-466.

Figures captions

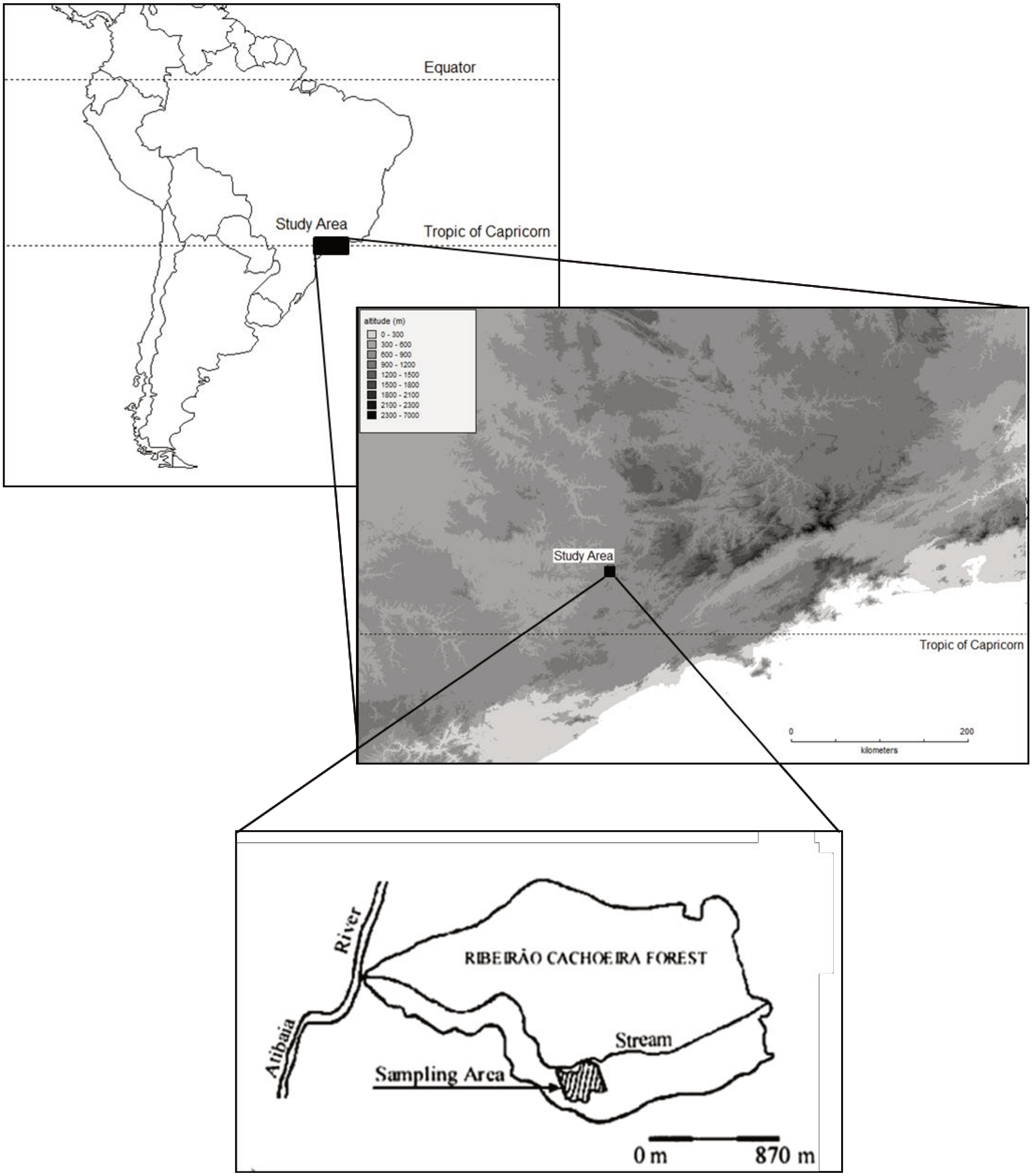

Fig.1 **–**The sampled forest and the location of the sampling area (6.5-ha), located at southeastern region of Brazil, South America.

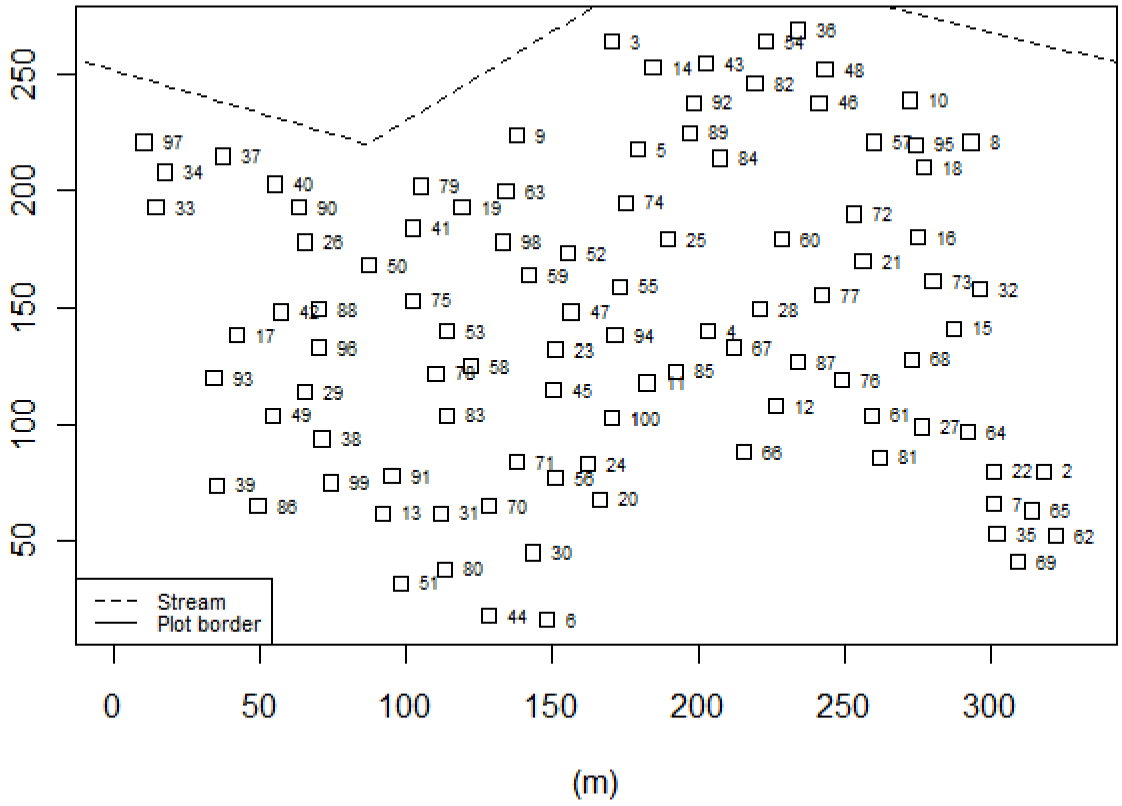

Fig.2 – Schematic *figure of the* **s**ampled area showing the 100 square plots of 100 m^2 and the relative position of water stream.

Tables

Table 1 – Topo-edaphic: forward-selected edaphic and topographic variables; Forest: forward-selected internal dynamic variables; Space: forward-selected spatial data variables, represented by principal coordinates of neighbor matrices (PCNM). Fraction of explained variation (adjusted R^2). All the testable model fractions were significant at 5% of significance.

Variables			**Fraction of Total Explanation**
Topo-edaphic			0.883%
	Forest		1.164%
		Space	9.879%
Topo-edaphic	+Forest		-0.031%
Topo-edaphic		+Space	3.583%
	Forest	+Space	1.938%
Topo-edaphic	+Forest	+Space	0.0539%
Residuals			82.05%

Table 2 – Redundancy Analysis (RDA) with all selected variables for liana community structure. Space variables are represented by principal coordinates of neighbor matrices (PCNM).

Variables	RDA axis 1	RDA axis 2	RDA axis 3
Altitude	0.51058	-0.72013	0.12135
CII	0.38912	0.463208	0.2456
Hmed	-0.13613	-0.31814	-0.15092
Hmax	-0.5173	-0.09709	-0.19978
PCNM 1	0.3125	-0.15346	-0.0622
PCNM 11	-0.01572	-0.26474	-0.55036
PCNM 14	-0.26289	0.199776	0.14612
PCNM 15	-0.26842	0.213589	0.28271
PCNM 18	0.01377	0.000804	-0.10991
PCNM 2	0.16222	0.315203	-0.32195
PCNM 20	-0.20264	0.04701	-0.04664
PCNM 22	0.10417	-0.24838	0.1542
PCNM 24	0.31633	0.177978	0.01991
PCNM 25	0.35919	0.231349	0.10356
PCNM 3	-0.35451	0.204505	0.09021
PCNM 31	-0.16895	-0.02647	0.16895
PCNM 4	-0.05339	-0.34188	0.06204
PCNM 5	-0.11087	0.429084	-0.17005
PCNM 56	0.08477	0.01363	-0.07997
PCNM 6	0.16816	0.050397	0.20753
PCNM 7	0.18841	0.065725	0.27127
PCNM 8	-0.1914	-0.25021	0.34682

Table 3 – Liana species with the strongest relationships (eight highest species module scores) with each of the first three constrained redundancy analysis (RDA) axes, which could be positive (+) or negative (-). The species are listed in order of decreasing absolute value of their scores. The explanatory variables consist of selected variables of space, internal dynamics, soil and relative elevation, listed in the table 2. 1 – Stem twiner liana; 2 – tendril liana.

RDA axis 1	**RDA axis 2**	**RDA axis 3**
+ *Adenocalymma marginatum*^{2}	+ *Banisteriopsis anisandra*^{1}	+ *Serjania laruotteana*^{2}
+ *Fridericia conjugata*^{2}	+ *Mikania glomerata*^{1}	+ *Forsteronia pubescens*^{1}
+ *Lundia obliqua*^{2}	+ *Urvillea laevis*^{2}	+ *Tynanthus fasciculatus*^{2}
+ *Pyrostegia venusta*^{2}	+ *Pristimera celastroides*^{1}	+ *Pyrostegia venusta*^{2}
+ *Rhynchosia phaseolata*^{1}	+ *Bredemeyera floribunda*^{1}	+ *Tanaecium selloi*^{2}
+ *Dicella bracteosa*^{1}	- *Mansoa difficilis*^{2}	- *Adenocalymma marginatum*^{2}
- *Elachyptera festiva*^{1}	- *Fridericia triplinervia*^{2}	- *Davilla rugosa*^{1}
- *Forsteronia australis*^{1}	- *Forsteronia pubescens*^{1}	- *Condylocarpon isthimicum*^{1}

Capítulo 2: Is the phylogenetic structure of climbing plants correlate with successional stage of forest?[2]

Autores:

Juliano van Melis

Fernando Roberto Martins

[2]Artigo segue normas de *Journal of Vegetation Science*

Title: Is the phylogenetic structure of climbing plants correlate with successional stage of forest?

Authors: Juliano van Melis, Fernando Roberto Martins

Aims: Distinguish the phylogenetic structure of climbing plants' community in a seasonal semideciduous forest, inferring if exist interspecific competitive exclusion or habitat filtering in climbing plants' community among different ecounits (treefall gaps and old-growth forest).

Location: 1 ha of Seasonal Semideciduous Forest, Southeastern Brazil.

Methods: We sampled all climbing ramets of climbing plants with DBH (Diameter at Breast Height) higher or equal to 1.0 cm in 100 plots (100m²). We calculate net relatedness index (NRI) considering all climbing plants species and restricting to the taxonomic scale of Bignoniaceae family. NRI measures tree-wide phylogenetic clustering and overdispersion of species. We used parametric variables of stand community as surrogates to the different ecounits of successional forest mosaic. We used generalized additive model (GAM) to assess which environmental params are correlated with NRI samples values.

Results: when we considered all climbing plants species, we found a random phylogenetic structure in 40/100 plots and significant phylogenetic clustering structure in 60/100 of plots. When we considered only Bignoniaceae species, only one plot presented an overdispersion structure, and almost all plots presented a random phylogenetic structure. Phylogenetic structure did not present a spatial structure and did not differentiate between sample groups. We found a slight correlation of tree height and proportion of present trees set in clustered phylogenetic samples.

Main Conclusions: Considering our surrogates to forest dynamic, climbing plants composition, in a scale of 100 m², presents a coexistence of close relatives, independent of ecounit (treefall gap or old-growth forest). But there is a trend to old-growth forest sites indicatins closer phylogenetic structure than treefall gap sites. We concluded that treefall gaps have more random phylogenetic structure than mature sites due to the convergent ecological traits of climbing plants to high light sites (treefall gaps).

Keywords: mean pairwise distance (MPD) values, treefall gap, Atlantic forest, lianas, vines

Introduction

Treefall gaps are important to maintain tropical biodiversity (Schnitzer & Carson 2001). They create high light habitats and species may specialize on and partition resources gradients that vary from gap center to forest interior, permitting species coexistence (Schnitzer et al. 2008). There is a considerable bibliography which complains the dissimilarity between pioneer and shade-tolerant tree species in tropical forests, which is important to species coexistence (Brokaw 1985; Pacala & Rees 1998; Wright 2002), but there is a deficiency for climbing plants' flora.

Lianas (woody and sub-woody climbers) represent about 25% of woody species in tropical forests (Schnitzer & Bongers 2002) and exhibit a massive abundance in disturbed sites and early successional stages in tropical forests (Balée & Campbell 1990, Pérez-Salicrup et al. 2001, Madeira et al. 2009, Malizia & Grau 2009). Furthermore, gaps sites have more lianas species per area and per stem than non-gaps sites (Schnitzer & Carson 2001). Gap sites provide, besides light, small-diameter supports that benefit lianas to climb to the canopy (Putz 1984, DeWalt et al. 2000, Laurance et al. 2001), leading to consider that climbing plants are a unique specialized functional group, although there is considerable variation among species (Gerwing 2004). In an old-growth Amazonian forest, Gerwing (2004) classified two of six studied vine species as late successional species and merely one as pioneer. In an Australian subtropical forest, 40% of the 38 more common lianas are considered as species of later succession (Hegarty 1991). Therefore, some perspectives are guided to study if lianas' species composition differences between gap and non-gap sites are due to successional niche (abiotic filter) or due to competition-colonization trade-off, as proposed to trees (Pacala and Rees 1998).

Biomechanical differences among climbing mechanisms may explain affinities concerning this trait and sites which belong to treefall gap or non-gap (old-growth forest). Tendril climbers present affinity to young forests and forest edges (DeWalt et al. 2000, Laurance et al. 2001, Malizia & Grau 2008) due to the limitation of tendril climbers to use smaller supports (Putz 1984, Putz & Chai 1987, Putz & Holbrook 1991) and twiner lianas present preference to old-growth forests (DeWalt et al. 2000). Yet, even tendril climbers have different life history strategies (Gerwing 2004). Besides, species of the same family or same genera tended to dominate different habitats suggesting that evolutionary niche differentiation has occurred within some liana phylogenetic lineages, which propose a purported evolutionary niche differentiation operating (Ibarra-Manriquez & Martinez-Ramos 2002). There is a strong trade-off between growth and survival for both trees and lianas at the seedling stage on Barro

Colorado Island (Gilbert et al. 2006), rejecting the hypothesis that lianas are essentially light-demanding due to their overlapping life history strategies with trees.

Chazdon (2008) describes a model of forest succession in three phases: stand iniciation, stem exclusion and understory reinitiation, where each phase presents a characteristic species composition and structure (Letcher 2010). During the stem exclusion phase of forest succession it has been observed a decrease of liana density (DeWalt et al. 2000; Chazdon 2008; Letcher and Chazdon 2009; Madeira et al. 2009; Letcher 2010), probably due to self-thining among lianas stems (but see Leicht-Young et al. 2011).

Habitat filtering and species interactions (competition or facilitation) structure community composition, and the phylogenetic relationships present a key to understand species' interactions when it is phylogenetic niche conservatism (Burns & Strauss 2011). Therefore, studies about the phylogenetic structure of an ecological community can provide insights into the relative importance of habitat filtering, species interactions or even random processes to structure that community (Webb et al. 2002, Kembel & Hubbell 2006).

A community with a clustered phylogenetic structure is constituted by closely related philogenetic taxa sharing traits that are important for the species persistence in a particular environment (Webb et al. 2002), or when competitive ability is conserved, leading to a clustering pattern due to competitive exclusion (Mayfield & Levine 2010). On the other hand, phylogenetic overdispersion can result either from the elimination of the closely related taxa with the most similar niche-use leading to a minimal niche overlap of the remaining species and phenotypical repulsion (interspecific competitive exclusion); or from the convergence of similar niche-use by distantly related taxa leading to phenotypical attraction (Webb et al. 2002).

Therefore, our objective in the this study is to detect the phylogenetic structure of climbing plants' community (woody and non-woody) in a seasonal semideciduous forest, inferring if exist interspecific competitive exclusion or habitat filtering in climbing plants' community among different ecounits (treefall gaps and old-growth forest). For this purpose we correlate parametric variables of tree stand community, as surrogates to the different ecounits of successional forest mosaic (Torquebiau 1986), with net relatedness index (NRI), which measures tree-wide phylogenetic clustering and overdispersion of species (Webb 2000).

Considering that tendril climbing plants have preference for young forest stages (DeWalt et al. 2000), we suppose climbing plants show an overall phylogenetic clustering in early successional stages due to the conservative trait of climbing mechanism, such as to Bignoniaceae-Bignonieae (Lohmann 2006), which shows tendrils. On the other hand, considering species interactions, especially competitive exclusion among closely related species (Prinzing et al. 2008), during stem exclusion (Chazdon 2008, Letcher 2010), we suppose phylogenetic overdispersion at family level in later successional stages (old-growth forest).

Material and Methods

Study Site

Located in a highly fragmented area at the municipality of Campinas, São Paulo state, SE Brazil, the sampled area vegetation may be classified as seasonal semideciduous forest due to the climatic seasonality and deciduousness observed in less of 50% of the trees during the dry season (IBGE 1992). There are no signs of recent anthropogenic disturbances in the area, such as tree burning or logging evidences. The studied stand shows an area of 6.5 ha and is situated in the south portion of a forest fragment (total area: 24.5 km²), called Ribeirão Cachoeira forest (22°49'S, 49°55'W). We sampled 100 random square plots with 100 m² each, totaling a sampled area of 10,000 m². The plots coordinates were defined by a simple generator of uniform pseudo-random numbers in a computer program (MS Excel), characterized as a simple random sampling design (Dutilleul 2011). The plots are separated with each other from 2m (nearest distance) to 270m (farest distance).

Sampling

From August to October 2008 we resampled all trees sampled by Cielo-Filho et al. (2007) and included all living trees with DBH ≥ 5.0 cm. From October 2008 to April 2009, following Gerwing et al. (2006), we sampled all climbing plants' stems (woody and non-woody) with DBH ≥ 1 cm that were rooted in each plot. We considered as a single individual each stem with no evident connection with other stem at soil surface. Vouchers were lodged in the UEC herbarium.

Environmental data

Since tropical forests are described as mosaics of ecologically uniform patches (Torquebiau 1986), we classified each tree as belonging to the past, present or future sets, according to Torquebiau

(1986). Past trees are those with visible signs of senescence or death, such as branches and parts of the tree or even the main trunk broken or dead, and/or presence of parasites and pathogens. Present trees are sustainable adults presenting a bole with morphological inversion point and having potential for extension and expansion, and even though their size is maximum, they can restore lost parts. Future trees have not yet reached their maximum height, have no bole with morphological inversion point, and the growth of the major orthotropic axis is led by an apical meristem. We used the proportion of past trees as an indicative of treefall gap, since a great proportion of trees showing senescence and/or falling branches characterizes a canopy gap area. In the same way, we used the proportion of present trees as an indicative of old-growth forest (Oldeman 1990).

We used the crown illumination index CII (Clark and Clark 1992) to assess light exposition of each tree. Keeling and Phillips (2007) found a strong positive correlation between average CII and gap openness; then we used average CII per plot as a measure of gap openness. We estimated forest canopy openness (%) with the aid of a spherical convex densitometer at the breast height (Lemmon 1956).

Forest disturbance is correlated with low tree height and small basal area and wood density (Laurance et al. 2001; Baker et al. 2004). We searched the literature to obtain wood density (WD) for each species. When data were absent for species, we used genus-level approximation for WD values, since WD is highly correlated with genus level (Chave et al. 2006).

Considering that we studied a seasonal semideciduous forest, we classified leaf phenodynamics of each species as evergreen, semideciduous or deciduous, following the literature. Scattered in every tropical seasonal semideciduous forest there are gaps of deciduousness, which correspond to momentary bright places that appear during the dry season under deciduous canopy trees when they are leafless (Gandolfi et al. 2009). As these deciduousness gaps can affect survival and development of seeds, seedlings, sapling and poles (Gandolfi et al. 2009), we assumed that they could also influence liana establishment and persistence.

The number of past trees (PT), present trees (PR), and Semi-deciduous and Deciduous Trees (SDT) was standardized by Wisconsin method, which is a common double standardization where “species” (in these cases, category of tree) are first standardized by maxima an then sites (each plot of 100 m^2) by site totals (function “wisconsin" in vegan package).

For each plot we considered the following variables as indicating the community internal dynamics: mean CII, median WD, median of log values of tree basal area (BAmed), median tree height (Hmed), height of the tallest tree (Hmax), PT, PR and SDT.

Phylogenetic data and structure

Firstly we verify taxon names for synonyms to match standardized names from the integrated taxonomic information system using Nix (Kembel 2007) but Bignoniaceae, which was conferred in iplants (L.G. Lohmmann & C. Ulloa Ulloa, *available online*), excluding undetermined individuals. Then, we constructed a phylogenetic tree for all climbing plants species sampled in the 100 plots using Phylomatic software (Webb & Donoghue 2005), a phylogenetic database and toolkit for the assembly of phylogenetic trees, based on Phylomatic reference tree R20100701 with APG III (Angiosperm Phylogeny Group 2009) phylogenetic classification of flowering plant families. In the absence of detailed information on phylogenetic relationships, we assumed polythomy. Additionally, we based Bignoniaceae phylogenetic distances on Lohmmann et al. (2013).

We performed analysis of phylogenetic structure using picante package. For our purpose we used the NRI metric (Webb et al. 2002), which corresponds to a Z-statistic based on mean pairwise distance (MPD) values. MPD is calculated as the average phylogenetic distance among all pairwise combinations of co-occurring species in each 100 m² plot. Thus, NRI is defined as:

$$NRI = -1*(MPD_s-MPD_r)*se_r^{-1},$$

where MPD_s is the MPD in a sample of taxa, observed on one site (plot), MPD_r is the MPD obtained from a set of randomized samples, in our case we used 999 permutations, and se_r is the standard error of MPD_r. Admitting 5% of significance, critical values of Z-statistics are ±1.96, where positive values means that observed MPD presents smaller value than randomized MPD ($NRI>+1.96$), and negative values means that observed MPD are higher than expected by chance ($NRI<-1.96$). Therefore, positive values of NRI, higher than 1.96, incomes meaningful clustered phylogenetic structure and negative NRI ($NRI<-1.96$) means overdispersed phylogenetic structure.

There is another phylogenetic clustering metric, the nearest taxon index (NTI), which is calculated in an analogous way to the NRI (Webb et al. 2002). But this metric is too sensitive to tree topology and may not be appropriate to compare among multiple trees, due to the difficult to interpret trees with little intrafamilial resolution (Letcher 2010). Therefore, we used only NRI metrics. To avoid a misunderstanding of NRI due to the dominance of structure of plots, we examined if Pielou's evenness of each plot was not related to NRI with linear regressions ($R^2_{All} = 0.023$, p-value $_{All} = 0.13$; $R^2_{Bignoniaceae} = 0.100$, p-value $_{Bignoniaceae} = 0.001$); therefore, NRI is not related to evenness in species abundances considering all species and when considering only species of Bignoniaceae family.

We also examined NRI values considering only Bignoniaceae, due to substantial proportion of species which belong to this family (21 of 90 species) and their almost ubiquity (occurring in 99/100 of plots), reducing a likely biased interpretation.

Data analysis

Firstly, we performed a clustering process to split the plots in groups based on the environmental data. We used the k-means cluster method, which aims to partition the points into k groups such that the sum of squares from points to the assigned cluster centres is minimized. At the minimum, all cluster centres are at the mean of their Voronoi sets (the set of data points which are nearest to the cluster centre) (R Developmental Core Team 2010). We aggruped the plots in three groups (k =3) based on the ward hierarchical clustering (Figure 1). This approach grouped the sampled plots that are most similar based solely on environmental data, representing forest dynamics surrogates, using Ward distance (incremental sum of squares) and nearest neighbor as the linkage. Secondly, we performed a one-way ANOVA to test if the clustered groups present differences in NRI, and Kruskal-Walis test with Bonferroni correction to test if the clustered groups present differences in species richness, abundance or diversity (H').

We performed a generalized additive model (GAM) with the environmental data that could explain the variation of phylogenetic structure of lianas. Generalized additive models (GAMs) are a useful tool to capture the shape of a relationship between predictive variables (x, in this case environmental data) and response variable (y, in this case NRI), regardless of its parametric form or forms (quadratic, logarithmic, exponential, logistic, reciprocal, etc), extending the range of application of generalized linear models (GLMs) by allowing non-parametric smoothers in addition to parametric forms (Crawley 2007). The regression surface in GAM is expressed as a sum of functions of each variable, so that each explanatory variable has an additive effect and can be interpret separately, but the assumption to do this is the lack of interaction among the explanatory variables (Yee and Mitchell

1991). For each environmental variable in the model 95% Bayesian confidence intervals can be plotted (Wood 2011a). GAM returns p-value for each term based on F-ratio test according to the estimated degrees of freedom under a null hypothesis that the estimator parameter is equal to zero (Wood 2011a). A p-dimensional smoother can be set to model the regression surface, the p-dimension or basis dimension of smoothers must be large enough for the model structure to include a reasonable approximation to the truth and simultaneously small enough to avoid power loss (Wood 2011b). Broadly GAM works by first constructing basis functions and one or more quadratic penalty coefficient matrices for each smooth term in the model formula, obtaining a model matrix for the strictly parametric part of the model formula, and combining these to obtain a complete model matrix and a set of penalty matrices for the smooth terms (Wood 2011b).

We executed a backward stepwise procedure in GAMs, excluding sequentially the variables with highest p-value and performing a model selection between the previous and next models through Akaike Information Criterion (AIC). Therefore, the selected GAM shows the lowest value of AIC. Since residual spatial autocorrelation could be understand as an evidence that one or more unmeasured spatially structured variables are required to explain all spatial structure in the data, a correlogram provides important clues with respect to the spatial scale at which these variables are operating (Hawkins 2012), we assessed the autocorrelation of GAM residuals using Moran's I statistics, which tests the null hypothesis of spatial independency, varies between -1 and +1, indicating negative or positive autocorrelation in the data, examinating their significances by Z-value (1.96<Z<-1.96, p-value<0.05).

All analyses were performed in R language version 2.12 (R Developmental Core Team 2010) with the aid of "vegan" (Oksanen et al. 2011), "picante" (Kembel et al. 2010) and "mgcv" packages (Wood 2011b).

Results

We sampled 3,806 living climbing plant stems of 90 species in 25 families, of which 19 were identified to genus only, two to family, and two (each with one individual) are still undetermined (*Supplemental Material 1*), excluding the latter two morphoespecies from our analysis. Each plot contained two to 25 species (median of 11) and five to 150 living stems (median of 31). We constructed a supertree with 88 climbing plants species sampled (Figure 2).

Considering all climbing plants species and comparing with the sampled supertree, we found a generalized and significant phylogenetic clustering and the phylogenetic structure did not present a spatial structure (Figure 3). From 100 plots, 62 presented NRI values for clustering pattern (Figure 4), differing significantly from the random null model (modal value higher than1.96). We found no plot with significant phylogenetic overdispersion (NRI<-1.96). Considering only Bignoniaceae family, we found a random phylogenetic structure but one site (Figure 4), which presented an overdispersed structure (NRI<-1.96). Regarding to clustered groups, we did not found significant differences between the groups for NRI values ($F_{1,98}$=0.603, p-value=0.439, Figure 5), species richness ($X^2_{df=2}$ =5.39, p-value>0.05), abundance ($X^2_{df=2}$ =6.71, p-value>0.03) and diversity ($X^2_{df=2}$ =3.29, p-value>0.05).

The best GAM (AIC=429.67, ΔAIC=-6.65) to explain NRI variance in backward stepwise analyses included three terms: Hmed, PR and Hmax. This model explain 17% of NRI variance, however only PR (proportion present trees set) showed a significant smooth term (p-value<0.05), with a negative correlation with NRI (Figure 6). Its residuals did not show spatial autocorrelation (Figure 7). We did not perform GAM analysis with Bignoniaceae family, since this family showed only one plot with significant NRI.

Discussion

At neighborhood scale we might observe the effect of individual-based interactions that lead to within-habitat filtering or “neighbor exclusion” (Webb et al. 2002). Therefore, considering our studied scale (100 m²), general conclusions of competitive exclusion or habitat filtering could emerge. Our results indicate that climbing plants composition in a scale of 100 m² shows coexistence of close relatives, independent of ecounit (based on our environmental data). Moreover, considering our surrogates to forest dynamic (proportion of present trees –PR, and median of tree heights), climbing plants’ phylogenetic pattern showed higher values of clustering values (lowest values of NRI) in old-growth forest than in gap sites, the opposite of our hypothesis. The expected explanation for clustering in distribution of sampled taxa on the phylogeny is due to the habitat filtering which causes phenotypic attraction over the species repulsion (Kraft & Ackerly 2010).

Letcher (2010) proposes strong biotic filtering during the stem exclusion phase, which causes lowest values of NRI, consequently overdispersion pattern of phylogeny. In this phase, high mortality of lianas and shrubs are noted, canopy closes, the recruitment of shade-tolerant seedling, sapling and trees happens and also the proeminent high mortality and growth suppression in understory and subcanopy of short-lived pioneer trees (with low WD density) (Chazdon 2008). Our supposed counterintuitive result of clustering in old-growth forest for climbing plants community, where Letcher (2010) found overdispersion nearly random structure for angiosperms, is due to a biotic filtering (Verdú et al. 2009). These sites could be more physiologically challenging than treefall gaps to climbing plants species. Climbing plants are a polyphyletic group of plants sharing a common growth strategy that centers on ascending to the canopy using the architecture of other plants, which leads to cogitate that climbing plants are adapted as a life-form light-demanding (Schnitzer and Bongers 2002). Their ability to grow rapidly in the high light levels resulting from a disturbance (Putz & Chai 1987, Schnitzer & Bongers 2002) and their more efficient physiology to use water, nitrogen and phosphorus, to fix more carbon and to present higher photosynthetic rates (Cai et al. 2009, Zhu & Cao 2010) could reflect that lianas species to grow at a high rate in treefall gaps than in non-gap sites, i.e., old-growth forest sites are more physiological restrictive to climbing plants.

Consequently, treefall gaps have more random phylogenetic structure than old-growth forest sites due to the convergent ecological traits of climbing plants to high light sites (treefall gaps) and an upcoming competitive exclusion, which causes primarily a random pattern of sample taxa on the phylogeny (Webb et al. 2002). Treefall gaps sites present higher lianas species richness than non-gaps sites (Schnitzer & Carson 2001), which was firstly explained by their light-demanding physiology. Gilbert et al. (2006) proposed three alternative hypotheses to explain high liana diversity in gaps: (1) greater persistence of established climbing plants after the creation of a canopy gap; (2) plastic growth response of climbing plants; and (3) adult climbing plants growth from nearby trees and that established liana seedlings and saplings also grow directionally into newly formed gaps from the nearby understory. Indeed, Malizia and Grau (2008) showed that surrounding environmental has a strong influence on climbing plants species composition and diversity, due to a likely increasing propagule input. For that reason we could consider that clustered phylogenetic structure of climbing plants on some gap sites is due to a resilient presence of previous individuals, keeping the property of phenotypical attraction of old-growth forest.

Differences of diversity, abundance, species richness and NRI between the groups based on our environmental data were not found. However, we found a general (weak) influence of some categorical characteristics of old-growth forest (proportion of present trees and tree height) on phylogenetic clustering of climbing plants. Treefall gaps seem to be less ecological restrictive to climbing plants species coexistence than old-growth forest, which results in a generalized random phylogenetic structure. We highlight that the overall phylogenetic cluster analysis of the climbing plants community did not reflect at family level. There may be a general pattern of scale dependency resulting from the taxonomic delineation of local assemblages where more finely taxonomically defined communities are more likely to be phylogenetically overdispersed (Swenson et al. 2006). Usually, NRI patterns could be achieved until the Order taxonomic scale (Swenson et al. 2006)

Further investigations must be taken, because positive interactions may also promote phylogenetic clustering when they enhance fitness of phylogenetically similar species (Cavender-Bares et al. 2009). Therefore, future directions could address the phylogenetic structure between different sizes of climbing plants, to investigate these two possibilities: positive interactions among climbing plants species in treefall gaps or resilient presence of phenotypical constrain in old-growth forest.

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References

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen T, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill D, Patiño S, Pitman N, Silva JNM, Vásquez-Martinez R (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545–562.

Brokaw, N.V.L. (1985) Gap-phase regeneration in a Tropical forest. Ecology 66(3): 682-687.

Burns JH, Strauss SY (2011) More closely related species are more ecologically similar in an experimental test. PNAS 108(13): 5302-5307.

Cai, Z-Q, Schnitzer, S.A., Bongers, F. (2009) Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. Oecologia 161:25-33.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. Ecology Letters 12:693-715.

Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006) Regional and Phylogenetic variation of wood density across 2456 Neotropical tree species. Ecological Applications 16: 2356-2367.

Chazdon RL (2008) Chance and determinism in tropical forest succession. In: Carson WP, Schnitzer SA (Eds.), Tropical Forest Community Ecology. Blackwell, Malden, USA, pp. 384–408.

Cielo-Filho R, Gneri MA, Martins FR (2007) Position on slope, disturbance, and tree species coexistence in a Seasonal Semideciduous Forest in SE Brazil. Plant Ecology 190:189-203.

Clark DB, Clark DA (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62(3): 315-344.

Crawley, M.J. (2007) The R book. John Willey & Sons. London, United Kingdom

DeWalt SJ, Schnitzer SA, Denslow JS (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. Journal of Tropical Ecology 16:1-19.

Dutilleul P (2011). Spatio-Temporal Heterogeneity: Concepts and Analysis. Cambridge Press. Cambridge, United Kingdom.

Gandolfi S, Joly CA, Leitão-Filho HF (2009) “Gaps of Deciduousness”: Cyclical gaps in tropical forests. Scientia Agricola 66(2): 280-284.

Gerwing J.J. (2004) Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. Forest Ecology and Management 190: 57–72

Gerwing JJ, Schnitzer SA, Burnham RJ, Bongers F, Chave J, DeWalt SJ, Ewango CEN, Foster R, Kenfack D, Martínez-Ramos M, Parren M, Parthasarathy M, Pérez-Salicrup DR, Putz EF, Thomas DW(2006) A standard protocol of liana censuses. Biotropica 38(2): 256-261.

Gilbert, B., Wright, S.J., Muller-Landau, H.C., Kitajima, K. & Hernandez, A. 2006. Life history trade-offs in tropical trees and lianas. Ecology 87: 1281–1288.

Hawkins, B.A. (2012) Eight (and a half) deadly sins os spatial analysis. Journal of Biogeography 39:1-9.

Hegarty, E.E. 1991. Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. Journal of Tropical Ecology 7: 201–214.

Ibarra Manríquez G, Martínez-Ramos M (2002) Landscape variation of liana communities in a Neotropical rain forest. Plant Ecology 160(1):91-112.

IBGE (1992) Manual técnico da vegetação brasileira. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Keeling HC, Phillips OL (2007) A calibration method for the crown illumination index for assessing forest light environments. Forest Ecology and Management 242:431-437.

Kembel, S.W., Hubbell, S.P. (2006) The phylogenetic structure of a neotropical forest tree community. Ecology 87(7): S86-S99.

Kembel, S.W. 2007. Nix: software for taxonomic informatics. http://phylodiversity.net/nix/

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26: 1463-1464.

Kraft, N.J. & Ackerly, D.D. (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs 80(3): 401-420.

Laurance, W.F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P.M., D’Angelo, S., Jerozolinski, A., Pohl, L., Lovejoy, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82: 105–116

Leicht-Young, S.A., Latimer, A.M., Silander Jr, J.A. 2011. Lianas escape self-thinning: Experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. Perspectives in Plant Ecology, Evolution and Systematics 13: 163-172.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314-320.

Letcher SG, Chazdon RL (2009) Lianas and self-supporting plants during tropical forest succession. Forest Ecology and Management 257: 2150–2156.

Letcher S (2010) Phylogenetic structure of angiosperm communities during tropical forest succession. Proc. R. Soc. B 277: 97-104.

Lohmmann, L.G., Bell, C.D., Calió, M.F., Winkworth, R.C. (2013) Pattern and timing of biogeographical history in the Neotropical tribe Bignonieae (Bignoniaceae). Botanical Journal of the Linnean Society: 171, 154–170

Malizia, A. & Grau, R.H. (2008) Landscape context and microenvironmental influences on lianas communities within treefall gaps. Journal of Vegetation Science 19: 597-604

Mayfield, M.M., Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085-1093.

Oksanen, J. Blanchet, F. G., Kindt, R., Legendre,P., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M. H. H., Wagner, H. (2011). vegan: Community Ecology Package. R package version 1.17-9. http://CRAN.R-project.org/package=vegan

Oldeman RAA (1990) Forests: elements of silvology. Springer-Verlag, Berlin, 624p

Malizia, A. & Grau, H.R. (2009) Landscape context and microenvironment influences on liana communities within treefall gap. Journal of Vegetation Science 19(5): 597-604.

Pacala SW, Rees M (1998) Models suggesting field experiments to test towo hyphotesis explaining successional diversity. American Naturalist 152(5):729-737.

Pérez-Salicrup DR, Sork VL, Putz FE (2001) Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33: 34-47.

Prinzing, A., Reiffers, R., Braakhekke, W.G., Hennekens, S.M., Tackenberg, O. Ozinga, W.A., Schaminée, J.H.J., van Groenendael, J.M. (2008) Less lineages – more trait variation: phylogenetically clustered plant communities are functionally more diverse. Ecology Letters 11: 809-819.

Putz, F.E. (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713-1724.

Putz, F.E. & Chai, P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. Journal of Ecology 75: 523-531.

Putz, F.E. & Holbrook, N. M. 1991. Biomechanical studies of vines. In Putz, F.E. & Mooney, H.A. (eds.) The biology of vines, pp. 73-97. Cambridge University Press, Cambridge, UK.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Schnitzer, S. A. & Carson, W. P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology, 82: 913-919.

Schnitzer, S. A. & Bongers, F. A. (2002) The ecology of lianas and their role in forests. Trends in Ecology & Evolution, 17 (5): 223-230.

Schnitzer, S.A., Mascaro, J., Carson, W.P. (2008) Treefall gaps and the maintenance of plant species diversity in tropical forests. In: Carson WP, Schnitzer SA (Eds.), Tropical Forest Community Ecology. Blackwell, Malden, USA, pp. 196–209.

Swenson, N.G., Enquist, B.J., Pither, J., Thompson, J. Zimmerman, J.K. (2006) The problem and promise of scale dependency in community phylogenetics. Ecology 87(10): 2418-2424.

Torquebiau EF (1986) Mosaics patterns in dipterocarp rain forest in Indonesia, and their implications for practical forestry. Journal of Tropical Ecology 2: 301-325.

Verdú, M., Rey, P.J., Alcántara, J.M., Siles, G. & Valiente-Banuet, A. (2009) Phylogenetic signatures of facilitation and competition in successional communities. Journal of Ecology 97: 1171-1180

Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalis 156: 145-155.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J. (2002) Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475-505.

Webb, C.O., Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. Molecular Ecology Notes 5:181-183.

Wood, S.N. (2011a) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73(1):3-36

Wood, S.N. (2011b) mgcv: GAMs with GCV/AIC/REML smoothness estimation and GAMMs by PQL. Version 1.7-9. http://CRAN.R-project.org/package=mgcv

Yee, T.W., N.D. Mitchell. (1991) Generalized additive models in plant ecology. Journal of Vegetation Science 2:587-602

Zhu, S.-D., Cao, K.-F. (2010) Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. Oecologia 163:591-599.

Figures

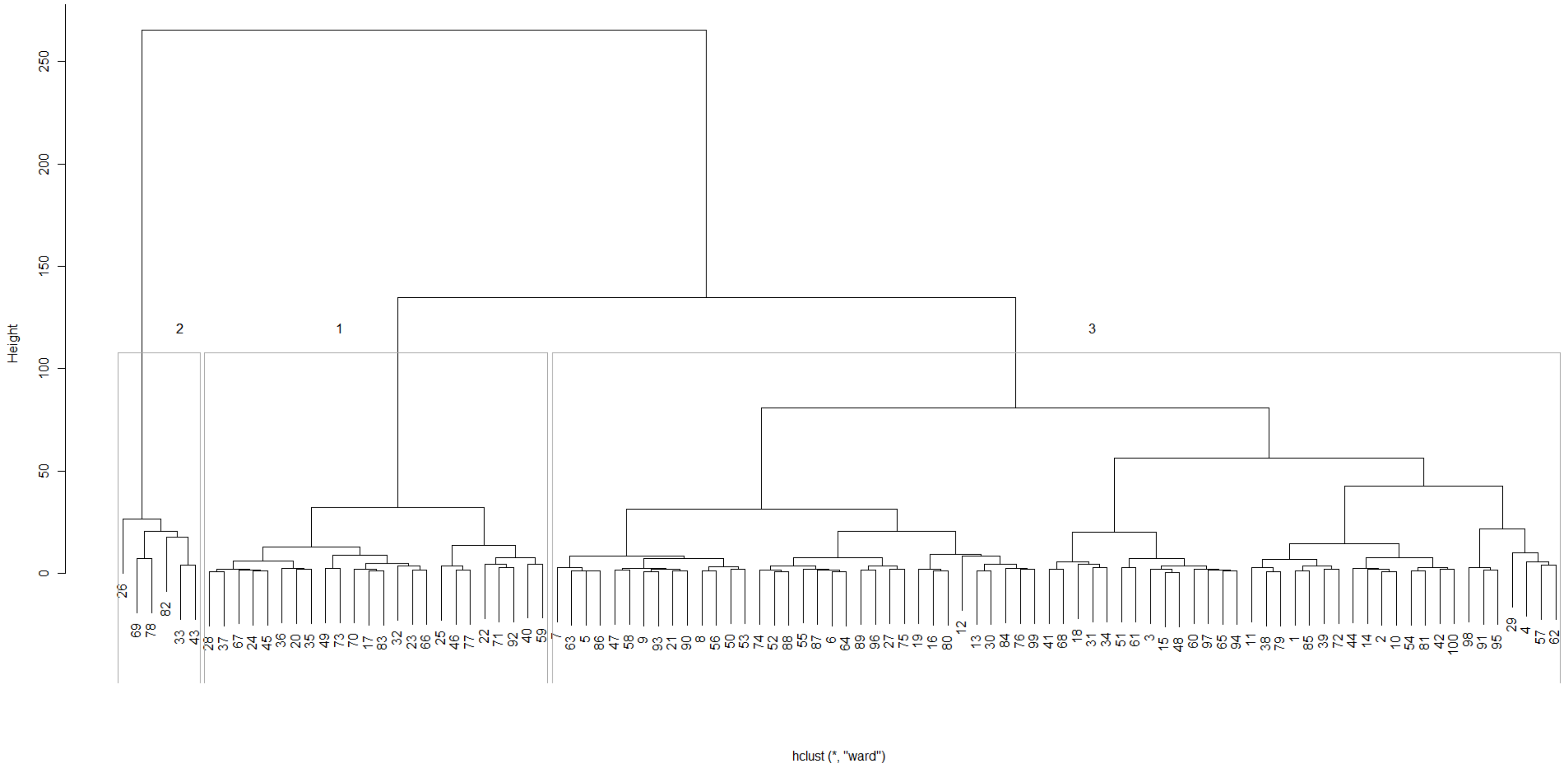

Figure 1 – Ward hierarchical clustering analysis (information retained at 30%) based on environmental data, representing forest dynamic surrogates.

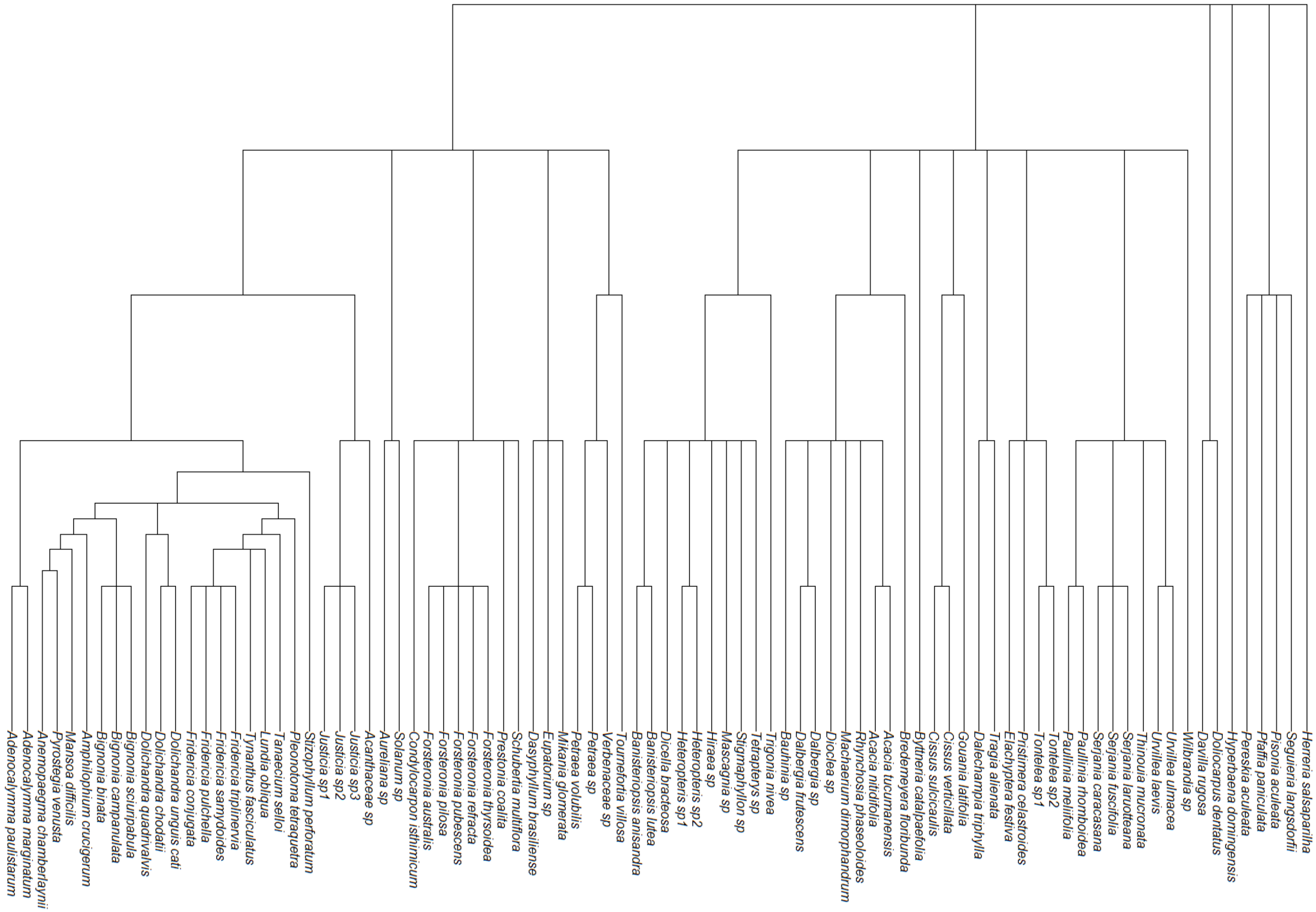

Figure 2 – Phylogenetic supertree of sampled climbing plants species in Ribeirão Cachoeira Forest, Campinas, Brazil

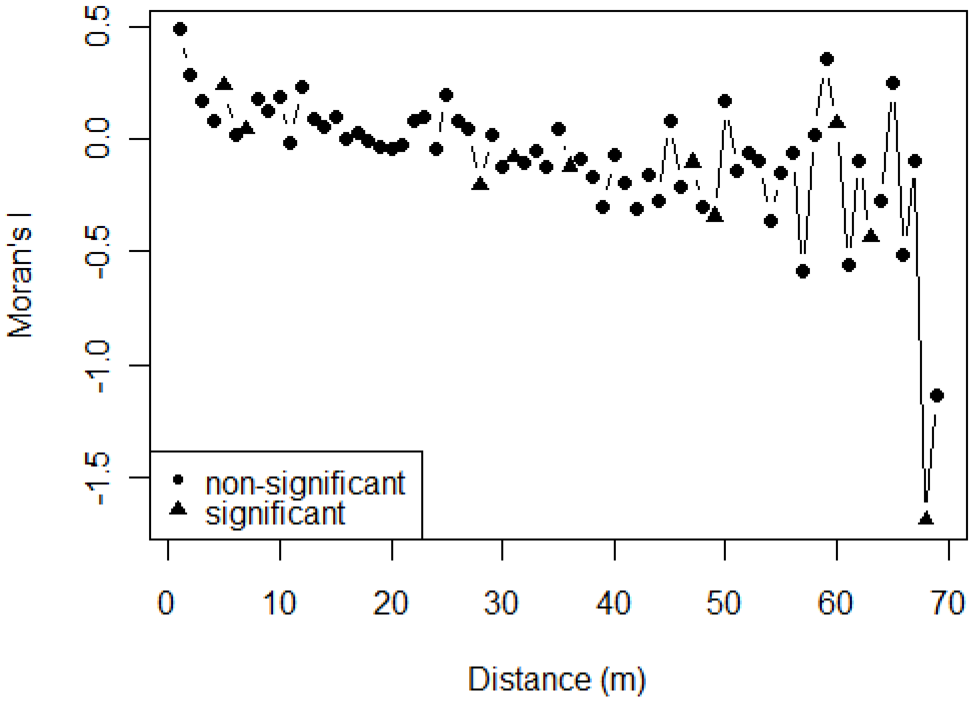

Figure 3 – Spatial autocorrelation of Net Relatedness Index (NRI) based on Moran's I coefficient. Significant autocorrelation distance classes at p-value less than 0.05 are represented by a triangle (▲).

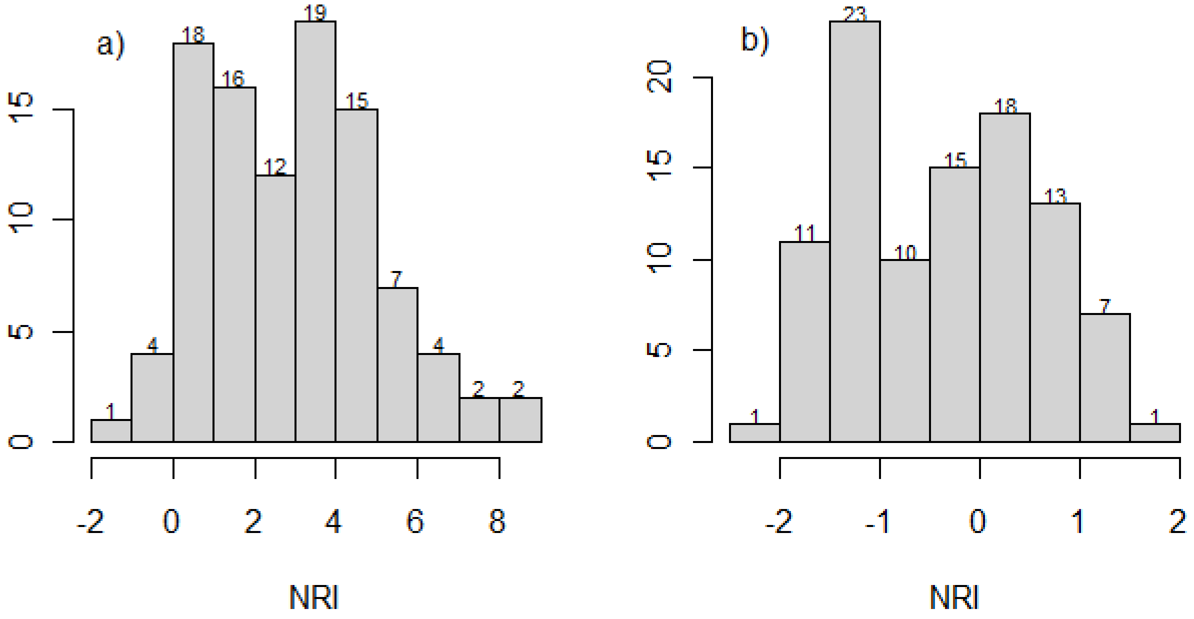

Figure 4 – Frequency distribution of the Net Relatedness Index of a Seasonal Semideciduous Forest considering all the sampled climbing plants' community (a) and only the species belonging to Bignoniaceae family (b).

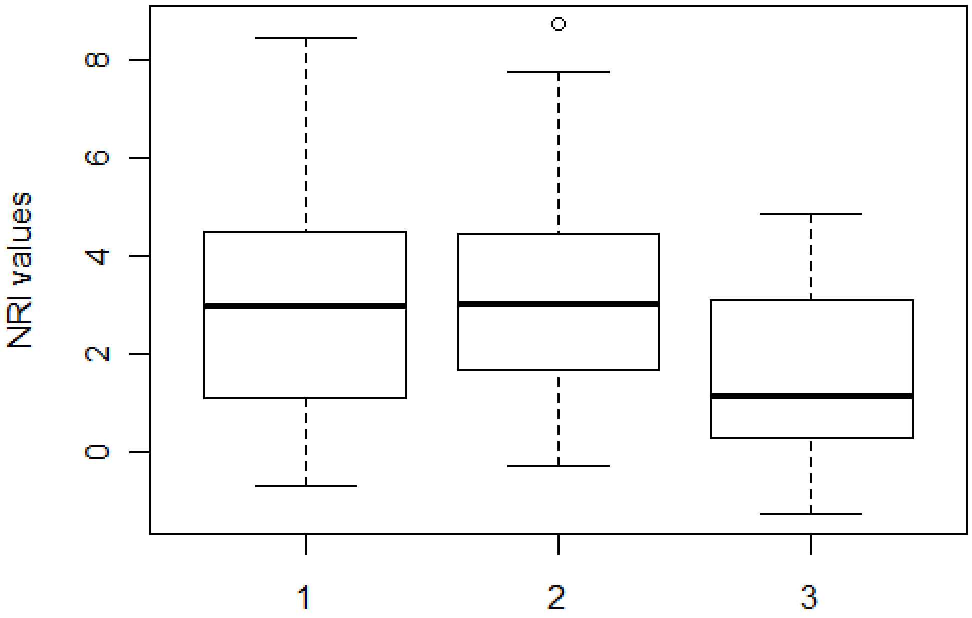

Figure 5 – Boxplots with Net relatedness index (NRI) values of the three clustered groups based on environmental data. Groups numbers are showed in Figure 1.

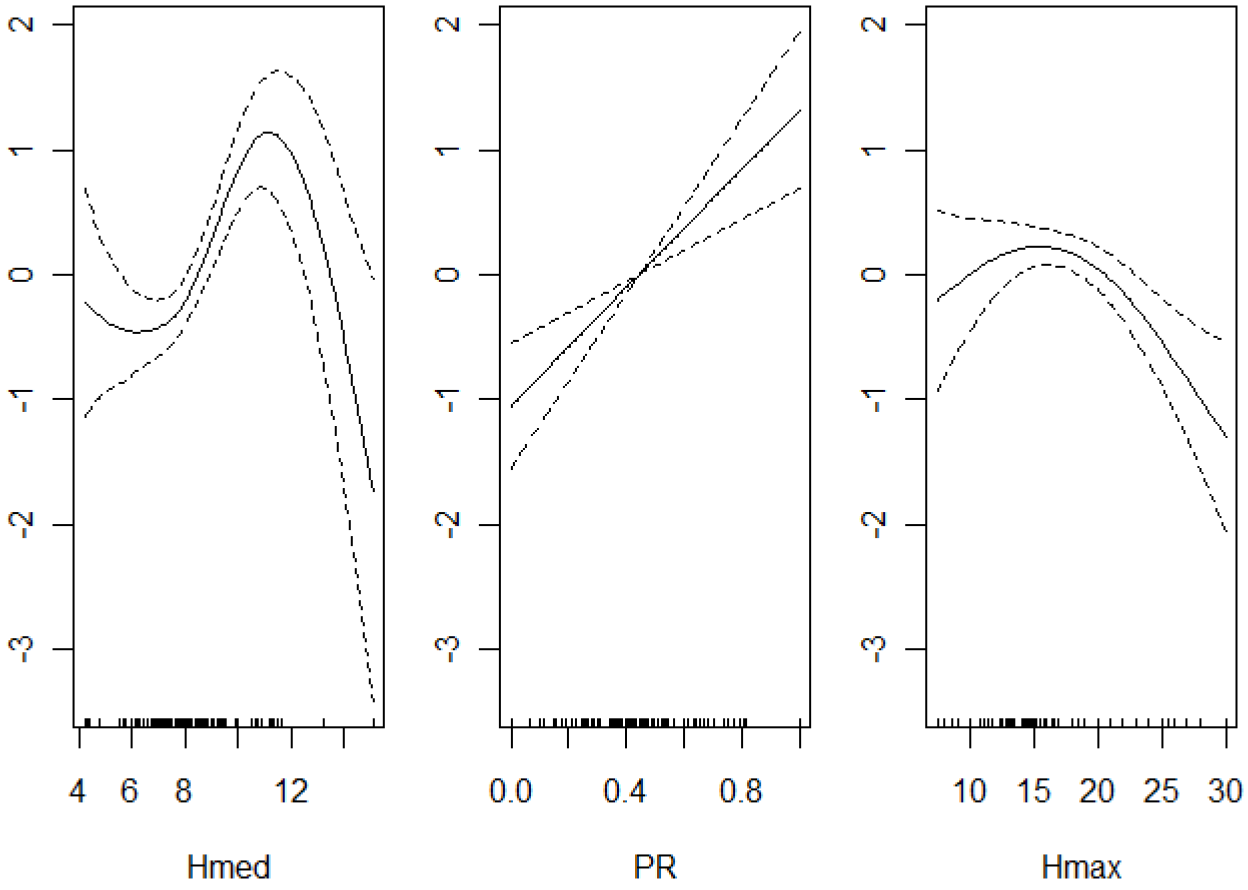

Figure 6 – Generalized Additive Model plots for the relationship of Net Relatedness Index (NRI) values with three environmental predictors (Hmed: Median Tree Height, PR: Proportion of Present Trees, Hmax: Maximum Tree Height). The y label is the smoothing of covariate and their estimated degrees of freedom. Dashed lines contain the 95% confidence interval for each response curve.

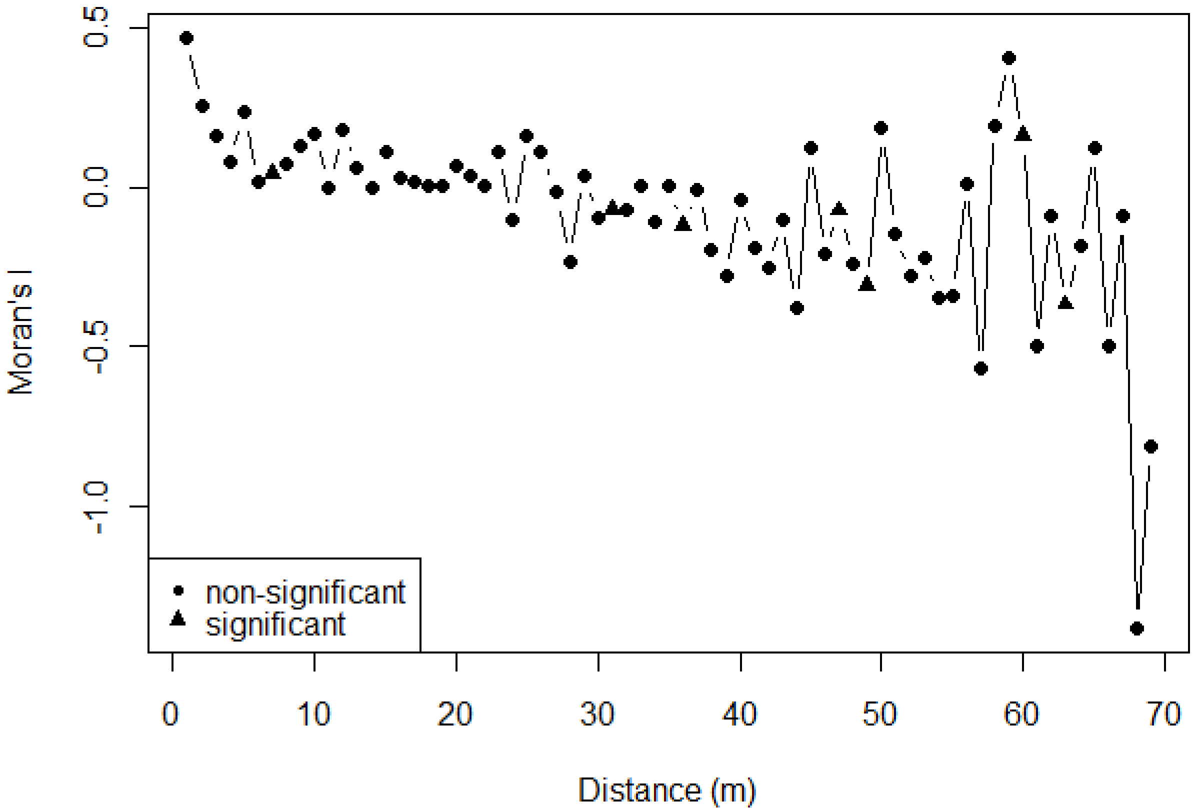

Figure 7 - Spatial autocorrelation of the residuals of Generalized Additive Model based on Moran's I coefficient. Significant autocorrelation distance classes at p-value less than 0.05 are represented by a triangle (▲).

Capítulo 3: Direct and Indirect factors to determine climbing plants community parameters on local-**scale: A Structural Equation Modeling approach.**[3]

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[3] Artigo segue normas de *Plant Ecology*

Indirect and direct factors to determine climbing plants community parameters on local-scale: A Structural Equation Modeling approach.

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Climbing plants are an imporntant plant group in the Tropics and their abundance are increasing. o evaluate an empirical model which tree community variables, tree canopy features and soil characteristics drive the abundance and species richness of climbing plants (woody, subwoody and herbaceous) we applied a Structural Equation Modeling (SEM) approach to test our hypotheses. At fine spatial scale in a Neotropical Seasonal Semideciduous Forest, located in Campinas, southeastern Brazil, we sampled all climbing plants with diameter larger than 1.0 cm and trees and shrubs with perimeter at breast height larger than 15 cm in 100 randomized plots of 100m² and obtained canopy characteristics, to evaluate surrogates of canopy disturbance, and edaphic data. Our first Structural Equation Model based on the theoretical background was not significant. Therefore, edaphic properties were excluded of analysis. A second SEM model was constructed and showed a good fit. The final SEM showed that the community parameters of trees and shrubs cause a significant change in climbing plants parameters but canopy disturbance exhibited higher influence. We conclude that edaphic properties do not show any importance in determine the climbing plants' community parameters (abundance and species richness). Trees and shrubs' parameters are direct important drivers to modify the variance of climbing plants' parameters but not indirectly by canopy disturbance. The most important factor on these parameters on a fine spatial scale is the direct influence of canopy disturbance.

Keywords: lianas, climbers, Neotropical Semideciduous Forest, Atlantic Forest

Introduction

Climbing plants, such as lianas (woody and sub-woody climbing plants), are often more abundant and show higher number of species richness and diversity in tropical seasonal dry forests than in others forests (Gentry 1991, Schnitzer 2005, van der Heijden and Phillips 2009). Climber species richness and the Shannon heterogeneity index of trees in SE Brazilian forests are correlated on large spatial scale, indicating that the heterogeneity of tree traits would be associated with the number of potential niches for climbers (Sfair and Martins 2011). It remains to be investigated whether this response similarity would be due to correlation of climbing plant and tree community assembling processes or to causation of trees on climbing plants at local scale.

At local scale, liana communities seem to be strongly influenced by canopy disturbance rather than by the abundance or species composition of canopy trees (Malizia et al. 2010). On the other hand, Garbin et al. (2012) asserted that subordinate woody species promote the diversity of climbing plants rather than dominant trees, specifying that is an outcome of subordinate woody plants facilitation to climbing plants. Canopy disturbance is overall highly correlated with liana abundance and species richness (Schnitzer and Bongers 2002, Dalling et al. 2012), where treefall gaps promote climbers diversity by increasing local resource availability and heterogeneity. Garbin et al. (2012) highlighted the importance of more studies which include different groups of plants at the same spatial scale, where multiple causal hypotheses are used to explain climber abundances, for example.

Unveil causality corresponds to the ideal method of science, but causes of variation often seem to be beyond control. Science deals with a group of characteristics or conditions that are correlated because of a complex of interacting, uncontrollable, and often obscure phenomena, which demand careful methods to distinguish between causality and modulation (Shipley 2000). Structural equation modeling (SEM) has attracted the interest of ecologists due to the possibility of this technique to link theoretical concepts and statistical techniques (Grace 2006, Yuan et al. 2011), allowing to understand if a theoretical model based on direct and indirect effects on some variable is truly valid. Van der Heijden and Phillips (2008, 2009) used SEMs to explain variation of abundance, basal area and species richness of lianas within Neotropical forests. However, to our knowledge, there is no study relating direct and indirect causal factors in liana community on fine spatial scale.

Macroecological constraints could not be the same constraints on local scales. For instance, some researchers have found no relationship between liana diversity and soils properties on local scale (Burnham 2002, Ibarra-Manríquez and Martínez-Ramos 2002, Dalling et al. 2012, but see Malizia et al. 2010), and on larger scales there is a likely association between liana species richness and soil properties obscured by soil correlation with climate (van der Heijden and Phillips 2009). Moreover, soil properties are correlated with forest dynamic on landscape scale, i.e. Tropical rain forests growing on more fertile soils have higher tree turnover and are more dynamics (Phillips et al. 1994, 2004), would causes an indirect effect on liana abundance and species richness.

Therefore, we propose and test a theoretical model to explain the main factors structuring the climbing plant community variables (abundance and species richness) at fine spatial scale in a Neotropical Seasonal Semideciduous Forest. Our aim is to investigate how soil properties, canopy disturbance or tree community influence on climbing plant community (woody and non-woody). For our purpose, we use structural equation modeling (SEM), which provides a perspective by partitioning direct from indirect effects and thereby revealing a variety of mechanisms behind the overall patterns, whereas conventional univariate relationships can lead to misleading impressions (Grace and Keeley 2006). Therefore, we use SEM with latent variables to investigate direct and indirect factors of climbing plant community structuring on a fine spatial scale. Our specifics questions are: (1) are tree community parameters positive causal effects on climbing plant diversity? (2) What are the indirect and direct environmental factors to explain climbing plant community on fine spatial scale?

Material and Methods

Study area

We studied an area of 6.5 ha (22°49’S and 46°55’W) located in the south portion of one forest fragment in the municipality of Campinas, SE Brazil. The sampling area is located on a slope, approximately 270 m in length, with average steepness of 15%, and 40 m of difference between the up and low ends. In the studied area, we settled down through simple randomization, 100 square plots with 100 m² each, totaling a sampled area of 10,000 m².

The vegetation is seasonal semideciduous forest with an accentuated rainfall seasonality and deciduousness observed in up to 50% of the canopy trees during the dry season (IBGE 1992). Altitude varies between 630 and 760 m above sea level. The predominant soil is Acrisoil (FAO nomenclature) with sandy texture and many rock fragments (Embrapa 1999). According to Koeppen's classification, the climate is Cwa, with hot, rainy summer and mild, dry winter. There are no signs of recent anthropogenic disturbances in the area, such as coal on the ground surface, soot on the tree trunks or logging evidences, characterizing as an "Old Growth" forest.

Structural Equation Modeling

A Structural Equation Modeling (SEM) is guided by an *a priori* theoretical knowledge of the investigator, considering general expectations (Figure 1). Through the use of a simultaneous analysis procedure, SEM derives results that seek to account for the roles of multiple factors in a single analysis (Grace and Keeley 2006). SEM models represent translations of a series of hypothesized cause-effect relationships between variables into composite hypothesis concerning patterns of statistical dependencies (Pugesek et al. 2003), which can work as a "confirmatory" model tests, testing against empirical data, or in an "exploratory" mode, which involves repeated applications of the same data in order to explore potential relationships between variables of interest (Pugesek et al. 2003).

Standardized path coefficients for the models are showed in the figures, where solid arrows represent significant path relations ($p\text{-value}<0.01$) and non-significant paths were shown with dashed lines ($p\text{-value}>0.05$). Standardized path coefficient shows the mean response, in standard deviations (SD) units of the dependent variable, to one standard deviation (SD) of change in the explanatory variable. The model-fit was characterized by its minimum function X^2 test and its p-value, where a well fitted model shows low value of X^2 and high value of p-value. Structural equation models are measured in a different way, compared to null hypotheses. In the latter, priority is given to the hypothesis of no relationship. This is the case no matter what our *a priori* knowledge is about the processes involved. In contrast, when evaluating overall fit of data to a structural equation model, priority is given to the model, and test results are used to indicate whether there are important deviations between model and data (Grace 2006). Therefore, in SEM, the *a priori* information used to develop the initial model is used as a basis for interpretation, highlighting that *a priori* hypothesis is very important.

The variables of interest could be classified as observed or latent variables. One of the distinctness characteristics between Path analysis and SEM is the incorporation of latent variables on the analysis. Latent variables are hypothetical or theoretical variables that cannot be observed directly, which give important reasons to use them (Grace 2006). Latent variables distinguish concepts from observations and adjust for the effects of measurement errors (see Grace 2006 for further information).

Latent variable represents shared information of indicators (observed variables) adding the effects of measurement errors. To make a good latent variable is necessary to see if the correlations between candidate indicators are strong but not redundant. We named our latent variables of our theoretical model as: “SOIL”, “CANOPY”, “TREES” and “LIANAS”. In advance, we explain which observed variables were used to these latent variables. We examined the significance of latent variable in blocks, i.e. viewing the higher significance (p-value closest to 1.0) and less covariance and variance values of observed variables.

The presence of spatial autocorrelation violates the assumption of independently distributed errors of regression models, inflating Type I errors of tests, and can affect inference from statistical models and our ability to evaluate the importance of explanatory variables (Legendre 1993, Dormann et al. 2007, Kissling et al. 2008). To check any spatial autocorrelation between variables, we calculate Moran’s I values on the residuals of our minimal adequate regression models. In the presence of spatial autocorrelation, we fitted spatial simultaneous autoregressive error models (Kissling and Carl 2008), which can include the spatial autocorrelation of a given data set. Spatial error term is predefined from a neighbourhood matrix and autocorrelation in the dependent variable estimated, and then the parameters are estimated using a Generalized Least Squares (GLS) framework (Kissling and Carl 2008, Beale et al.2010). SAR (simultaneous autoregressive) models augmented the multiple regressions with an additional term that accounted for patterns in the response variable that were related to values in neighboring locations. If (and only if) the OLS (ordinary least squares) and SAR coefficients are the same, we can trust the OLS coefficients. We found closer values of OLS and SAR coefficients. Moreover, in all SAR the residuals spatial autocorrelation still remained, thus we assumed that standardized coefficients of SEM are trustful due to the robustness of correlations despite the spatial autocorrelation.

All statistical analyses were performed with software R version 12.2 (R Development Core Team 2011). SEMs were performed in ‘lavaan’ package, variables standardization with ‘vegan’ package, Principal Component Analyses (PCAs) were performed with “FactoMineR” and “nFactors” packages, and SAR were calculated with ‘spdep’ and ‘ncf’ packages. Normality of observed data was reached after transformation (described in advance) and standardization.

Climbing plants, shrubs and trees inventory.

From August to October 2008 we resampled all the living trees and shrubs with DBH (diameter at breast height) larger or equal to 5.0 cm in the plots that were sampled in 2001 by Cielo-Filho et al. (2007). Following Gerwing et al. (2006), from October 2008 to April 2009 we sampled all the climbing plant stems (woody and non-woody) with DBH $\geq$ 1 cm that were rooted in each plot. We considered as a single individual each stem with no evident connection with other stem at the soil surface. Vouchers were lodged in the UEC herbarium.

The latent variables named “LIANAS” and “TREES” are theoretical constructs of both plant groups which explain their abundance and species richness values per plot. Therefore, “TREES” latent variable explain the observed abundance and observed number of species of trees and shrubs in each plot (100m²), incorporating measurement errors of observed variables. “LIANAS” latent variable was constructed in the same way for climbing plants. Lianas species richness (^2/3) and liana abundance (log) reached the normality after transformation.

Soil

Firstly, we collected superficial soil samples (0-20 cm in depth) in the center of each plot for physico-chemical analyses, which were performed by the Instituto Agronômico de Campinas. Chemical analyses determined total cation exchange capacity (CEC), extractable bases (SB), base saturation (V), organic matter (OM), potential acidity (H+Al), pH, exchangeable cations (Ca, Mg, K) and extractable phosphorus (P). Texture analysis quantified percentages of clay, silt and sand. To reach the normality we transformed K, Ca, H+Al, S.B., Clay with their natural logarithm values.

Secondly, we examined which observed edaphic variables (SB, V, OM, H+Al, pH, Ca, Mg, K and P) demonstrated less variance and covariance, and which constructed a latent variable with higher p-value. We excluded one plot of analyses because its outlier values of edaphic variables, visualized with PCA factor map. The observed variables which better represent the “SOIL” latent variable were: pH, CEC and Mg. Finally, we tested if “SOIL” latent variable represents a causal relationship of altitude of plots or soil texture. The SEM model indicating covariance between soil texture and “SOIL” was not significant (p-value=0.559), despite the fact the SEM model showed a good acceptance (p-value equals to 0.701). However, the SEM which shows a causal relationship of altitude on “SOIL” showed a good acceptance (minimum function $X^2 = 3.073$ with 2 degrees of freedom, p-value = 0.215) and a significant regression (p-value <0.001, standardized parameter = 0.376).

Canopy

Since canopy disturbance promotes the diversity and abundance of lianas (Schnitzer and Bongers 2002), we investigated some forest characteristics which are highly correlated with canopy structure (treefall to old-growth forest).

According to Torquebiau (1986), we classified each tree as belonging to the past, present or future sets. We considered the proportion of past trees as an indicative of treefall gap, since "past" trees present senescence and broke boles, and a large proportion of this set characterizes a canopy gap. In the same way, we used the proportion of present trees as an indicative of old-growth forest (Oldeman 1990). Also, we used the crown illumination index CII (Clark and Clark 1992) to assess light exposition of each tree. Keeling and Phillips (2007) found a strong positive correlation between average CII and gap openness; so, we used average CII per plot as a measure of gap openness. Since many canopy gaps become colonized by lianas very soon after gap formation (Schnitzer et al. 2004), we estimated the forest canopy cover index for each plot using a spherical convex densitometer at the breast height (Lemmon 1956).

Forest disturbance is correlated with low tree height and small basal area, and shows trees with low wood densities (Laurance et al. 2001; Baker et al. 2004). Therefore, we obtained tree heights with the aid of a Crain ® Fiberglass Telescoping Measuring Rod, measuring until the end of tree bole. Basal area values of the trees were got with a metric-tape. We searched the literature to obtain wood density (WD) for each tree species we sampled. When data were absent for species, we used genus-level approximation for WD values (Chave et al. 2006).

Considering that we studied a seasonal semideciduous forest, we classified leaf phenodynamics of each species as evergreen, semideciduous or deciduous, following the literature. Scattered in every tropical seasonal semideciduous forest there are gaps of deciduousness, which correspond to momentary bright places that appear during the dry season under deciduous canopy trees when they are leafless (Gandolfi et al. 2009). As these deciduousness gaps can affect survival and development of seeds, seedlings, sapling and poles (Gandolfi et al. 2009), we assumed that they could also influence climbing plant establishment and persistence.

The number of past trees (PT), present trees (PR), and semi-deciduous and deciduous trees (SDT) was standardized by Wisconsin method, which is a common double standardization where “species” (in these cases, category of tree) are first standardized by its maxima (highest abundance per plot), and then sites (each plot of 100 m²) are standardized by site totals (function “wisconsin" in the R software vegan package). This standardization is necessary in order to compare variables expressed in incompatible units. Therefore, for each plot we considered the following surrogates of the community internal dynamics: mean CII, median WD, median of log values of tree basal area (BAmed), median tree height (Hmed), height of the tallest tree (Hmax), PT, PR and SDT. We used natural logarithm transformation of CII, CO, SDT and Hmed to reach the normality.

We dealt with “CANOPY” latent variable as we did with “SOIL” latent variable, searching for less variance and a SEM model with higher p-value and significant parameters. The evaluated indicators of “CANOPY” latent variable were CII, WD and PR.

Results

We sampled 90 morphospecies in 3806 living ramets of climbing plants and 137 species in 1211 sampled individuals of shrubs and trees. We excluded dead stems from these analyses. Our first model (Figure 2) did not fit with the relationships considered in our theoretical model (Figure 1). The X^2 statistic (64.454; p-value=0.005 with 38 degrees of freedom) indicates that the model cannot be accepted. Seeing the parameters and significance of regressions of the first tested model (Table 1), there is no significant relationship between “SOIL” characteristics with “TREES” or with “LIANAS”. Therefore, we decided to exclude the “SOIL” latent variable of analysis, and perform a new model.

This second SEM model (Figure 3) fit indicates that the model shall be accepted (X^2 statistic = 8.419; p-value=0.675 with 11 degrees of freedom) with significant parameters of regressions (Table 2). Therefore, we consider this reduced SEM as the final plausible representation of the direct and indirect factors on climbing plant community parameters on the fine spatial scale studied (Neotropical Semideciduous Forest).

We can infer the latent variables with their standardized path coefficients involved with their observed variables. “LIANAS” and “TREES” highly indicate that each plant group abundance and species richness increase their SD when the latent variable SD increase. Therefore, we consider that any positive effect on “LIANAS” and “TREES” causes a positive effect on SD of abundance and species richness of both groups.

Any increase in the “CANOPY” latent variable indicates increament in the mean of Wood density (WD), in the proportion of present trees (PR) and in the canopy illumination index (CII). Therefore, we considered that lower value of “CANOPY” latent variable designates lower canopy disturbance (old-growth forest). Crown Illumination Index (CII) is positively related with “CANOPY” latent variable due to the likely occurrence of emergent trees with higher incidence of sunlight in their crowns in these sites. Reinforcing, we consider that higher values of “CANOPY” latent variable indicates a old-growth forest with emergent trees.

According to our final SEM model, a shift in one SD unit in the TREES latent variable increase the SD of LIANAS in 0.26 unit, in a situation which the remaining variables of SEM model maintain constant – without variance. Conversely, an increase in one unit SD of the CANOPY latent variable decreases the SD of LIANAS in -0.53. Indirect effects, which are mediated by other variables, are estimated by multiplying the standardized path coefficients involved. Consequently, the indirect effect of CANOPY mediated by TREES in LIANAS was only 0.06 (0.28*0.24). Moreover, the relationship between CANOPY latent variable and TREES was marginally significant (p=0.06, Table 2). Additive effects – mediated and direct effects – are simply calculated by summing the values of mediated path coefficient and direct standardized path coefficient. Therefore, the total effect of CANOPY in LIANA community is -0.47 (-0.53 + 0.06). All measurement errors are displayed in Table 2.

Discussion

Our results support the importance of trees and shrubs abundance and species richness in climbing plants’ community and also show a parallel influence of canopy disturbance in climbing plants’ community parameters (abundance and species richness). We emphasize the term “parallel” because canopy disturbance showed a weak indirect influence on climbing plants, when mediated by trees. Abundance and species richness of climbing plants was positively influenced by abundance and species richness of trees and shrubs on fine spatial scale, and undisturbed canopy (higher values of CANOPY latent variable) contracted climbing plants’ community parameters, with low influence on trees and shrubs parameters.

Structural equation modeling (SEM) is a powerful tool (Shipley, 2000), although interpretation requires profound examinations (Grace and Bollen, 2005). There are a number of statistical fixes that can be used to deal with specific problems with SEM, but space is limited (Hawkins 2011). However, none of the existing observed variables in our final SEM model showed spatial autocorrelation. Thus, we shall exclude a spurious causal effect, triggered by spatial autocorrelation, in our model.

Previously, van Melis and Martins (unpublished – *first chapter of this thesis*) revealed that composition of this liana community, which we investigated in the Neotropical Seasonal Semideciduous Forest fragment, is determined by stochastic factors and dispersal limitation, showing a strong spatial autocorrelation of liana community composition (species abundance differences). However, spatially structured variables in this Neotropical Seasonal Semideciduous Forest were not important to drive any difference in liana community structural parameters (species richness and abundance), since OLS and SAR coefficients did not differentiated.

Malizia et al. (2010) already stated that liana communities are strongly influenced by canopy disturbance rather than the abundances of canopy trees. Garbin et al. (2012) highlighted the great influence of subordinate trees to the existence of the climbing plants, providing trellis (support to growth) to them. This balance of influences between canopy disturbance (treefall openness) and tree abundance (trellis) reflects different ecological filters in different life stages of the climbing plants, as elucidated by previous authors (Nesheim and Økland 2007, Nogueira et al. 2011).

The majority of lianas species are positively associated with areas recently disturbed by treefalls (Dalling et al. 2012), indicating a preference for gap-phase microsites. This strong association reflects in the fact that, on one hand species richness of self-supporting vegetation increases with forest age, on the other hand species richness of lianas shows no change or a slight decline with forest age (Letcher and Chazdon 2009). Abundance of lianas in the first phase of succession (stand initiation phase) is often high, decreasing in the second phase (stem exclusion), and with large lianas abundance increasing in old-growth forests (Chazdon 2008). Our results show a decrease in SD of liana parameters as a response of higher values of CANOPY values, inferring an increase in SD of liana parameters (species richness and abundance) in sites with lower values of CII (shaded trees), WD (denoting pioneer species) and present trees (typical set of old-growth forest).

Pairing these two main factors in climbing plants' community parameters in our model, canopy disturbance and tree community parameters (species richness and abundance), we set up a stronger causal effect of canopy disturbance on liana parameters than a direct effect of trees and shrubs. Therefore, despite the fact that trees and shrubs abundance and species richness influence climbing plants' community parameters, we conclude that the existence of canopy disturbance increase the abundance and species richness of climbing plants on fine spatial scale, based on our results. The most important factor on these climbing plants' parameters is the direct influence of canopy on climbing plants abundance and species richness in a Neotropical Seasonal Forest.

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References

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D., Patiño, S., Pitman, N., Silva, J.N.M. and Vásquez-Martinez, R. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biology 10:545–562.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. and Elston, D.A. 2010. Regression analysis of spatial data. Ecology Letters 13:246-264.

Burnham, R.J. 2002. Dominance, diversity and distribution of lianas in Yasuni, Ecuador: who is on top? Journal of Tropical Ecology, 18, 845–864

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H. and Webb, C.O. 2006. Regional and Phylogenetic variation of wood density across 2456 Neotropical tree species. Ecological Applications 16: 2356-2367.

Chazdon, R.L. 2008. Chance and determinism in tropical forest succession. In Carson, W.P., Schnitzer, S.A. (Eds.), Tropical Forest Community Ecology. Blackwell, USA. pp. 384–408.

Cielo-Filho, R., Gneri, M.A. and Martins, F.R. 2007. Position on slope, disturbance, and tree species coexistence in a Seasonal Semideciduous Forest in SE Brazil. Plant Ecology 190:189-203.

CIIAGRO/IAC. 2012. (Centro Integrado de Informações Agrometereológicas – Instituto Agronômico de Campinas). Dados históricos 1992-2012. http://www.ciiagro.sp.gov.br/ciiagroonline/Quadros/QTmedPeriodo.asp

Clark, D.B. and Clark, D.A. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62(3): 315-344.

Dalling, J.W., Schnitzer, S.A., Baldeck, C., Harms, K.E., John, R., Mangan, S.A.,Lobo, E., Yavitt, J.B. and Hubbell, S.P. 2012. Resource-habitat associations in a neotropical liana community. Journal of Ecology 100:1174-1182.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R.,Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. and Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609–628.

EMBRAPA (1999) Sistema brasileiro de classificação de solos. Empresa Brasileira de Pesquisa Agropecuária - Centro Nacional de Pesquisa de Solos, Brasília

Gandolfi, S., Joly, C.A. and Leitão-Filho, H.F. 2009. “Gaps of Deciduousness”: Cyclical gaps in tropical forests. Scientia Agricola 66(2): 280-284.

Garbin, M.L., Carrijo, T.T., Sansevero, J.B.B., Sánchez-Tapia, A. and Scarano, F.R. 2012. Subordinate, not dominant, woody species promote the diversity of climbing plants. Perspectives in Plant Ecology, Evolution and Systematics 14: 257-265.

Gentry, A.H. 1991. The distribution and evolution of climbing plants, p. 3-49. In F.E. Putz and H.A. Mooney (eds.). The Biology of Vines. Cambridge University, Cambridge, U.K.

Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, M., Pérez-Salicrup, D.R., Putz, E.F. and Thomas, D.W. 2006. A standard protocol of liana censuses. Biotropica 38(2): 256-261.

Grace, J.B. 2006. Structural Equation Modeling and Natural Systems. Cambridge University, Cambridge, U.K.

Grace, J.B. and Keeley, J.E. 2006. A Structural Equation Model analysis of postfire plant diversity in California shrublands. Ecological Applications 16(2): 503-514.

Hawkins, B.A. 2011. Eight (and a half) deadly sins of spatial analysis. Journal of Biogeography 39(1): 1-9.

Ibarra-Manríquez, G. and Martínez-Ramos, M. 2002. Landscape variation of liana communities in a Neotropical rain forest. Plant Ecology, 160, 91–112.

IBGE. 1992. Manual técnico da vegetação brasileira. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Keeling, H.C. and Phillips, O.L. 2007. A calibration method for the crown illumination index for assessing forest light environments. Forest Ecology and Management 242:431-437.

Kissling, W.D. and Carl, G. 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. Global Ecology and Biogeography 17: 59–71

Kissling, W.D., Field, R. and Böhning-Gaese, K. 2008. Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? Global Ecology and Biogeography 17:327-339.

Laurance, W.F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P.M., DÁngelo, S., Jerozolinski, A., Pohl, L. and Lovejoy, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82: 105–116

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659-1673.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314-320.

Letcher, S.G. and Chazdon, R.L. 2009. Lianas and self-supporting plants during tropical forest succession. Forest Ecology and Management 257:2150-2156.

Malizia, A., Grau, H.R., Lichstein, J.W. 2010. Soil phosphorus and disturbance influence liana communities in a subtropical montane forest. Journal of Vegetation Science 21(3): 551-560.

Nesheim, I. and Økland, R.H. 2007. Do vine species in neotropical forests see the forest or the trees? Journal of Vegetation Science 18: 395–404.

Nogueira, A., Costa, F.R.C. and Castilho, C.V. 2011. Liana abundance patterns: the role of ecological filters during development. Biotropica 43: 442–449.

Oldeman RAA (1990) Forests: elements of silvology. Springer-Verlag, Berlin, 624p

Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. and Vásquez-Martínez, R. 1994. Dynamics and species richness of tropical rain forests. Proceedings of the National Academy of the Sciences USA, 91, 2805–2809.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W.F., Lewis, S.L., Lloyd, J., Terborgh, J., Vásquez Martıínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patin ˜o, S., Pitman, N., Quesada, C.A., Saldias, M., Torres Lezama, A. and Vinceti, B. 2004. Pattern and process in Amazon tree turnover, 1976–2001. Philosophical Transactions of the Royal Society B: Biological Sciences 359: 381–407.

Pugesek, B.H., Tomer, A. and von Eye, A. 2003. Structural Equation Modeling: Applications in Ecological and Evolutionary Biology. Cambridge University, Cambridge, U.K.

R Development Core Team. 2011. R: A language and Environment for statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.

Schnitzer, S.A. and Bongers, F. 2002. The Ecology of lianas and their role in forests. Trends in Ecology and Evolution 17:223-230.

Schnitzer, S.A., Parren, M.P.E. and Bongers, F. 2004. Recruitment of lianas into logging gaps and the effects of pre-harvesting climber cutting. Forest Ecology and Management 190: 87–98.

Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166(2): 262-276.

Sfair, J.C. and Martins, F.R. 2011. The role of heterogeneity on climber diversity: is liana diversity related to tree diversity? Global Journal of Biodiversity Science and Management 1(1):1-10

Shipley, B. 2000. Cause and Correlation in Biology. Cambridge University, Cambridge, U.K.

Torquebiau, E.F. 1986. Mosaics patterns in dipterocarp rain forest in Indonesia, and their implications for practical forestry. Journal of Tropical Ecology 2: 301-325.

van der Heijden, G.M.F. and Phillips, O.L. 2008.What controls liana success in Neotropical forests? Global Ecology and Biogeography 17:372-383.

van der Heijden, G.M.F. and Phillips, O.L. 2009. Environmental effects on Neotropical liana species richness. Journal of Biogeography 36(8): 1561-1571.

Yuan, Z., Gazol, A., Wang, X., Xing, D., Lin, F., Bai, X., Zhao, Y., Li, B. and Hao, Z. 2011. What happens below the canopy? Direct and indirect influences of the dominant species on forest vertical layers. Oikos 121(7): 1145-1153.

Figures

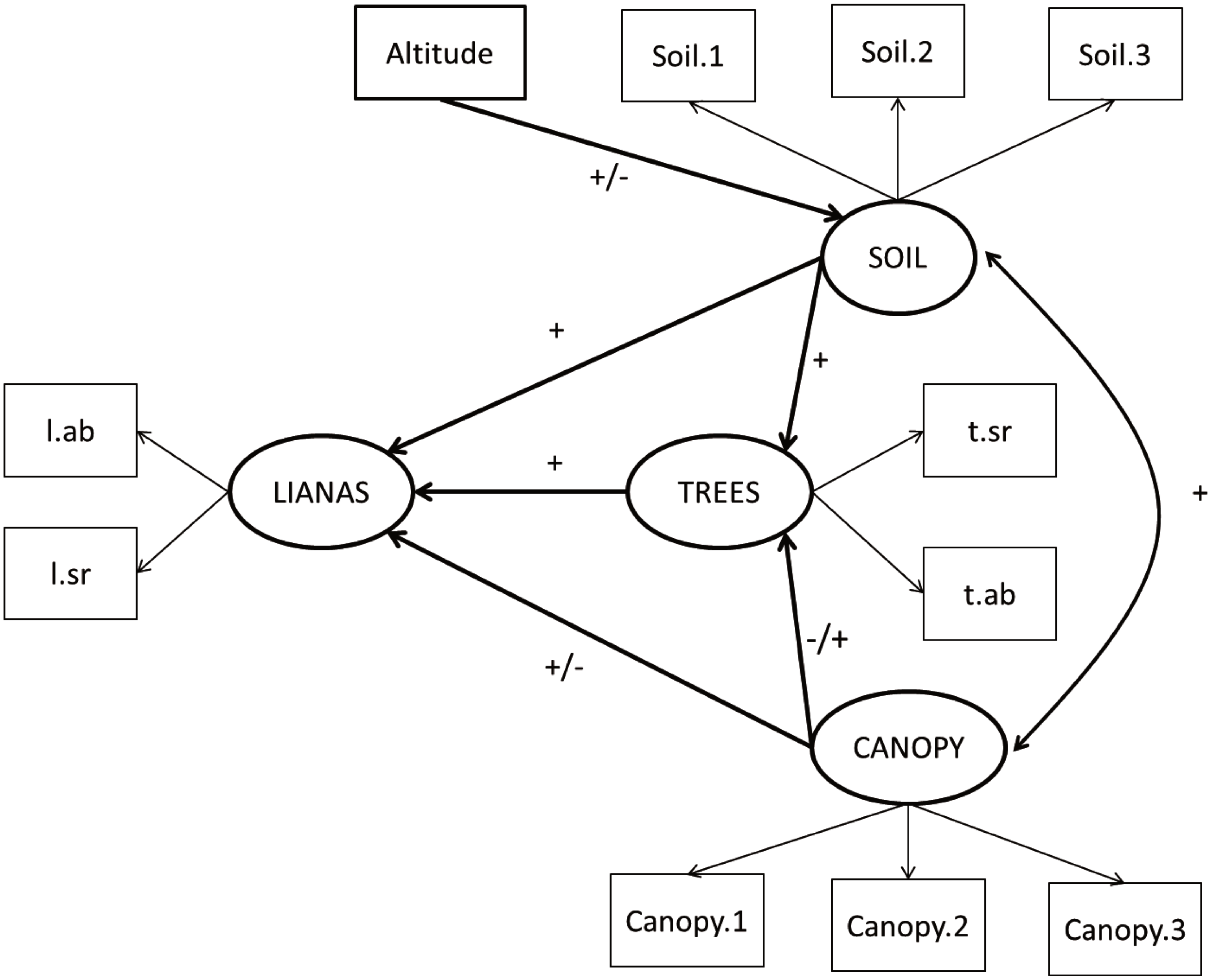

Figure 1 – Theoretical Model showing direct and indirect factors which influence climbing plants' community patterns (abundance and species richness). Squared variables are observed variables, rounded variables are latent variables. The following observed variables are: climbing plants' species richness (l.sr); climbing plants' abundance (l.ab); trees and shrubs' species richness (t.sr); trees and shrubs' abundance (t.ab). Each value corresponds to values in each plot. Signal + supposes positive causal influence; Signal +/- supposes a negative or positive causal influence, which depends of the construction of latent variable.

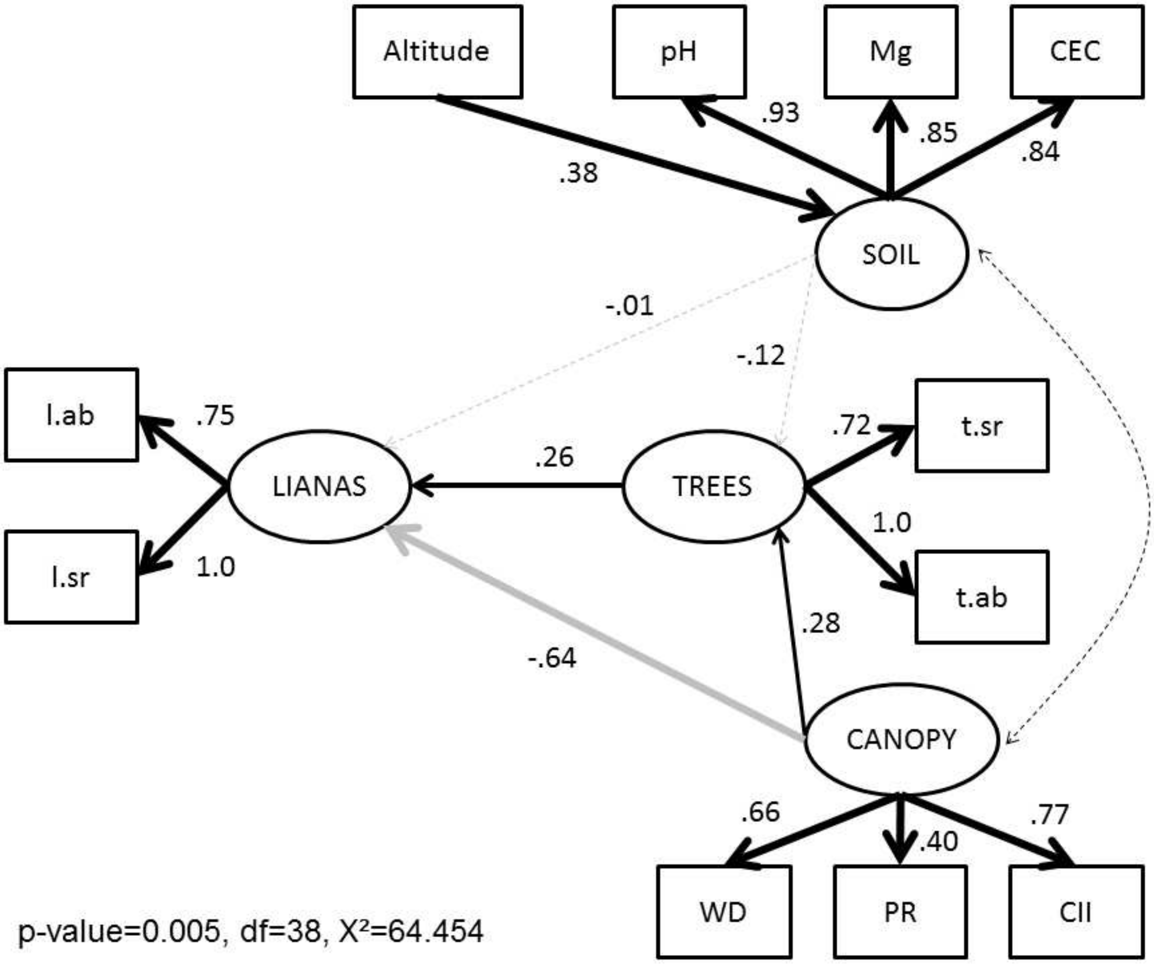

Figure 2 – First calculated Structural Equation Model. Squared variables are observed variables, rounded variables are latent variables. The following observed variables are: climbing plants' species richness (l.sr); climbing plants' abundance (l.ab); trees and shrubs' species richness (t.sr); trees and shrubs' abundance (t.ab); Wood density (WD); proportion of "present" trees (PR); mean of crown illumination index (CII); pH; Quantity of exchangable Magnesium (Mg); total cation exchange capacity (CEC). Each value corresponds to values in each plot. Gray arrows correspond to negative causal influences in variance; black bold arrows correspond to positive causal influences in variance.

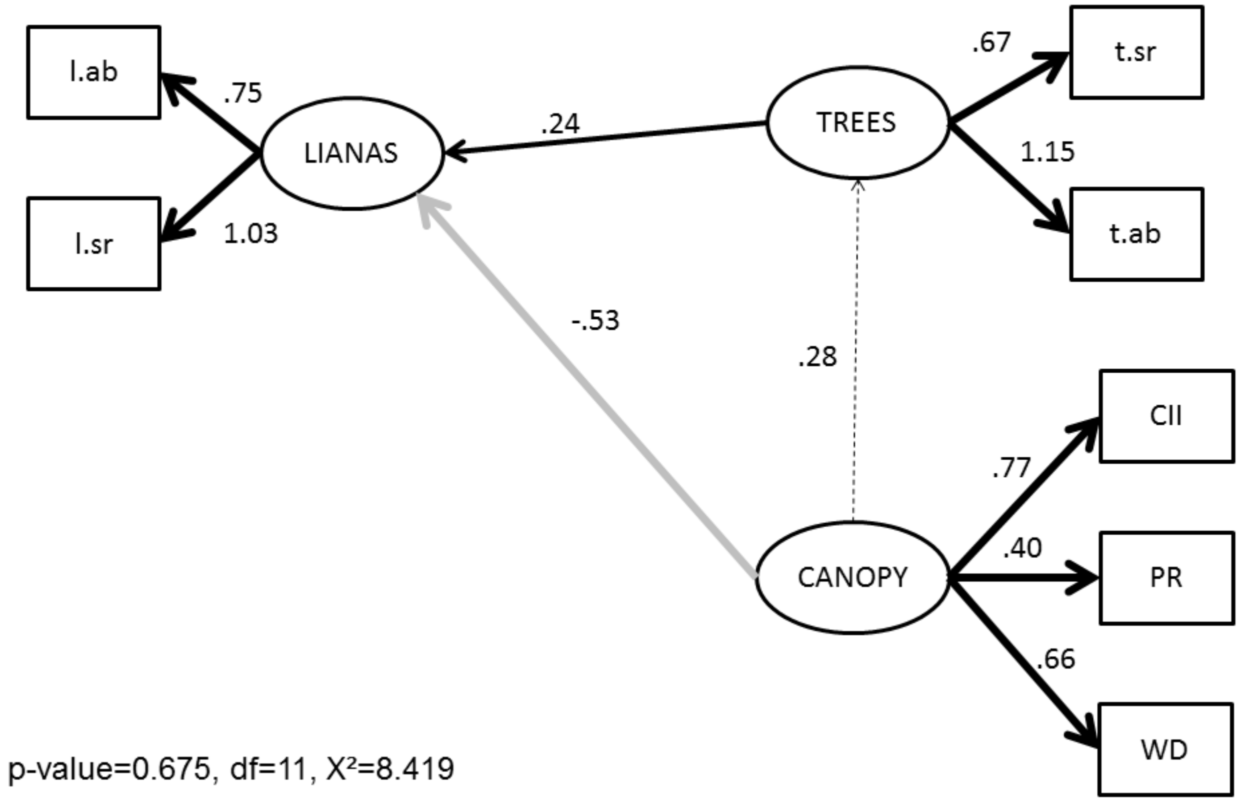

Figure 3 – Structural Equation Modeling with selected variables. The following observed variables are: climbing plants' species richness (l.sr); climbing plants' abundance (l.ab); trees and shrubs' species richness (t.sr); trees and shrubs' abundance (t.ab); Wood density (WD); proportion of "present" trees (PR); mean of crown illumination index (CII). Each value corresponds to values in each plot. Gray arrows correspond to negative causal influences in variance; black bold arrows correspond to positive causal influences in variance.

Tables

Table 1 – Paths results of latent variables and regressions of the previous model. Only significant paths remain in the final model. Unstd. Coefficient: unstandardized coefficient; Std. Coef.: standardized coefficient; Std.Error: standard error.

Pathway	Unstd. Coef.	Std. Coef.	Std. Error	Z-Value	p-value
Latent variables					
CANOPY→ CII	1.000	0.772			
CANOPY→ WD	0.858	0.662	0.182	4.706	0.000
CANOPY→PR	0.513	0.396	0.158	3.250	0.001
SOIL→pH	1.000	0.931			
SOIL→CEC	0.903	0.840	0.080	11.299	0.000
SOIL→Mg	0.910	0.847	0.079	11.451	0.000
TREES→t.sr	1.000	0.723			
TREES→t.ab	1.470	1.063	0.370	3.969	0.000
LIANAS→l.sr	1.000	1.023			
LIANAS→l.ab	0.731	0.748	0.142	5.164	0.000
Regressions					
SOIL←					
Altitude	0.352	0.378	0.091	3.875	0.000
LIANAS←					
CANOPY	-0.714	-0.539	0.183	-3.896	0.001
SOIL	-0.009	-0.008	0.105	-0.087	0.930
TREES	0.372	0.263	0.134	2.777	0.005
TREES←					
CANOPY	0.259	0.276	0.131	1.980	0.048
SOIL	-0.094	-0.121	0.079	-1.192	0.233
Covariances					
SOIL↔CANOPY	-0.108	-0.164	0.083	-1.296	0.195

Tables 2 - Values of measurement errors (standardized coefficient) of latent and observed variables.

Pathway	Unstd. Coef.	Std. Coef.	Std. Error	Z-Value	p-value
Latent variables					
CANOPY→ CII	1.000	0.765			
CANOPY→ WD	0.861	0.658	0.183	4.697	0.000
CANOPY→PR	0.525	0.401	0.158	3.286	0.001
TREES→t.sr	1.000	0.666			
TREES→t.ab	1.729	1.152	0.370	3.073	0.002
LIANAS→l.sr	1.000	1.027			
LIANAS→l.ab	0.725	0.745	0.142	5.147	0.000
Regressions					
LIANAS←					
CANOPY	-0.710	-0.529	0.183	-3.859	0.000
TREES	0.365	0.237	0.133	2.749	0.006
TREES←					
CANOPY	0.244	0.280	0.134	1.882	0.060
Measurement errors	**Estimate**	**Std. error**			
CII	0.411	0.120			
WD	0.561	0.113			
PR	0.830	0.126			
t.sr	0.550	0.155			
t.ab	-0.325	0.403			
l.sr	-0.054	0.180			
l.ab	0.441	0.114			
CANOPY	0.579	0.165			
TREES	0.405	0.152			
LIANAS	0.766	0.222			

Considerações Finais

1. Nossa investigação mostrou que as características nutricionais do solo em uma escala fina apresentaram pouca importância na variação da composição das espécies de lianas e na determinação da abundância e número de espécies de trepadeiras (lenhosas e não lenhosas maiores que 1.0 cm de diâmetro) na floresta estudada.

2. Porém, a altitude apresentou-se um fator importante na variação da composição das espécies de lianas, possivelmente sendo o reflexo de um gradiente de umidade no solo (que não foi abordado nesta tese).

3. A dinâmica florestal, representada pelas variáveis Hmax (altura da maior árvore), Hmed (mediana das alturas das árvores) e CII (média do índice de iluminação da copa), mostrou pouca importância na determinação da composição de espécies de lianas.

4. A montagem da comunidade de lianas mostrou forte agregação espacial, independente dos fatores ambientais (dinâmica florestal e fatores topoedáficos), possivelmente devido à limitação por dispersão (clonalidade e dispersão anemocórica das lianas).

5. Grande parte da variação (82%) da composição de espécies não foi explicada pelas variáveis estudadas: fatores topoedáficos, dinâmica florestal e autocorrelação espacial. 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. Outros fatores determinísticos, como conteúdo da água do solo, interações interespecíficas e modos de dispersão, devem ser investigados,de modo a reduzir a proporção não explicada (82%) de variação na composição de espécies de lianas.

6. A determinação da composição de lianas (trepadeiras lenhosas) por fatores ligados à dinâmica florestal não foi importante na Floresta Estacional Semidecídua estudada, mas não reflete na variação da densidade e riqueza de trepadeiras provocada por esses fatores da dinâmica florestal. Encontramos que áreas de clareira não são filtros ambientais importantes para a determinação e variação da composição de espécies de lianas, mas áreas de floresta madura apresentam menor agregação filogenética, menor número de espécies e caules de trepadeiras na Floresta Estacional Semidecídua.

7. As variáveis utilizadas como fatores quantitativos substitutos à dinâmica florestal se comportaram de forma inconstante. Em dois capítulos (1 e 2) a altura das árvores foi um fator importante para os fatores estudados, mas em outros dois (capítulos 2 e 3) a variável "proporção de árvores do presente" foi importante para a variação dos fatores estudados.

8. Apesar de não ser discutido de forma aprofundada nesta tese, destacamos a grande riqueza de espécies de trepadeiras amostradas na área estudada (90 espécies de trepadeiras, anexo 2), sendo a maior riqueza por área encontrada para um estudo fitossociológico de trepadeiras no estado de São Paulo.

Anexo 1: Scripts das análises realizadas nesta tese (R versão 2.12, Windows 7)

Capítulo 1

```
library(vegan)

library(packfor)

setwd("C:/Users/Juliano/Documents/Rib Cachoeira/dados gerais/brutos")

set.seed(42) # the answer to the life, universe and everything else.

#############

read.csv("RC_lianas_table.csv", row.names=1,sep=";")->l # it's a
table, containing abundance of each species in each plot

dim(l)

l[-4,-91]->l#excluding outlier plot & dead

l[apply(l,2,FUN=sum)>=10]->l ## excluding rare spp (<10 stems)

make.cepnames(colnames(l))->colnames(l)

sum(l)

l.hel<-decostand(l,"hellinger")

read.csv("RC_plots.csv", head=T, sep=";")->p # plot

p[,20]->CO

xy<-p[-4,c(2,3)] # x and y of each plot

p[-4,(4:17)]->e # edaphic

as.factor(p$plot)->plot

as.list(levels(plot))->plot

read.csv("RC_trees_selected.csv",sep=";")->t

aggregate(t$cii,by=list(plot=t$Plot),FUN=mean,na.rm=T)->pCII

aggregate(t$WD,by=list(plot=t$Plot),FUN=median,na.rm=T)->pWD

log((t$PBH^2)/4*pi)->t$AB
```

```
aggregate(t$AB,by=list(plot=t$Plot),FUN=median,na.rm=T)->pAB

aggregate(t$final,by=list(plot=t$Plot),FUN=median,na.rm=T)->pHmed

aggregate(t$final,by=list(plot=t$Plot),FUN=max,na.rm=T)->pHmax

table(t$Plot,t$torquebieu)->tpt

table(t$Plot,t$pheno)->tff

wisconsin(tpt)->ppt # normality reached

as.vector(tff[,1]+tff[,4])->SSD

data.frame(as.vector(tff[,2]),as.vector(tff[,3]),SSD)->TFF

wisconsin(TFF)->feno

d<-
data.frame(pCII$x,pWD$x,pAB$x,pHmed$x,pHmax$x,as.vector(ppt[,2]),as.v
ector(ppt[,3]),feno$SSD,CO)

colnames(d)<-
c("CII","WD","BAmed","Hmed","Hmax","PT","PR","SDT","Canopy")
#internal dynamic

rm(TFF,pAB,feno,pCII,pHmax,pHmed,pWD,ppt,plot,tff,tpt,t,SSD)

d[-4,]->d#excluding outlier plot

data.frame(d,e)->f

### MAP


plot(xy$X, xy$Y, xlab="(m)",ylab="", pch=0,xlim=c(0,330),bty="l")

text(xy$X, xy$Y, rownames(p), cex=0.55, pos=4, col="black")

rc<-data.frame(x=c(-10, 87,164, 263, 360),y=c(255, 220, 279, 279,
250))

lines(rc, lty=2)

legend(x="bottomleft",c("Stream","Plot border"),lty=c(2,1),cex=0.7)

## PCAs
```

```
# **** SEARCH  FOR PCA significance !!!
(din.pca<-rda(d, scale=T))
summary(din.pca)
cor(d)
summary(env.pca<-rda(e, scale=T))
biplot(env.pca)
(l.h.pca<-rda(l.hel))
summary(l.h.pca)
########## RDA #############
(rda(l.hel~.,e,scale=T)->e.rda)
RsquareAdj(e.rda)
(aov.edaf<-anova.cca(e.rda,by="axis",step=1000)) # <1min
(rda(l.hel~.,d,scale=T)->d.rda)
RsquareAdj(d.rda)
(aov.both<-anova.cca(d.rda,by="axis",step=1000)) # <1min
# WAIT !!
# 3 axes
(rda(l.hel~.,f,scale=T)->f.rda)
RsquareAdj(f.rda)
(anova.cca(f.rda,by="axis",step=1000)) # 2min
# WAIT !!
# Constrained e= 0.166; d=0.1181; f=0.2777 # 6 axes
############ PCNM #########
summary(dnearneigh(as.matrix(xy),0,20))
d.liana<-dist(xy)
```

```
library(PCNM)

liana.PCNM<-PCNM(d.liana) # <1m

# WAIT !!

length(liana.PCNM$values) # number of eigenvalues = 65

liana.PCNM$expected_Moran

liana.PCNM$Moran_I

data.frame(liana.PCNM$vectors)->liana.space

(pcnm.rda<-rda(l.hel~.,data=data.frame(liana.PCNM$vectors)))

RsquareAdj(pcnm.rda)

## Forward selection. For each variable category.

summary(l.edaf<-rda(l.hel~.,e,scale=T))

R2.all.chem<-RsquareAdj(l.edaf)$adj.r.squared

forward.sel(l.hel,e,adjR2thresh=R2.all.chem,nperm=1000) #edaphic =
only altitude

l.dim<-rda(l.hel~.,d,scale=T)

R2.all.dim<-RsquareAdj(l.dim)$adj.r.squared

forward.sel(l.hel,d,adjR2thresh=R2.all.dim,nperm=1000) # dynamic =
CII, Hmax, Hmed

l.pcnm<-rda(l.hel~.,liana.space)

R2.all.spa<-RsquareAdj(l.pcnm)$adj.r.squared

(liana.PCNM.fwd<-forward.sel(l.hel,liana.space,
adjR2thresh=R2.all.spa,nperm=1000))

### Variation partitioning with selected variables (without space)

edaf.pars<-e[,1]

dim.pars<-d[,c(1,4,5)]

(spe.part<-varpart(l.hel,edaf.pars,dim.pars))
```

```
plot(spe.part,digits=2) # selected edaf > dim

spe.part.all<-varpart(l.hel,e,d)

plot(spe.part.all,digits=2) # all variables e > d

## selected forest + topo-edaphic variables. Verifying.

anova.cca(l.edaf,step=1000) # a+b

anova.cca(l.dim,step=1000) # b+c

env.pars<-cbind(edaf.pars,dim.pars)

anova.cca(rda(l.hel,env.pars,scale=T),step=1000) # a+b+c

anova.cca(rda(l.hel,edaf.pars,env.pars,scale=T),step=1000) # a

anova.cca(rda(l.hel,dim.pars,env.pars,scale=T),step=1000) # c

##### Including Space

(PCNM.sin<-sort(liana.PCNM.fwd[,1]))

PCNM.pars<-liana.space[,c(PCNM.sin)]

(spe.pars<-varpart(l.hel,edaf.pars,dim.pars,PCNM.pars))

plot(spe.pars,digits=2) # selected space > edaf > dim

cbind(f,liana.space)->all

cbind(edaf.pars,dim.pars,PCNM.pars)->selected

##RDA with all variables together.

(spe.rda.all<-rda(l.hel~.,data=all,scale=T)) # all

vif.cca(spe.rda.all)

(spe.rda.sel<-rda(l.hel~.,data=selected,scale=T)) # selected

summary(spe.rda.sel)

vif.cca(spe.rda.sel)

R2a.all<-RsquareAdj(spe.rda.all)$adj.r.squared

forward.sel(l.hel,all,adjR2thresh=R2a.all) ##
alt,CII,X15,X1,X8,Hmax,Hmed,OM,X56,X14
```

```
#

step.forward<-ordistep(rda(l.hel~1,data=all,scale=T),
scope=formula(spe.rda.all),direction="forward",pstep=1000) # ~30min
!!

## Wait!

step.forward # alt, CII, Hmax, Canopy + 12 PCNMs ##

summary(step.forward)

RsquareAdj(step.forward)

RsquareAdj(spe.rda.sel)

RsquareAdj(spe.rda.all)

## best model

rda(l.hel ~ alt + CII + X15 + Hmax + X11 + X8 + Canopy +X1 + X25 + PT
+ X51 + X39 + X48 + X3 + X19 + X40 + X18, data = all,scale=T)-
>forward.rda.pars

vif.cca(forward.rda.pars)

anova.cca(rda(l.hel ~ alt + CII + X15 + Hmax + X11 + X8 + Canopy +X1
+ X25 + PT + X51 + X39 + X48 + X3 + X19 + X40 + X18, data =
all,scale=T),step=1000,by="axis") # WAIT!


summary(forward.rda.pars)

# end
```

Capítulo 2

```
library(vegan)

path<-"C:/Users/Juliano/Documents/Rib Cachoeira/dados gerais/brutos/"

###################### Forest DATA #####################

read.csv(paste(path,"RC_trees_selected.csv",sep=""),sep=";")->t

read.csv(paste(path,"RC_plots.csv",sep=""), head=T, sep=";")->p #
plot

p[,20]->CO

table(t$Plot,t$species)->tt

as.factor(t$Plot)->parcela

as.list(levels(parcela))->plot

aggregate(t$cii,by=list(plot=t$Plot),FUN=mean,na.rm=T)->pCII

aggregate(t$WD,by=list(plot=t$Plot),FUN=median,na.rm=T)->pWD

log((t$PBH^2)/4*pi)->t$AB

aggregate(t$AB,by=list(plot=t$Plot),FUN=median,na.rm=T)->pAB

aggregate(t$final,by=list(plot=t$Plot),FUN=median,na.rm=T)->pHmed

aggregate(t$final,by=list(plot=t$Plot),FUN=max,na.rm=T)->pHmax

table(t$Plot,t$torquebieu)->tpt

table(t$Plot,t$pheno)->tff

wisconsin(tpt)->ppt # dados chegaram mais perto da normalidade

as.vector(tff[,1]+tff[,4])->SSD

data.frame(as.vector(tff[,2]),as.vector(tff[,3]),SSD)->TFF

wisconsin(TFF)->pheno

forest<-
data.frame(pCII$x,pWD$x,pAB$x,pHmed$x,pHmax$x,as.vector(ppt[,2]),as.v
ector(ppt[,3]),pheno$SSD,CO)
```

```
colnames(forest)<-
c("CII","WD","BAmed","Hmed","Hmax","PT","PR","SDT","CO")

rm(TFF,pheno,pAB,pCII,pHmax,pHmed,pWD,t,ppt,tpt,tt,parcela,SSD,plot,t
ff,p,CO)

summary(forest)

#

################# ANALYSIS ################

# Ward Hierarchical Clustering

clust.forest <- hclust(dist(forest), method="ward")

plot(clust.forest, main="",xlab="") # display dendogram

rect.hclust(clust.forest, k=5, border="red")

rect.hclust(clust.forest, k=4, border="green")

rect.hclust(clust.forest, k=3,border="darkgrey")

text(x=68,y=120,label="3")

text(x=16,y=120,label="1")

text(x=5,y=120,label="2")

# Model Based Clustering

library(cluster)

library(fpc)

fit0 <- kmeans(forest, 2)

fit1 <- kmeans(forest, 3)

fit2 <- kmeans(forest, 4)

fit3 <- kmeans(forest, 5)

# Cluster Plot against 1st 2 principal components

# vary parameters for most readable graph
```

```
clusplot(forest, fit0$cluster, color=TRUE, shade=TRUE,labels=2,
lines=0)

clusplot(forest, fit1$cluster, color=TRUE, shade=TRUE,labels=2,
lines=0)

clusplot(forest, fit2$cluster, color=TRUE, shade=TRUE,labels=2,
lines=0)

clusplot(forest, fit3$cluster, color=TRUE, shade=TRUE,labels=2,
lines=0)

# Centroid Plot against 1st 2 discriminant functions

plotcluster(forest, fit0$cluster)

plotcluster(forest, fit1$cluster)

plotcluster(forest, fit2$cluster)

plotcluster(forest, fit3$cluster)

#

#

# NMDS

library(MASS)

(NMDS.forest <- isoMDS(dist(forest), k=2)) # k is the number of dim

x <- NMDS.forest$points[,1]

y <- NMDS.forest$points[,2]

plot(x, y, xlab="Coordinate 1", ylab="Coordinate 2",

     main="Nonmetric MDS", type="n")

text(x, y, labels = row.names(forest), cex=.7)

abline(h=0,lty="dotted")

abline(v=0,lty="dotted")

######### PCA #####

(rda(forest,scale=T)->pca.data)
```

```
summary(pca.data)

pca.data$CA$v.eig[,1:3]

pca.data$CA$u.eig[,1:4]->axes

pca.data$CA$v.eig[,1]->x

pca.data$CA$v.eig[,2]->y

dev.off()

biplot(pca.data,bty="l")

text(x[1]-.5,y[1]+.4,"CII")

text(x[2]+.3,y[2]-.2,"WD")

text(x[3]-.2,y[3]+.8,"BA.med")

text(x[4]+.5,y[4]+.6,"H.med")

text(x[5]+.4,y[5]+.3,"H.max")

text(x[6]-.5,y[6]-.3,"PT")

text(x[7]+.5,y[7]+.2,"PR")

text(x[8]-.4,y[8]+.4,"SDT")

text(x[9]-.4,y[9]-.1,"CO")

rm(x,y)

################### Phylogenetic analysis ###########

library(picante)

########## Phylogeny DATA #####

read.tree(paste(path,"nice_try5.txt",sep=""))->phy_lianas

par(mar=c(0,0,0,0))

plot(phy_lianas, cex=1.0)

read.csv(paste(path,"RC_lianas_table1.csv",sep=""),sep=";",row.names=
1)->comm_lianas
```

```
comm_lianas[,-c(89,90,91)]->comm_lianas#excluding dead and unknown stems

# to verify if any species is not present in any data (e.g.: wrong name),

# we perform the following two lines:

allright<-sort(phy_lianas$tip.label)==names(comm_lianas)

sort(phy_lianas$tip.label)[!allright] # if character(0), it is OK!

# NRI

phydist<-cophenetic(phy_lianas)

ses.mpd(comm_lianas,phydist)->ses.mpd.result # NRI = z.ses.mpd

#############  WAIT !!!!!!!!!!!!!!! ###########################

-1*ses.mpd.result$mpd.obs.z->NRI_all

## selecting

subtrees(phy_lianas)->l

plot(l[[4]],sub=paste("Node",l[[4]]$node.label[4]),cex=0.6)

bigdist<-cophenetic(l[[4]])

comm_lianas[,c("Adenocalymma_paulistarum","Adenocalymma_marginatum","Anemopaegma_chamberlaynii","Pyrostegia_venusta","Mansoa_difficilis","Amphilophium_crucigerum","Bignonia_binata","Bignonia_campanulata","Bignonia_sciuripabula","Dolichandra_quadrivalvis","Dolichandra_unguis_cati","Fridericia_conjugata","Fridericia_pulchella","Fridericia_samydoides","Fridericia_triplinervia","Tynanthus_fasciculatus","Lundia_obliqua","Tanaecium_selloi","Pleonotoma_tetraquetra","Stizophyllum_perforatum")]->big.comm

ses.mpd(big.comm,bigdist)->big.mpd.result # NRI for bignoniaceae

###########  WAIT !!!!!!!!!!!!!!! ##############

-1*big.mpd.result$mpd.obs.z->NRI_big

par(mar=c(7,2,7,2),mfrow=c(1,2))

hist.1<-hist(NRI_all)
```

```
hist.2<-hist(NRI_big)

plot(hist.1, col="lightgray", xlab="NRI", main="")

text(hist.1$mids, hist.1$counts+.5, label=c(hist.1$counts),cex=.7)

text(hist.1$mids[1],hist.1$count[1]+17,label="a)")

plot(hist.2, col="lightgray", xlab="NRI", main="")

text(hist.2$mids, hist.2$counts+.5, label=c(hist.2$counts),cex=.7)

text(hist.2$mids[1],hist.2$count[1]+21,label="b)")

##

dev.off()

par(mar=c(0,0,0,0))

plot(phy_lianas, show.tip.label = FALSE, main = "")

tiplabels(tip = which(phy_lianas$tip.label %in%
colnames(comm_lianas)[comm_lianas[NRI_all>=1.96,]>0]), pch = 19)

str(phy_lianas)

########### Spatial structure of NRI ###########

read.csv(paste(path,"RC_plots.csv",sep=""),sep=";",row.names=1)->xy

xy[,c(1,2)]->xy

(NRI_all[NRI_all<=-1.96]->od.all) ## Didn't occurred

length(NRI_all[NRI_all>=1.96]->cl.all) # 61/100

length(NRI_all[NRI_all<=1.96&NRI_all>=-1.96]->rdm.all) #39/100


length(NRI_big[NRI_big<=-1.96]->od.big) #1/100 +1NA

(NRI_big[NRI_big>=1.96]->cl.big) ## didn't occurred = NA

length(NRI_big[NRI_big>=-1.96&NRI_big<=1.96]->rdm.big) #98/100 +1NA

# Moran's I

library(spdep)
```

```
library(ncf)

nb.w<-nb2listw(dnearneigh(as.matrix(xy),0,30), glist=NULL, style="W",
zero.policy=FALSE)

localmoran(NRI_all,nb.w)->local.moran

(local.moran[,5]<=.05)->sign

cor.NRI<-correlog(x=xy$X, y=xy$Y, z=NRI_all, increment=5, resamp=100)

# Plot Moran' I for NRI

par(mar=c(6,6,6,6),mfrow=c(1,1))

plot(cor.NRI$correlation, type="b", xlab="Distance (m)",
ylab="Moran's I",pch=16+sign)

legend(x="bottomleft",c("non-
significant","significant"),pch=c(20,17))

moran.test(NRI_all,nb.w)

moran.plot(NRI_all,nb.w)

################### Diversity ###########

plot(specaccum(comm_lianas))

length(apply(comm_lianas,1,FUN="specnumber")->l.sr)

length(apply(comm_lianas,1,FUN="sum")->l.ab)

length(apply(comm_lianas,1,FUN="diversity")->l.H)

data.frame(l.ab,l.sr,l.H)->liana.data

### specialist vs generalists

clamtest(comm_lianas,fit0$cluster)->clam.lianas

plot(clam.lianas)

##

summary(lm(l.H~NRI_all))

summary(lm(apply(big.comm,1,FUN="diversity")~NRI_big) )
```

```
plot(apply(big.comm,1,FUN="diversity")~NRI_big)

boxplot(NRI_all~fit1$cluster,ylab="NRI values")

summary(aov(fit1$cluster~NRI_all))

(kruskal.test(l.sr~as.factor(fit1$cluster)))

(kruskal.test(l.ab~as.factor(fit1$cluster)))

(kruskal.test(l.H~as.factor(fit1$cluster)))

plot(l.sr~as.factor(fit1$cluster))

plot(l.ab~fit1$cluster)

plot(l.H~as.factor(fit1$cluster))

############ GAM ##############

library(mgcv)

str(forest)

cor(forest)

pairs(forest, panel=function(x,y) { points(x,y); lines(lowess(x,y))}
)

attach(forest)

fit.NRI.0<-
gam(NRI_all~s(CII)+s(Hmed)+s(BAmed)+s(PR)+s(Hmax)+s(CO)+s(WD)+s(PT))
# AIC=436.92

fit.NRI.1<-gam(NRI_all~s(Hmed)+s(PR)+s(Hmax))# AIC = 439.28

fit.NRI.2<-gam(NRI_all~s(PR)) # AIC = 436.37

AIC(fit.NRI.0,fit.NRI.1,fit.NRI.2)

AIC(fit.NRI.0)-AIC(fit.NRI.1)# delta AIC

anova(fit.NRI.2,fit.NRI.1,fit.NRI.0,test="Chi")

boxplot(fit.NRI.2$residuals,fit.NRI.1$residuals,fit.NRI.0$residuals)

# best model
```

```
summary(fit.NRI.1)

par(mfrow=c(1,3),mar=c(5,2,2,1),cex=1)

plot(fit.NRI.1)

#

plot(fit.NRI.1,residuals=T)

dev.off()

plot(PR,fitted(fit.NRI.2))

#

moran.test(fit.NRI.1$residuals,nb.w)

moran.plot(fit.NRI.1$residuals,nb.w)

localmoran(fit.NRI.1$residuals,nb.w)->local.moran

(local.moran[,5]<=.05)->sign

cor.GAM<-correlog(x=xy$X, y=xy$Y, z=fit.NRI.1$residuals, increment=5,
resamp=100)

plot(cor.GAM$correlation, type="b", xlab="Distance (m)",
ylab="Moran's I",pch=16+sign)

legend(x="bottomleft",c("non-
significant","significant"),pch=c(20,17))

# GAM diversity

summary(gam(NRI_all~s(l.H))->fit.sr)

plot(fit.sr)

##

plot(l.H,fitted(fit.sr))

# end
```

Capítulo 3

```
library(FactoMineR)

library(vegan)

library(nFactors)

library(lavaan)

path<-"C:/Users/MyDocuments/"

qq.norm<-function(X){

  qqnorm(X)

  qqline(X)

}

######## Diversity DATA #############

read.csv("RC_lianas_table.csv", row.names=1,sep=";")->l # it's a
table, containing abundance of each species in each plot

l[,-91]->l#excluding dead stems

make.cepnames(colnames(l))->colnames(l)

specnumber(l)->l.sr

apply(l,1,FUN="sum")->l.ab

apply(l,1,FUN="diversity")->l.H

data.frame(l.ab,l.sr,l.H)->liana.data

# trees

read.csv(paste(path,"RC_trees_table.csv",sep=""),
row.names=1,sep=";")->t #100x138

t[,-138]->t#excluding dead stems

make.cepnames(colnames(t))->colnames(t)

apply(t,1,FUN="specnumber")->t.sr

t.H<-apply(t,1,FUN="diversity")

t.ab<-apply(t,1,FUN="sum")

data.frame(t.sr,t.ab,t.H)->trees.data
```

```
rm(t.sr,t.H,t.ab,l.ab,l.sr,l.H)

### Topo-Edaphic DATA ####

read.csv(paste(path,"RC_plots.csv",sep=""), head=T,
row.names=1,sep=";")->p # plot

xy<-data.frame(p$X,p$Y) # x and y of each plot

colnames(xy)<-c("x","y")

p$alt->alt

edap<-p[4:17]

###################### Forest DATA ####################

read.csv(paste(path,"RC_trees_selected.csv",sep=""),sep=";")->t

as.factor(t$Plot)->parcela

as.list(levels(parcela))->plot

aggregate(t$cii,by=list(plot=t$Plot),FUN=mean,na.rm=T)->pCII

aggregate(t$WD,by=list(plot=t$Plot),FUN=median,na.rm=T)->pWD

log((t$PBH^2)/4*pi)->t$AB

aggregate(t$AB,by=list(plot=t$Plot),FUN=median,na.rm=T)->pAB

aggregate(t$final,by=list(plot=t$Plot),FUN=median,na.rm=T)->pHmed

aggregate(t$final,by=list(plot=t$Plot),FUN=max,na.rm=T)->pHmax

table(t$Plot,t$torquebieu)->tpt

table(t$Plot,t$pheno)->tff

wisconsin(tpt)->ppt # nornality

as.vector(tff[,1]+tff[,4])->SSD

data.frame(as.vector(tff[,2]),as.vector(tff[,3]),SSD)->TFF

wisconsin(TFF)->pheno

forest<-
data.frame(pCII$x,pWD$x,pAB$x,pHmed$x,pHmax$x,as.vector(ppt[,2]),as.v
ector(ppt[,3]),pheno$SSD,p[,19])

colnames(forest)<-
c("CII","WD","BAmed","Hmed","Hmax","PT","PR","SDT","CO")
```

```
str(forest)
rm(TFF,pheno,pAB,pCII,pHmax,pHmed,pWD,ppt,tpt,parcela,SSD,plot,tff,l,
t,p)


# PCA #
PCA(forest[-4,])
cor(forest)
print(factanal(forest, 3, rotation="varimax"), digits=2, cutoff=.3,
sort=TRUE)
#BAmed redundant with Hmed, PR with PT
nScree((eigen(cor(forest)))$values,
(parallel(subject=nrow(forest),var=ncol(forest),
rep=100,cent=.05))$eigen$qevpea)
# 3 optimal coordinates; 1 accelarion factor
(princomp(edap[-4,],cor=T,scale=T))$scale
biplot(princomp(edap[-4,],cor=T,scale=T))
PCA(edap[-4,]) # plot4 outlier
cor(edap[-4,])
#redundants: Ca , CEC, OM & S.B.; silt & Sand coarse; pH & H_Al;
############ standardization #################################
data.frame(trees.data,liana.data,alt,edap,forest,xy)->data
data[-4,]->data.1
log(data.1$WD)->x1 #testing
x1[x1==-Inf]<-0
data.1$WD^2/3->x1
shapiro.test(x1)
qqnorm(x1)
qqline(x1)
shapiro.test(data.1$PT)
```

```
# x^2/3 = l.sr, l.H
data.1$l.sr^2/3->data.1$l.sr
data.1$l.H^2/3->data.1$l.H
#log = l.ab, K, Ca, H_Al,S.B.,CEC,clay, Hmed
log(data.1$CII)->data.1$CII
log(data.1$SDT)->data.1$SDT
data.1$SDT[data.1$SDT==-Inf]<-0
log(data.1$l.ab)->data.1$l.ab
log(data.1$K)->data.1$K
log(data.1$Ca)->data.1$Ca
log(data.1$H_Al)->data.1$H_Al
log(data.1$S.B.)->data.1$S.B.
log(data.1$CEC)->data.1$CEC
log(data.1$Clay)->data.1$Clay
log(data.1$Hmed)->data.1$Hmed
log(data.1$CO)->data.1$CO
data.1$CO[data.1$CO==-Inf]<-0
# WD -> did not reacch the normality
# ok = t.ab, Mg, pH, sand_coarse, Hmax, alt,P, PT,V
##### standard Z ####
data.2<-matrix(data=0,nrow=nrow(data.1),ncol=ncol(data.1))
for (i in 1:nrow(data.1)){
  for(j in 1:ncol(data.1)){
   data.2[i,j]<-(data.1[i,j]-mean(data.1[,j]))/sd(data.1[,j])
  }
}
colnames(data.2)<-colnames(data.1)
```

```
as.data.frame(data.2)->data.2

############ Selecting soil variables to Soil latent variable #######

pairs(data.2[,c(8:17)])

cor(data.2[,7:21])

model.soil<-'soil=~pH+CEC+Mg

  texture=~Sand_coarse+Silt+Clay

  soil~~texture

'

(sem(model.soil,data=data.2)->sem.soil)

summary(sem.soil)

standardizedSolution(sem.soil)

model.soil<-'soil=~pH+CEC+Mg

  soil~alt'

(sem(model.soil,data=data.2)->sem.soil)

summary(sem.soil)

standardizedSolution(sem.soil)

####### Selecting canopy variables to Canopy latent variable #

pairs(data.2[,22:30])

cor(data.2[,22:30])

PCA(data.2[,22:30])

print(factanal(data.2[,22:30], 3, rotation="varimax"), digits=2,
cutoff=.3, sort=TRUE)

nScree((eigen(cor(data.2[,22:30])))$values,
(parallel(subject=nrow(data.2[,22:30]),var=ncol(data.2[,22:30]),
rep=100,cent=.05))$eigen$qevpea)

model.canopy<-'canopy=~CII+PT+CO

'

(cfa(model.canopy,data=data.2)->sem.canopy)

summary(sem.canopy)
```

```
standardizedSolution(sem.canopy)
################# ------- Analysis - SEM - ##########################
# first, testing theoretical
model.final<-'Soil=~pH+CEC+Mg
  Soil~alt
  Canopy=~CII+PR+PT
  Soil~~Canopy
  trees=~t.sr+t.ab
  trees~Canopy+Soil
  lianas=~l.sr+l.ab
  lianas~Canopy+Soil+trees
  '
(sem.final<-sem(model.final,data=data.2)) #low p-value
summary(sem.final,fit.measures=T) # NS! -> Soil-> lianas & Trees;
standardizedSolution(sem.final)
# without topo-edaphic
model.final<-'
  Canopy=~CII+PR+PT
  trees=~t.sr+t.ab
  trees~Canopy
  lianas=~l.sr+l.ab
  lianas~Canopy+trees
  '
(sem.final.1<-sem(model.final,data=data.2))
summary(sem.final.1,fit.measures=T)
standardizedSolution(sem.final.1)
model.final.2<-'
```

```
  Canopy=~CII+WD+PT

  lianas=~l.sr+l.ab

lianas~Canopy

'

(sem.final.2<-sem(model.final.2,data=data.2))

summary(sem.final.2,fit.measures=T)

standardizedSolution(sem.final.1)

# Comparing SEMs

# available at
http://jarrettbyrnes.info/ubc_sem/lavaan_materials/lavaan.modavg.R

source('C:/Users/Juliano/Documents/Disciplinas/SEM -
lectures/2/lavaan.modavg.r')

aictab.lavaan(list(sem.final.2,sem.final.1),c("old","new"))

## --------------------------- SAR ---------------------------------##

library(spdep)

library(ncf)

coords<-cbind(data.1$x,data.1$y)

coords<-as.matrix(coords)

nb<-dnearneigh(coords,0,30)

nb.w<-nb2listw(nb, glist=NULL, style="W", zero.policy=FALSE)

## TESTING VARIABLE ###

cor.t.sr<-correlog(x=data.1$x, y=data.1$y, z=data.1$t.sr, na.rm=T,
increment=5, resamp=10)

plot(cor.t.sr$correlation, type="b", pch=1, xlab="distance",
ylab="Moran's I", main="Trees SR")

cor.l.sr<-correlog(x=data.1$x, y=data.1$y, z=data.1$l.sr, na.rm=T,
increment=5, resamp=10)

plot(cor.l.sr$correlation, type="b", pch=1, xlab="distance",
ylab="Moran's I", main="Lianas SR")

### CONTINUING SAT ###
```

```
ols<-lm(data.1$l.sr~data.1$t.sr)

summary(ols)

res.ols <- residuals(ols)

cor.ols.res<-correlog(data.1$x, data.1$y, z=residuals(ols), na.rm=T,
increment=10, resamp=10)

plot(cor.ols.res$correlation, type="b", pch=1, xlab="distance",
ylab="Moran's I", main="OLS")

## SARerr ##

sem.nb.w<-errorsarlm(ols, na.action=na.fail,listw=nb.w)

res.sem.nb.w <- residuals(sem.nb.w)

cor.sem.nb.w<-correlog(data.1$x, data.1$y, z=residuals(sem.nb.w),
na.rm=T, increment=1, resamp=10)

#Plot correlogram

plot(cor.sem.nb.w$correlation, type="b", pch=4,xlab="distance",
ylab="Moran's I", main="SARerr")

## SARlag ##

slm.nb.w<-lagsarlm(ols, listw=nb.w, na.action=na.fail, type="lag")

summary(slm.nb.w)

res.slm.nb.w <- residuals(slm.nb.w)

cor.slm.nb.w<-correlog(data.1$x, data.1$y, z=residuals(slm.nb.w),
na.rm=T, increment=1, resamp=1)

plot(cor.slm.nb.w$correlation, type="b", pch=2,ylim=c(-0.5, 1),
xlab="distance", ylab="Moran's I",main="SARlag")

 ## SARmix ##

smm.nb.w<-lagsarlm(ols, listw=nb.w, na.action=na.fail,type="mixed")

summary(smm.nb.w)

res.smm.nb.w <- residuals(smm.nb.w)

cor.smm.nb.w<-correlog(data.1$x, data.1$y, z=residuals(smm.nb.w),
na.rm=T, increment=1, resamp=1)

plot(cor.smm.nb.w$correlation, type="b", pch=3, xlab="distance",
ylab="Moran's I", main="SARmix")
```

```
## ploting altogether

plot(cor.ols.res$correlation, type="b", pch=1, cex=1.5, lwd=1.5,
ylim=c(-2, 3), xlab="Distance class", ylab="Moran's I", cex.lab=1.5,
cex.axis=1.5);abline(h=0)

# then SARlag model residuals

points(cor.slm.nb.w$correlation, pch=2,
cex=1.2);lines(cor.slm.nb.w$correlation, lwd=1.5)

# then SARmix model residuals

points(cor.smm.nb.w$correlation, pch=3, cex=1.2)

lines(cor.smm.nb.w$correlation, lwd=1.5)

# then SARerr model residuals

points(cor.sem.nb.w$correlation, pch=4,
cex=1.2);lines(cor.sem.nb.w$correlation, lwd=1.5)

# annotate legend

legend(x=0, y=3.5, legend=c("OLS residuals", "SAR lag residuals","SAR
mix residuals", "SAR err residuals"), pch=c(1, 2, 3, 4), bty="n",
cex=1.1)

# End (?)
```

Anexo 2: Tabela fitossociológica das trepadeiras inventariadas na “Mata Ribeirão Cachoeira” - Um hectare de Floresta Estacional Semidecídua, Campinas, estado de São Paulo, Brasil.

Tabela 1 – Tabela com descritores fitossociológico das trepadeiras amostradas em um hectare de Floresta Estacional Semidecídua. Mata Ribeirão Cachoeira, Campinas, São Paulo.

Espécies	L/SL/H	NInd	NAm	TotRam	IVI
Bignonia campanulata Cham.	L	814	96	834	40.6
Mansoa difficilis (Cham.) Bureau & K. Schum.	L	556	90	562	32
Dolichandra quadrivalvis (Jacq.) L.G.Lohmann	L	201	75	203	17.4
Fridericia triplinervia (Mart. ex DC.) L.G.Lohmann	L	137	46	144	14.2
Fridericia conjugata (Vell.) L.G. Lohmann	L	127	37	134	11.9
Bignonia sciuripabula (K. Schum.) L.G. Lohmann	L	153	48	157	10.9
Adenocalymma marginatum (Cham.) DC.	L	186	31	189	10.8
Forsteronia pubescens A.DC.	L	130	39	135	10
Morta †	L	110	60	110	9.94
Elachyptera festiva (Miers) A.C. Sm.	L	134	40	146	9.91
Banisteriopsis anisandra (A. Juss) Wonders & B. Gates	L	83	34	88	8.07
Stizophyllum perforatum (Cham.) Miers	L	86	37	89	8.07
Condylocarpon isthimicum (Vell.) A. DC.	L	102	38	105	8.06
Urvillea laevis Radlk.	L	81	37	85	7.9
Adenocalymma paulistarum Bureau & K. Schum.	L	86	40	93	7.52
Pristimera celastroides (Kunth) A.C. Sm.	L	75	27	81	6.11
Tynanthus fasciculatus (Vell.) Miers	L	49	26	50	5.5
Pereskia aculeata Mill.	SL	51	29	52	4.94
Serjania caracasana (Jacq.) Willd.	L	59	25	61	4.81
Forsteronia pilosa Müll. Arg.	L	52	14	55	4.63
Thinouia mucronata Radlk.	L	23	10	24	4.27
Tanaecium selloi (Spreng.) L.G. Lohmann	L	46	15	50	4.17
Serjania laruotteana Cambess.	L	34	19	40	3.75
Dolichandra unguis-cati (L.) L.G. Lohmann	L	23	14	24	3.39
Davilla rugosa Poir.	L	33	14	35	3.31
Dicella bracteosa (A. Juss) Griseb.	L	44	19	45	3.25
Acacia nitidifolia (Sw.) DC.	L	37	16	41	3.08
Acacia tucumanensis Griseb.	L	16	11	18	2.95
Banisteriopsis lutea (Griseb.) Cuatrec	L	10	5	11	2.84
Pyrostegia venusta (Ker Gawl.) Miers	L	36	17	38	2.67
Lundia obliqua Sond.	L	30	12	30	2.39
Mikania glomerata Spreng.	SL	31	15	34	2.38
Bredemeyera floribunda Willd.	L	14	10	17	1.85
Forsteronia australis Müll.Arg.	L	15	10	15	1.73
Doliocarpus dentatus (Aubl.) Standl.	L	18	9	18	1.66

Espécies	**L/SL/H**	**NInd**	**NAm**	**TotRam**	**IVI**
Serjania fuscifolia Radlk.	L	20	8	23	1.64
Pleonotoma tetraquetra (Cham.) Bureau	L	14	9	14	1.29
Stigmaphyllon sp	L	13	10	13	1.26
Petrea volubilis L.	L	9	8	9	1.04
Trigonia nivea Cambess.	L	12	5	12	1.01
Pfaffia paniculata (Mart.) Kuntze	L	9	8	10	0.97
Rhynchosia phaseoloides (Sw.) DC.	L	19	3	20	0.95
Forsteronia thyrsoidea (Vell.) Müll. Arg.	L	13	3	13	0.93
Heteropteris sp2	L	8	6	8	0.82
Tontelea sp1	L	9	3	10	0.69
Dalbergia sp	L	4	3	4	0.62
Bignonia binata Thunb.	L	5	5	5	0.58
Dalechampia triphylla Lam.	SL	5	5	5	0.58
Hiraea sp	L	5	4	5	0.53
Forsteronia refracta Mull.Arg.	L	4	4	4	0.49
Byttneria catalpaefolia Jacq.	L	4	3	4	0.47
Dioclea sp	L	4	2	4	0.47
Heteropteris sp1	L	3	2	3	0.41
Seguieria langsdorffii Moq.	L	4	3	4	0.4
Cissus verticillata (L.) Nicolson & C.E. Jarvis	SL	3	3	3	0.34
Urvillea ulmacea Kunth.	L	3	3	3	0.34
Wilbrandia sp	SL	3	3	3	0.34
Anemopaegma chamberlaynii (Sims) Bureau & K. Schum.	L	4	2	5	0.32
Acanthaceae sp1	SL	2	2	2	0.31
Fridericia samydoides (Cham.) L.G.Lohmmann	L	3	1	3	0.3
Justicia sp2	SL	4	2	4	0.3
Tontelea sp2	L	3	2	3	0.28
Bauhinia sp	L	2	2	2	0.27
Mascagnia sp	L	2	2	2	0.27
Amphilophium crucigerum (L.) L.G.Lohmann	L	2	2	3	0.26
Dalbergia frutescens (Vell.) Britton	L	2	2	2	0.26
Eupatorium sp	SL	2	2	2	0.25
Fridericia pulchella (Cham.) L.G.Lohmann	L	2	2	2	0.25
Paullinia meliifolia Juss.	L	3	1	3	0.25
Petrea sp	L	2	1	2	0.24
Gouania latifolia Reissek	L	2	2	2	0.23
Tragia alienata (Didr.) Múlgura & M.M. Gut.	H	2	2	2	0.22
Machaerium dimorphandrum Hoehne	L	1	1	1	0.19
Dolichandra chodatii (Hassl.) L.G.Lohmmann	L	1	1	1	0.18
Hyperbaena domingensis (DC.) Benth.	L	2	1	2	0.18
Prestonia coalita Mull.Arg.	L	1	1	1	0.18

Espécies	**L/SL/H**	**NInd**	**NAm**	**TotRam**	**IVI**
Aureliana sp	L	2	1	2	0.16
Tournefortia villosa Salzm. ex DC.	L	2	1	2	0.16
Unknown sp2	L	1	1	1	0.16
Cissus sulcicaulis (Baker) Planch.	SL	2	1	2	0.15
Pisonia aculeata L.	L	1	1	1	0.15
Schubertia multiflora Mart.	L	2	1	2	0.15
Verbenaceae sp	L	1	1	1	0.15
Unknown sp1	L	1	1	1	0.13
Justicia sp1	L	1	1	1	0.12
Paullinia rhomboidea Radlk.	L	1	1	1	0.12
Tetrapterys sp	L	1	1	1	0.12
Dasyphyllum brasiliense (Spreng.) Cabrera	SL	1	1	1	0.11
Herreria salsaparilha Mart.	H	1	1	1	0.11
Justicia sp3	L	1	1	1	0.11
Solanum sp	L	1	1	1	0.11
TOTAL	L: 79 SL: 10 H: 02	3916	100	4055	300

Onde:

L/SL/H: trepadeira com tecido lenhoso (L), sublenhoso (SL) ou herbáceo (H);

NInd: Número de indivíduos amostrados;

NAm: número de amostras (parcelas de 100m²) em que as espécies foram encontradas;

IVI: Índice de Valor de Importância. *IVI = DRe + FRe +DoRe*;

DRe: Densidade relativa da espécie (porcentual da contribuição do número de indivíduos ao total da comunidade)

FRe: Frequência relativa da espécie (porcentual de amostras em que a espécie esteve presente)

DoRe: Dominância relativa (porcentual da contribuição da área basal da espécie para a área basal da comunidade)

Anexo 3 – Gráficos de pontos baseadas nas matrizes utilizadas nas análises ambientais.

Figura 1 – Gráfico de pontos baseado na matriz de dinâmica utilizada, sendo **CII**: índice de iluminação da copa médio das árvores presentes na parcela; **WD**: densidade da madeira médio das árvores presentes na parcela, **BAmed**: Mediana da área basal das árvores presentes em cada parcela; **Hmed**: Mediana das alturas das árvores encontradas em cada parcela, **Hmax**: Altura da árvore mais alta presente em cada parcela, **PT**: proporção de árvores caracterizadas como árvores do "passado" em relação ao total, **PR**: proporção de árvores caracterizadas como árvores do "passado" em relação ao total; **SDT**: Proporção de árvores com deciduidade total ou parcial da copa durante o período seco; e; **Canopy**: Abertura do Dossel, medido com um reflectómetro.

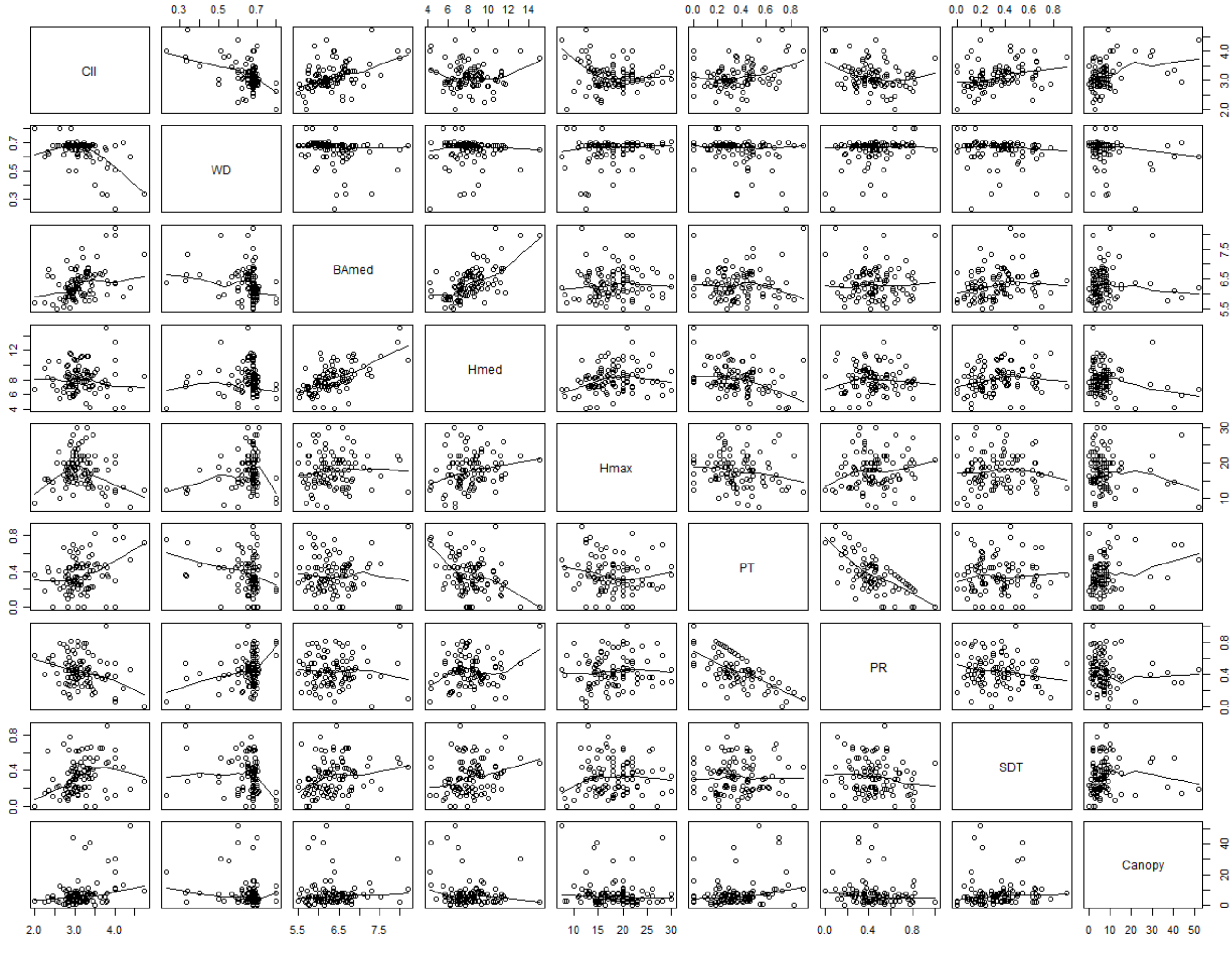

Figura 2 - Gráfico de pontos baseado na matriz de dados edáficos e altitude. Sendo: **alt**: altitude relativa da parcela (em relação ao nível do rio Ribeirão Cachoeira; **OM**: Matéria Orgânica; **pH**: medida de atividade do íon hidrogênio dissolvido; **P**: Concentração de Fósforo extraível; **K**: Concentração de cátions de Potássio; **Ca**: Concentração de Cátions de Cálcio; **Mg**: Concentração de Cátions de Magnésio, e; **H_Al**: acidez potencial.

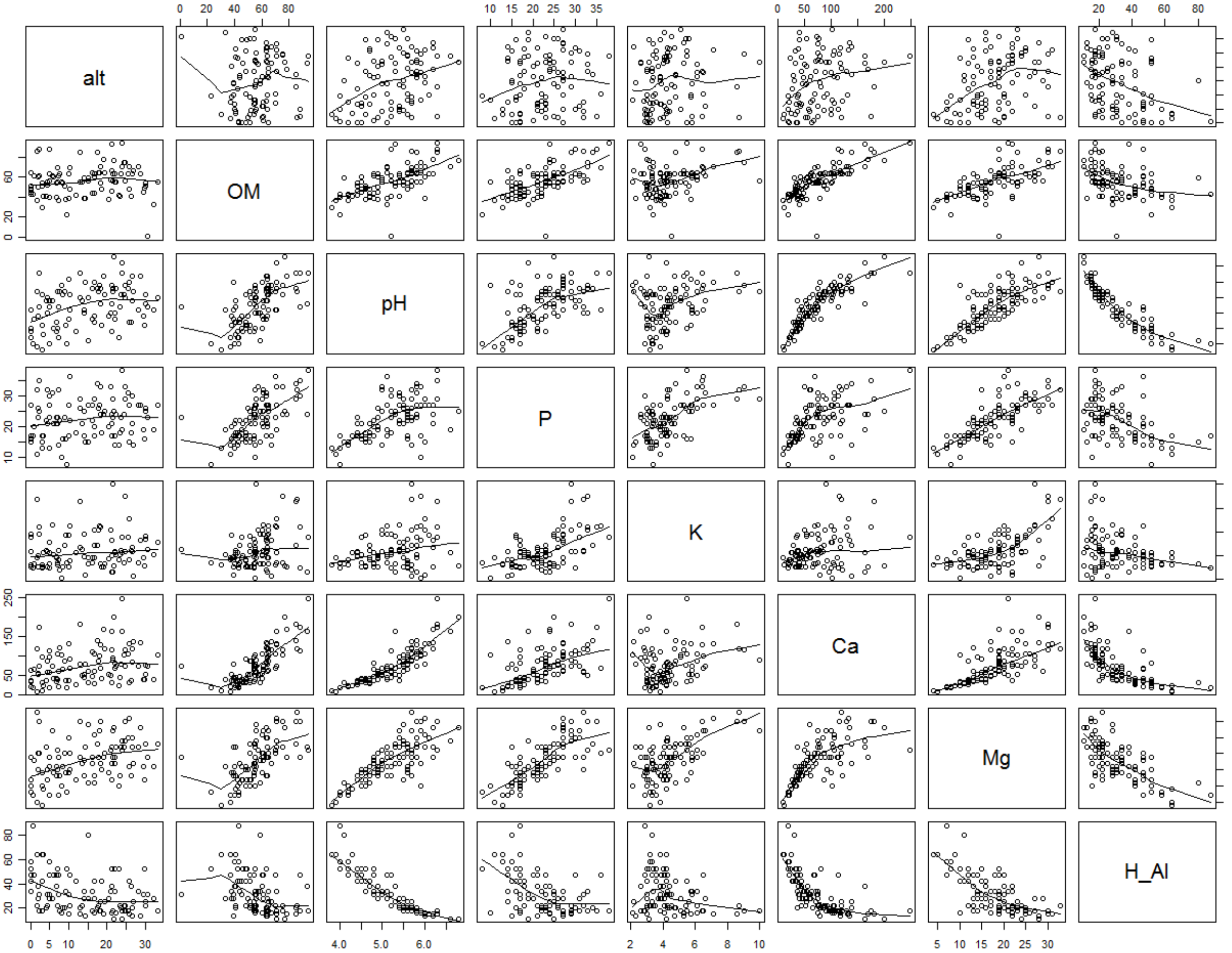

Figura 3 - Gráfico de pontos baseado na matriz de dados edáficos, texturais e altitude. Sendo: **alt**: altitude relativa da parcela (em relação ao nível do rio Ribeirão Cachoeira; **S.B.**: soma de bases trocáveis; **CEC**: Capacidade de troca de Cátions; **V**: saturação de bases (em %); **Clay**: Proporção da porção de argila (<0.002 mm) no solo; **Silt**: proporção da porção de silte (0.053-0.002 mm) no solo e, **Sand_tot**: Proporção da porção de areia total (2.00-0.053 mm) no solo.