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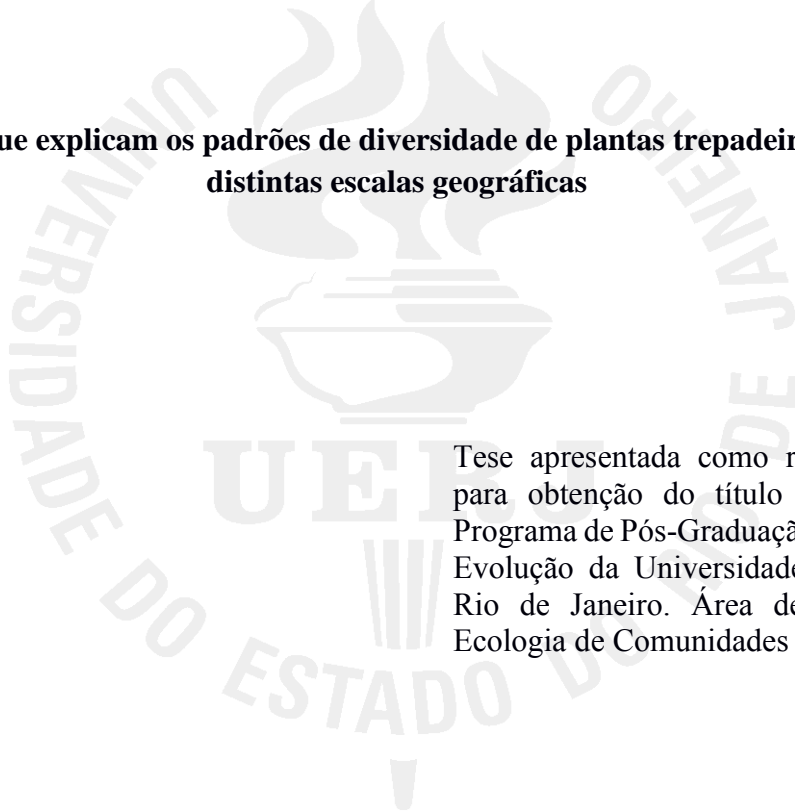
**Mecanismos que explicam os padrões de diversidade de plantas trepadeiras
ao longo de distintas escalas geográficas**

Rio de Janeiro

2018

Thiago de Azevedo Amorim

Mecanismos que explicam os padrões de diversidade de plantas trepadeiras ao longo de distintas escalas geográficas



Tese apresentada como requisito parcial para obtenção do título de Doutor, ao Programa de Pós-Graduação em Ecologia e Evolução da Universidade do Estado do Rio de Janeiro. Área de concentração: Ecologia de Comunidades e Ecossistemas.

Orientador: Prof. Dr. Bruno Henrique Pimentel Rosado

Coorientador: Prof. Dr. André Felipe Nunes-Freitas

Rio de Janeiro

2018

CATALOGAÇÃO NA FONTE

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A524	<p>Amorim, Thiago de Azevedo. Mecanismos que explicam os padrões de diversidade de plantas trepadeiras ao longo de distintas escalas geográficas / Thiago de Azevedo Amorim. – 2018. 145 f. : il.</p> <p>Orientador: Bruno Henrique Pimentel Rosado. Coorientador: André Felipe Nunes-Freitas. Tese (Doutorado em Ecologia e Evolução) - Universidade do Estado do Rio de Janeiro. Instituto de Biologia Roberto Alcântara Gomes.</p> <p>1. Ecologia vegetal – Teses. 2. Trepadeiras – Influência do meio ambiente - Teses. I. Rosado, Bruno Henrique Pimentel. II. Nunes-Freitas, André Felipe. III. Universidade do Estado do Rio de Janeiro. Instituto de Biologia Roberto Alcântara Gomes. IV. Título.</p> <p style="text-align: right;">CDU 581.522.4</p>
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Rinaldo Magallon *CRB/7-5016* – Responsável pela elaboração da ficha catalográfica.

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Assinatura

Data

Thiago de Azevedo Amorim

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Aprovada em 28 de fevereiro de 2018

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Rio de Janeiro

2018

Dedico este trabalho em homenagem a todos os anônimos que investem seu tempo e recursos à conservação da diversidade biológica brasileira.

AGRADECIMENTOS

Nas palavras de São Paulo, “dou graças ao Deus e Pai de Jesus Cristo”! Gratidão resume esse momento. Obrigado por mais uma etapa concluída. Pelos momentos alegres e difíceis que me fizeram chegar até aqui. Sou grato por todo aprendizado que acumulei. Meu desejo é que como discípulo, eu saiba compartilhar generosamente o que aprendi.

Agradeço à minha amada esposa, Eliziane Braga, por todo suporte e companhia. Obrigado por sua paciência nas minhas ausências e pelo carinho e cuidado quando ao teu lado. Obrigado por harmonizar a minha vida de um jeito que nem eu faria. Essa conquista é nossa.

Meu pai, William, minha mãe Harialda e minha irmã Luanna. Sempre ao meu lado, cada um ao seu modo, oferecendo a mim cuidado, amor, aconchego e muitas risadas. Obrigado por me mostrar que nenhum estudo no mundo vale mais que uma família feliz e saudável. Viu mamãe, o menino curioso acerca dos seres vivos já na pré-escola, se tornou um cientista conforme “profetizado” pela professora Helen.

Agradeço minha família, que sempre foi um porto seguro. Tios e tias, primos e primas e vovó. Em especial agradeço minhas tias Lane, Nete, Bete, Zete e Vanda. Parte do homem que me tornei com certeza se deve ao fato de diariamente conviver com o exemplo dessas mulheres, fortes, batalhadoras e corajosas! Obrigado pelos barulhentos encontros de família.

Ao Departamento de Botânica (DeBot) da Universidade Federal Rural do Rio de Janeiro (UFRRJ) na pessoa da sua atual chefe a docente, Rejane Gomes. Agradeço aos colegas pela anuência para cursar o doutorado. Além disso, agradeço sem exceção aos técnicos administrativos e docentes pela contribuição à minha formação acadêmica desde quando ingressei nessa casa, no ano de 2004. Minha trajetória acadêmica-profissional está profundamente ligada a esse Departamento o qual tenho uma dívida de gratidão. Aos docentes Marilena Conde, minha mãe acadêmica e sábia conselheira; Genise Somner, com sua alegria contagiante sempre me estimulando e me fazendo dar risadas nos dias difíceis e ao Marcelo Souza pelo seu exemplo de afino e cuidado com o Herbário RBR. À professora Solange Brandolini, diretora do Instituto de Ciências Biológicas e da Saúde (UFRRJ), e sua equipe por todo suporte durante a realização dessa tese em especial durante a solicitação do afastamento para cursar a bolsa sanduíche.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa de estudos para cursar o estágio sanduíche na *University of South Bohemia*, República

Tcheca (processo número 88881.135051/2016-01). Essa oportunidade foi muito valiosa e produtiva!

À professora Gisele Lobo, atual coordenadora do Programa de Pós-Graduação em Ecologia e Evolução (PPGEE) da UERJ, e a ex-coordenadora, professora Rosana Mazzoni juntamente com as secretárias Sonia Pereira e Verusca Machado. Vocês sempre foram solícitas e atenciosas quanto as minhas demandas junto à secretaria do PPGEE-UERJ. À professora Nena Bergalo por ser uma grande coordenadora e entusiasta de projetos e estudos científicos na Ilha Grande. Ao doutorando Rodrigo Zucarato, à Carlota Enrice e demais membros do laboratório de ecologia de pequenos mamíferos (UERJ) pelo auxílio em campo.

Ao meu “queridão” orientador Bruno Rosado. Brunão, você é inspirador! Ao longo destes quatro anos tive a honra de ser orientado por um dos mais brilhantes e entusiasmados ecólogos que eu já conheci. Tive o privilégio ser sua “cobaia” como o seu primeiro aluno de doutorado (é claro que compartilhei isso com o Lucas). Tenho a plena convicção que boa parte do avanço que tive durante o curso do doutorado é por conta da sua influência. Agora, com o fim da tese eu acho que dá para gente ir assistir um jogo do Botafogo no Engenhão! Ao meu orientador André Freitas. André me acompanha desde o fim da minha graduação. Obrigado pela confiança e ensinamentos ao longo destes anos. Obrigado por aquela conversa nos idos anos de 2013 que viria a ser o embrião deste projeto de doutorado. Ao docente Jeronimo Sansevero (UFRRJ) que contribuiu com a melhoria da qualidade do texto desta tese desde a etapa da qualificação.

Aos companheiros do Laboratório de Ecologia Vegetal (LEV) da UERJ, minha mais sincera gratidão. Obrigado pela grande ajuda nas atividades em campo e no laboratório: Ilaine Matos (também pelas considerações valiosas nas apresentações de seminários), Michele Lima, Pedro Rajão, Sara Petrocchi, Jessica Castelo Branco, Brigiti Bandini, Valquiria Gouveia, Rodrigo Brantes, Ágata Silva, Carol, Maria Paula e Lidiane Almeida. Dario Paiva e Lais Barbalioli. Essa dupla dinâmica foi muito prestativa nas etapas de campo desta tese! MUITÍSSIMO obrigado! Ao meu amigo e companheiro de doutorado Lucas Lopes; seu auxílio foi imprescindível! Desconfio que ainda estaria coletando e medindo atributos funcionais se não fosse a sua cooperação. Muito obrigado por cada ajuda, não só em campo, mas também encurtando distâncias e resolvendo situações para mim quando estive impossibilitado de estar na UERJ. Ao professor André Dias (Universidade Federal do Rio de Janeiro, UFRJ) pelas suas sempre tão pertinentes colocações e contribuições não só pontualmente nesta tese, mas durante as discussões e convívio no LEV. Aos queridos Ruralinos que estiveram comigo me auxiliando em campo: Yago Mesquita, Bernardo Lars, André Brandão, Allan Chagas, Thiago Costa,

Nathan Borges e Caio de Paula. Ao Felipe Cito por todas influências ecológicas durante minha formação.

I thank all the team of the ecology laboratory, Department of Botany - University of South Bohemia, Czech Republic. Thank you all for your contribution improving the quality of my scientific skills. Enrique Valencia, Thomas Galland, Anna Vojtkó, Lars Götzenberger, Julia Sfair, Hana Dvořáková and Javier Puy. Thank you also for the moments of fun and relaxation! Nagore Medina, ¡muchas gracias por la atención prestada y por la gran ayuda en los análisis estadísticos! Particularly, I thank Professor Francesco de Bello who was my supervisor during this period. His experience and critical view brought valuable contributions to the development of this thesis. No podría olvidarme: ¡un abrazo a “comunidad” española que vive en České Budějovice!

I am thankful to the friends I made in České Budějovice: Petr Falc, Pter “Lynxxi” Pavliska, Tim Ha, Pavel Luksch, Jakub “Kuba” Houra, Zdeněk Bečvář, Miroslav “Mira” Peroutka and Robert Keno. Thank you so much! You received me as part of your family. We will “roll” in a near future! Oss! Čau! Amigos da equipe de jiu-jitsu Claudio Barbosa e ao mestre Claudio pelos ensinamentos, amizade e descontração dentro e fora do dojo que me ajudaram a aliviar o estresse decorrido da execução de um doutoramento.

Aos taxonomistas Genise Somner (Sapindaceae), André Amorim (Malpighiaceae) pelo auxílio nas identificações do material botânico. À curadora do herbário RB (Intituto de Pesquisas Jardim Botânico do Rio de Janeiro), Rafaela Forzza, pela permissão de consulta à coleção para identificação dos espécimes. À toda equipe do Centro de Estudo Ambientais e Desenvolvimento Sustentável (CEADS-UERJ) por todo apoio logístico durante este projeto. Ao Instituto Estadual do Meio Ambiente (INEA-RJ) pela concessão de autorização de coleta e apoio logístico no Parque Estadual da Ilha Grande. A todos aqueles que de algum modo contribuíram para a execução deste trabalho e que por um infortúnio não foram nominados.

“... estudar demais deixa exausto o corpo”.

Eclesiastes 12.12

RESUMO GERAL

AMORIM, T. A. *Mecanismos que explicam os padrões de diversidade de plantas trepadeiras ao longo de distintas escalas geográficas*. 2018 145 f. Tese. (Doutorado em Ecologia e Evolução) - Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro 2018.

Plantas trepadeiras são organismos que se apoiam sobre outros vegetais para utilizá-los como suporte físico, já que investem menos na produção de tecidos para suporte mecânico, mantendo-se enraizadas no solo por todo o seu ciclo de vida. São consideradas um dos grupos funcionais mais típicos em florestas tropicais, onde apresentam as maiores abundâncias. Nestes sistemas, elas participam de importantes processos e da dinâmica das florestas tropicais, influenciando a taxa de mortalidade de árvores, contribuindo no aporte de nutrientes na serapilheira e como fonte de recurso para a fauna. Dada a importância deste grupo para o funcionamento de florestas tropicais e dos serviços ambientais, são necessárias investigações sobre a estruturação de comunidades de plantas trepadeiras, focando, se possível, em mais de um aspecto da diversidade biológica. Assim, este trabalho buscou preencher algumas lacunas no conhecimento ecológico da estrutura de comunidade de plantas trepadeiras, através de uma abordagem multiescalar, com perguntas que avaliam a estruturação das suas comunidades desde a escala global até a escala local. Nós revisamos a explicação atual para o padrão global de abundância de lianas, demonstrando algumas evidências empíricas que contrapõem a explicação vigente sobre raízes profundas. Além disso, propomos uma explicação alternativa, baseada em uma abordagem multifuncional e na estratégia de crescimento típicas das plantas trepadeiras. Nós investigamos como fatores climáticos e espaciais podem influenciar a estrutura de comunidade de plantas trepadeiras em termos de diversidade taxonômica e filogenética. Detectamos uma preponderância da influência de processos climáticos sobre os padrões de diversidade alfa filogenética e beta taxonômica enquanto os processos espaciais possuíram maior influência nos padrões de diversidade beta filogenética e alfa taxonômica. Já em escala local, investigamos como a variação altitudinal poderia influenciar na montagem de comunidades de lianas, focando nos aspectos funcionais da comunidade. Verificamos a influência da altitude sobre as características funcionais da comunidade e incorporamos em nossa abordagem a variação intraespecífica das características funcionais (VIE). Demonstramos como a inclusão da VIE pôde permitir detalhar e esclarecer importantes aspectos da montagem de comunidades de plantas. Ainda em escala local, realizamos um estudo focando em responder perguntas sobre como gradiente ambiental associado a uma variação geográfica afeta o padrão e a estrutura filogenética de árvores e lianas. Verificamos que árvores e lianas possuem diferenças sobre a predominância do processo responsável por estruturar a comunidade em termos filogenéticos. Ressaltamos que essas diferenças são muito provavelmente advindas da diferença nas estratégias de colonização entre os grupos funcionais. Finalmente destacamos que os achados desta tese fornecem informações sobre o entendimento de como comunidades vegetais são estruturadas em diferentes escalas geográficas.

Palavras-chave: Variação-na-escala-espacial. Plantas-escandentes. Condições-climáticas. Condições-espaciais. Condições-ambientais. Montagem-de-assembleia. Diversidade-taxonômica. Diversidade-filogenética. Diversidade-funcional.

GENERAL ABSTRACT

AMORIM, T. A. *Mechanisms explaining patterns of climbing plant diversity across geographic scales*. 2018 145 p. Tese. (Doutorado em Ecologia e Evolução) - Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro 2018.

Climbing plants are a functional group that rely on other plants for physical support, as they do not invest in the production of tissues that provide mechanical support to your body. However, they remain rooted in the ground during their whole lifespan. They are considered one of the most typical plant functional group in tropical forests, where they present their peak of abundance. Climbing plants participate in important processes and dynamics in tropical forests, such as influencing the mortality rate of trees, contributing with nutrients cycling, providing died biomass to litter decomposers. Given the importance of this functional group to the functioning of tropical forests and environmental services, there is a need for research on how climbing plants communities are structured, focusing, if possible, on more than one aspect of biological diversity. This work was a comprehensive effort to fill some gaps in ecological knowledge regarding the community structure of climbing plants. This endeavor corresponded an investigation of topics about community structure from the global scale to the local scale. We review the current explanation for the global pattern of lianas abundance, demonstrating some empirical evidence that conteresposes the current explanation. In addition, we elaborate an alternative explanation, based on a multifunctional approach and on the growth strategy typical of climbing plants. We investigate how climatic and spatial factors can influence the community structure of climbing plants in terms of taxonomic and phylogenetic diversity. We detected an alternation of preponderance between the two processes according to the type of diversity investigated. At the local scale, we investigated how the altitudinal variation could influence the assembly of liana communities, focusing on the functional aspects of the community. We verified the influence of altitude on the functional characteristics of the community. We incorporated in our approach the intraspecific variation of functional characteristics (ITV). We showed how the inclusion of ITV allowed to detail and clarify important aspects of the assembly of plant communities. Furthermore, at the local scale, we performed another study focusing on answering questions about how the environmental gradient associated with a geographic variation affects the pattern and phylogenetic structure of trees and lianas. We verified that trees and lianas have differences on the predominance of the process responsible for structuring the community in phylogenetic terms. We argued that these differences were due to the differences in colonization strategies between these functional groups. Finally, we highlight that the findings of these studies provide information on the understanding how plant communities are structured at different geographic scales.

Keywords: Variation-in-geographic-scale. Vines. Woody-climber. Climatic constraints. Spatial variables. Environmental variables. Community-assembly. Taxonomic-diversity. Phylogenetic-diversity. Functional-diversity.

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INTRODUÇÃO GERAL

As lianas (ou trepadeiras lenhosas) são um dos grupos funcionais entre os vegetais mais típicos e diversificados nos neotrópicos e podem representar até 45 % da riqueza específica de plantas lenhosas nas florestas tropicais (Schnitzer & Bongers, 2002). Por serem plantas lenhosas de hábito trepador, dependem de outras plantas (forófitos), normalmente árvores, como suporte físico. As lianas desempenham funções importantes na estrutura, dinâmica e manutenção das florestas nos neotrópicos (Tang et al., 2012) e mesmo que esses papéis sejam reconhecidos, pouco se sabe sobre os fatores que estruturam as comunidades de lianas comparativamente às outras plantas lenhosas nos neotrópicos. As razões para isso podem estar relacionadas à dificuldade de coleta de espécimes e sua consequente identificação, já que normalmente as folhas e ramos reprodutivos das lianas estão no dossel da floresta (Schnitzer & Bongers, 2002). Contudo, já parece estar claro que as comunidades de lianas em áreas florestais tendem a ser favorecidas por distúrbios antrópicos (Schnitzer and Bongers 2011). Normalmente esses distúrbios resultam em incremento da abundância das populações e riqueza das espécies nos locais da floresta onde os níveis de distúrbio são intermediários (Madeira et al., 2009). Esse fato geralmente é atribuído à eficiência das lianas para obtenção de energia luminosa devido ao hábito trepador, que proporciona fácil acesso ao dossel, ou também a características ecofisiológicas que permitem um melhor balanço entre a atividade fotossintética e o custo metabólico (Gianoli et al., 2012). No momento que parte da vegetação é removida nas florestas, as lianas seriam favorecidas pela maior disponibilidade de luz, crescendo mais e tornando-se mais abundantes. Contudo desde escalas geográficas locais ainda existem uma série de questões que necessitam ser elucidadas.

Nos últimos anos, alguns estudos vêm buscando elucidar processos de montagem de comunidades em escala regional e global (Gallagher et al. 2011; Gallagher & Leishman, 2012; Hu et al. 2010). Estes estudos até o momento são uns dos poucos que integraram diferentes aspectos da diversidade biológica, considerando questões sobre a diversidade taxonômica, funcional e filogenética. Entender processos de montagem em escalas mais abrangentes que considerem mais de um aspecto da diversidade biológica podem ser muito importantes para melhor esclarecer como comunidades de lianas poderão responder às mudanças ambientais. A resultante do efeito das mudanças climáticas globais sobre a diversidade de plantas trepadeiras poderá ser melhor elucidada, prevista ou até mesmo mitigada se houver estudos que façam a conexão entre as mudanças das condições e recursos e a resposta das espécies a tais fatores (Rosado et al., 2013).

Além das lacunas teóricas sobre montagem de comunidades em escala global e regional, ainda há um grande déficit de estudos que incorporem a resposta funcional de plantas trepadeiras à variação ambiental e microclimática relacionada à variação de altitude. Os estudos que englobam o fator “altitude” em sua maioria buscam responder questões somente ligadas à diversidade taxonômica (e.g. Jimenez-Castillo et al., 2007; Homeier et al., 2010, Alves et al., 2011). Normalmente, os trabalhos que investigam essa possível influência consideram que a variação em altitude traz consigo mudanças na topografia e em propriedades físicas do solo como maior rochosidade e solo mais arenoso (Benites et al. 2007). Além disso, ocorrem também reduções na pressão atmosférica e umidade relativa e aumento da radiação (Körner 2007). Esses fatores podem contribuir para que o ambiente se torne progressivamente mais seco com a elevação da altitude (Leuschner, 2000). Outro fator considerado é a redução da temperatura com o aumento da altitude, também pela menor pressão atmosférica que tem menor capacidade de retenção do calor gerado pela energia luminosa incidente no solo (Leuschner 2000). Recentemente foi demonstrado que, em florestas tropicais, mesmo variações altitudinais entre 100 e 1000m promovem um aumento significativo da demanda evaporativa do ar em função de fatores como menor pressão parcial do CO₂ atmosférico e maior radiação que favorecem a evaporação de água em altitudes elevadas (Rosado et al. 2010; Rosado et al. 2016), causando mudanças em atributos funcionais das árvores (Rosado et al., 2016). Mas porque estudos que consideram a variação altitudinal podem ser tão apropriados para entender a resposta de plantas a fatores climáticos?

Estudos realizados ao longo de variações altitudinais têm sido considerados como poderosos experimentos naturais especialmente no contexto de mudanças ambientais (Körner 2007) e a necessidade destes estudos se mostra ainda maior a partir da constatação que, embora se assuma que os principais fatores limitantes em Florestas Tropicais chuvosas sejam luz e nutrientes, já existem evidências que ocorra déficit hídrico na Floresta Atlântica (Rosado et al., 2016). Com isso, as plantas que vivem nesses ambientes podem ser negativamente afetadas pela menor disponibilidade de água e temperatura mais baixa. Assim, é provável que as comunidades de lianas em áreas sujeitas à variação altitudinal apresentem comunidades menos diversificadas com aumento da altitude.

Os resultados dos poucos trabalhos já realizados não revelaram uma clara consonância conquanto ao padrão acima citado (e.g. Jimenez-Castillo et al., 2007; Homeier et al., 2010, Alves, et al., 2012), de modo que os padrões de riqueza e abundância das lianas não foram fortemente alterados diante do aumento da altitude. Isso pode significar que de modo geral, as espécies de lianas de uma dada área possuem características que as permitam lidar com a

variação ambiental associada a variação de altitude sem, contudo, experimentarem mudanças expressivas nos padrões de riqueza e abundância. Porém, essas características dos indivíduos que podem regular a riqueza e abundância da comunidade merecem ser investigadas e provavelmente consistem em atributos das plantas trepadeiras em nível morfo-fisiológico.

Recentemente, Dias (2013) demonstrou que lianas podem investir de maneira distinta em atributos foliares como área foliar específica e dos ramos como densidade da madeira de acordo com o tipo de Floresta (Ombrófila ou Estacional). Essas diferenças nos atributos foliares e dos ramos expressaram, respectivamente, o investimento foliar na demanda entre atividade fotossintética e longevidade (Wright et al., 2004) foliar e maior condutividade hidráulica e suscetibilidade à cavitação (Ewers et al., 2015). Embora Dias (2013) não tenha abordado a questão da influência de fatores ambientais associados à variação de altitude sobre as espécies de lianas, seus resultados podem contribuir para questionar o papel de atributos foliares e dos ramos como descritores das respostas das espécies de lianas em diferentes altitudes. Isso pode ser deduzido, pois Dias (2013) se deparou com variações ambientais entre as florestas estudadas semelhantes àquelas que podem ser encontradas por conta de variação altitudinal em uma mesma área.

Além das questões relativas somente as comunidades de lianas, diversos estudos vem buscando comparar a performance entre árvores e lianas, por serem as formas de vida lenhosa predominantes em Florestais Tropicais (e.g. Asner et al. 2007, Dewalt et al. 2010, Schntizer et al. 2005). Entretanto, poucos estudos se propuseram descrever e comparar simultaneamente como variações nas condições ambientais e espaciais podem afetar a variação na composição e estrutura de lianas e árvores. (e.g. Letcher et Chazdon 2009, Madeira et al. 2009, Pérez-Salicrup et Sork. 2001). Esses tipos de estudos podem fornecer informações valiosas sobre como diferentes formas de vida poderão responder a variações ambientais, especialmente no contexto das mudanças climáticas globais. Ainda sim, aspectos da diversidade como por exemplo diversidade filogenética não figuram nestes trabalhos, muito em parte pela carência de tecnologias que permitissem tais investigação no período em que foram realizados, além é claro da popularização de informações científicas por meio da internet.

Os trabalhos que vêm abordando os temas apresentados até aqui, de modo geral, adotaram uma abordagem mais clássica, buscando investigar aspectos da diversidade normalmente ligados a riqueza e abundância espécies e tamanho dos espécimes. Contudo, já se sabe que incorporação de métricas de diversidade que considerem as características dos indivíduos e suas relações evolutivas como fator condicionante à seu sucesso, estabelecimento e manutenção nas comunidades (i.e. diversidade funcional – sensu Violle et al., 2007 e diversidade filogenética –

sensu Faith, 1992) podem aumentar o poder descritivo sobre as regras as quais as comunidades foram montadas além de maior poder preditivo sobre como as comunidades poderão responder dado uma mudança nos filtros ambientais espaciais (Manson & de Bello, 2013). Outrossim, a tentativa de investigar esses aspectos em diversas escalas focando em mais de uma dimensão da diversidade biológica pode fornecer informações valiosas sobre a abrangência determinadas teorias ecológicas e proposições de mecanísticas para explicar padrões de diversidade biológica. É exatamente nesse contexto que esta tese se insere.

O presente estudo se propõe a investigar quatro grandes tópicos sobre aspectos ecológicos acerca da montagem de comunidades de plantas trepadeiras em distintas escalas geográficas. Esses tópicos foram organizados em capítulos que em linhas gerais versam sobre:

- Capítulo 1 – Consistiu em uma revisão em literatura sobre o atual mecanismo explanatórios dos padrões de abundância em escala global de lianas. Neste capítulo nós demonstramos as limitações para a explicação vigente e apresentamos uma explicação alternativa baseada em uma abordagem multifuncional e nas estratégias de colonização de lianas.
- Capítulo 2 – Compreendeu em um levantamento feito majoritariamente em literatura e bases de dados científicas eletrônicas envolvendo 18 unidades de conservação no estado do Rio de Janeiro para responder a seguinte questão: Como variáveis climáticas e a estrutura espacial podem determinar os padrões e diversidade taxonômica e filogenética de planta trepadeiras em uma escala regional?
- Capítulo 3 – Realizamos uma amostragem de características funcionais ligadas ao uso da água de uma comunidade de lianas ao longo de dez parcelas ao em uma variação altitudinal com vistas a responder a seguinte questão: qual é o efeito da filtragem ambiental associada a variação de altitude sobre as características funcionais ligadas ao uso da água em lianas neotropicais? A hipótese central é que em maiores altitudes, partindo da premissa de maiores déficits de pressão de vapor da atmosfera (DPV) (Rosado et al., 2016) as espécies de lianas apresentarão valores de atributos positivamente relacionados a um uso mais conservativo de água.
- Capítulo 4 – Neste capítulo amostramos árvores e lianas em 30 parcelas além de variáveis ambientais e espaciais. Em seguida relacionamos com as variáveis ambientais e espaciais com os padrões de diversidade filogenética afim de responder a seguinte questão: Qual a contribuição relativa de variáveis espaciais e ambientais sobre os padrões diversidade filogenética de árvores e lianas?

- Os esforços empenhados neste trabalho consistem em investigação sobre os mecanismos que operam nos padrões de diversidade de plantas trepadeiras ao longo de distintas escalas geográficas.

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GENERAL INTRODUCTION

Climbing plants are one of most typical and diversified functional group in the Neotropics and can reach up to 45% of the specific richness of plants in tropical forests (Schnitzer and Bongers, 2002). Due the climbing habit, they depend on other plants (phorophytes), usually trees, as physical support. The lianas play important roles in the structure, dynamics and maintenance of forests in the Neotropics (Tang et al. 2012). Even though these roles are recognized, little is known about the factors that structure the liana communities compared to other woody plants in the Neotropics (Schnitzer and Bongers 2002, Schnitzer 2005, Schnitzer and Bongers 2011). The reasons for this may be related to the difficulty of collecting specimens and their consequent identification, since normally the leaves and reproductive branches of the lianas are in the forest canopy (Schnitzer and Bongers 2002). However, it already seems clear that liana communities in forest areas tend to be favored by anthropic disturbances (Schnitzer and Bongers 2011). These disturbances usually result in increased population abundance and species richness in forest sites where disturbance levels are intermediate (Madeira et al. 2009). This fact is generally attributed to the liana efficiency to obtain light due to their climbing habit, which provides access to the canopy, or also to the ecophysiological characteristics that allow a better balance between the photosynthetic activity and the metabolic costs (Gianoli et al. 2012). As part of the vegetation is removed in the forests, the lianas would be favored by the greater availability of light, growing more and becoming more abundant. However, from local to global geographic scales many gaps still remain and that still need to be elucidated.

In recent years, some studies have sought to elucidate how communities are assembled on regional and global scale (Gallagher et al. 2011, Gallagher and Leishman, 2012, Hu et al. 2010). To date, these studies are the ones which have integrated different aspects of biological diversity, considering topics about taxonomic, functional and phylogenetic diversity. Understanding assembling processes at more comprehensive scales that consider more than one aspect of biological diversity can be very important to better clarify how communities of lianas can respond to environmental changes. Hence, the consequences of global climate change on the diversity of climbing plants may be better elucidated, predicted or even mitigated if studies could link the changes in conditions and resources to the response of species to such factors (Rosado et al. 2013, Marvin et al. 2015).

In addition to the theoretical gaps in community assembling of lianas on a global and regional scale, there is still a large deficit of studies that incorporate the functional response of climbing plants to environmental and microclimatic variation related to altitudinal variation.

The study of the “altitude variation” in the majority of the studies aimed to answer questions related only to taxonomic diversity (e.g. Jimenez-Castillo et al. 2007, Homeier et al. 2010, Alves et al. 2011). Normally, the studies that investigate this possible influence consider that the variation in altitude brings changes in the topography and physical properties of the soil such as increasing in rocky and sandy soil (Benites et al. 2007). In addition, there are also reductions in atmospheric pressure and relative humidity and increase in radiation (Körner 2007). These factors may contribute to the environment becoming progressively drier with higher elevation (Leuschner 2000). Another factor considered is the reduction of the temperature with the increase of the altitude, also by the lower atmospheric pressure that has less capacity of retention of the heat generated by the light energy incident on the ground (Leuschner 2000). It has recently been shown that in tropical forests, even altitudinal variations between 100 and 1000 m promote a significant increase in air evaporative demand due to factors such as lower partial pressure of atmospheric CO₂ and higher radiation that favor evaporation of water at high altitudes (Rosado and Mattos 2010, Rosado et al. 2016), causing changes in tree functional traits (Rosado et al. 2016). Yet, why studies that consider altitudinal variation can be so appropriate to understand the response of plants to climatic factors?

Studies carried out along altitudinal variations have been considered as powerful natural experiments especially in the context of environmental changes (Körner 2007). There is a need studies addressing the influence of altitude in Tropical rainforests over plant traits once there is evidence that water deficit occur in the Atlantic Forest (Rosado et al. 2016). Thus, plants living in these environments may be negatively affected by lower water availability and lower temperature. Thus, liana communities in areas subject to altitudinal variation are likely to present less diverse communities with increasing in altitude.

The results of the few studies already carried out across altitudinal variation did not reveal a clear consonance with the trend mentioned above (e.g. Jimenez-Castillo et al. 2007, Homeier et al. 2010, Alves, et al. 2012). The patterns of richness and abundance of lianas were not strongly altered by the increase in altitude. This may indicate that, in general, the species of lianas in a given area have traits that allow them to cope with the environmental variation associated with altitude variation without, however, experiencing significant changes in patterns of richness and abundance. However, these characteristics of the individuals that can influence the richness and abundance of the community deserve to be investigated and probably consist to functional traits.

Recently, Dias (2013) has shown that lianas can invest differently in leaf traits such as specific leaf area and in branches traits as wood density according to the forest type (aseasonal

a seasonal). These differences in leaf and branch traits express, respectively, trade-off between leaf photosynthetic activity and longevity (Wright et al. 2004) and higher hydraulic conductivity and susceptibility to cavitation (Ewers et al. 2015). Although Dias (2013) did not address the influence of environmental factors associated with altitude variation on liana species, their results may contribute to question the role of leaf and branch trait as descriptors of the responses of liana species to altitudinal variation. This can be inferred because Dias (2013) found environmental variations among the studied forests similar to those that can be found due to altitudinal variation in the same area.

In addition to the issues related to liana communities, several studies have sought to compare performance among trees and lianas due the predominance of these two woody plant groups in tropical forests (e.g. Asner et al. 2007, Dewalt et al. 2010, Schntizer et al. 2005). However, few studies have proposed describe and compare simultaneously how changes in environmental and spatial conditions can affect variation in composition and structure of lianas and trees. (e.g. Letcher and Chazdon 2009, Madeira et al. 2009, Pérez-Salicrup and Sork 2001). These types of studies can provide valuable insights into how different life forms may respond to environmental variations, especially in the context of global climatic change. However, aspects of diversity such as phylogenetic diversity were not included in these studies, in part due to the lack of technologies that allowed such research in the period in which they were carried out, besides of the popularization of scientific information through the internet.

The studies that have been addressing the topics presented so far, in general, adopted a more classical approach, seeking to investigate aspects of diversity usually related to species richness and abundance and size of specimens. However, it is already known that incorporation of diversity metrics that consider the characteristics of individuals and their evolutionary relationships as a factor determining their success, establishment and maintenance in the communities (i.e. functional diversity - sensu Violle et al. 2007 and phylogenetic diversity - sensu Faith, 1992) can increase descriptive power about how plant communities are assembled. Moreover, such approach can also improve predictive power about the responses of plant community given a change in environmental and spatial filters (Manson and de Bello, 2013).

Furthermore, researching these aspects at distinct scales focusing on more than one dimension of biological diversity may provide valuable insights into the scope of some ecological theories and mechanistic propositions that attempt to explain patterns of biological diversity. This thesis consists precisely in an effort in this direction.

The present study aims at investigating how ecological communities are assembled considering four different perspectives and encompassing different geographic scales. The investigations were organized in chapters. The chapters dealt with the following issues:

- Chapter 1 - Consisted of a literature review on the current explanatory mechanism of global patterns of liana abundance. In this chapter we demonstrated the limitations to the current explanation and presented an alternative explanation based on a multifunctional approach and lianas' colonization strategy.
- Chapter 2 - Consisted in a survey made mostly in the literature and electronic scientific databases involving 18 Protected Areas in the state of Rio de Janeiro, Brazil to answer the following question: How climatic variables and spatial structure can determine the patterns and taxonomic diversity and phylogenetics of climbing plants?
- Chapter 3 - We performed a sampling of functional traits linked to the water use of a liana community over ten plots. These plots were set up across an altitudinal variation. We aimed at answering the following question: what is the effect of environmental filtering associated to altitudinal variation on the functional traits related to the use of water in Neotropical lianas? The central hypothesis is that at higher altitudes, considering the premise of higher atmospheric vapor pressure deficits (VPD) (Rosado et al. 2016), liana species will trait value positively related to a more conservative water use.
- Chapter 4 - In this chapter we sampled trees and lianas in 30 plots. In each plot we measured environmental gradient and spatial variables. Then we correlated the environmental and spatial variables to the phylogenetic diversity patterns in order to answer the following question: What is the relative contribution of spatial and environmental variables to the patterns of phylogenetic diversity of trees and lianas?

The efforts undertaken in this thesis consist of research on the mechanisms that act on the patterns of climbing plant diversity along different geographic scales.

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1 DIGGING TO THE ROOT OF THE PATTERN: REVISITING THE HYPOTHESIS FOR INCREASING LIANA ABUNDANCE IN SEASONAL FORESTS

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Running headline: Revisiting the deep rooting paradigm

Note: A modified version of this chapter was published online on June 26th, 2018 in the scientific journal *Plant and Soil*. See: (<https://doi.org/10.1007/s11104-018-3730-6>).

1.1 Abstract

2. About ten years ago, the Mechanistic Explanation for Liana Global Abundance (MELGA) aimed to answer the following question: “Why are lianas most abundant in seasonal tropical forests across the globe?” MELGA relied on the assumption that lianas have a higher maximum root depth than trees and therefore are able to tap water from relatively deeper soil layers, giving lianas a competitive advantage especially during the drought season.
3. We here revisit the assumption of liana deep roots and propose an alternative explanation based on a multi-trait approach gathering comparative information about lianas and trees. We also describe a particular growth strategy of lianas (termed here as multifocal growth) as an important mechanism providing ecological advantages to lianas.
4. The additional hypothesis proposed here has important implications because it can potentially modify interpretation of community structure and processes involving lianas species, as well as predictions of future scenarios particularly in the context of global climatic change.

Keywords: Acquisitive-strategy. Drought. Foliar-water-uptake. Hydraulic-redistribution. Maximum-root-depth. Multifocal-growth. Tropical-forest. Woody-vine.

1.2 Introduction

Investigating mechanisms able to predict shifts in community assembly due to environmental changes has been one of the most prominent approaches in ecology (Fauset et al. 2012, Sutherland et al. 2013). In this sense, the use of functional traits as proxies to these mechanisms has been a remarkable approach, once traits (i.e., morphological, physiological and phenological organism features; (Violle et al. 2007) describe how species respond to environmental drivers (Bello et al. 2010, Fauset et al. 2012, Bello et al. 2013, Rosado et al. 2016). Despite the advantages of using a trait-based approach (Shipley et al. 2016), a complex and important task is the correct selection of functional traits able to describe how species cope with a given environmental filtering (Rosado et al. 2013, Pivovarovoff et al. 2016, Shipley et al. 2016, Rosado et al. 2016). Additionally, the identification of the correct traits to be measured when identifying how species are responding to a specific environmental driver also depends on the scale and the use of multiple traits to correctly identifying how the organisms may respond (Rosado et al. 2013, Pivovarovoff et al. 2016, Shipley et al. 2016, Rosado et al. 2016).

In this sense, there is an important debate in the literature on the mechanisms underpinning the increases in liana abundance under intensification of seasonality. It has been shown an increase in liana abundance with reductions in mean annual precipitation. This pattern, observed in more than 60 pantropical sites, suggests that this life-form does possess a mechanism that confer the ability to withstand drought (Schnitzer 2005, DeWalt et al. 2010). It has been hypothesized that deep roots is the way lianas can increase their abundance during increases in water deficits. The reasoning behind the idea of deep root patterning would be that lianas use other plants for support and hence do not need to invest in mechanical support. Instead, lianas can invest in stem and root elongation (Schnitzer 2005). Thus, compared to trees, lianas could develop roots to access deep water, allowing them to cope with drought and to be more photosynthetically active in seasonal tropical forests (Schnitzer 2005). This robust hypothesis, however, does not excludes other alternative mechanisms explaining this pattern and, while some studies indicate that deep roots in lianas is an important mechanism to thrive water deficits other studies indicate lacking evidence for deep roots (Powers, 2014, Santiago et al. 2014). We argue that the main problem arises when, even under such controversy, the presence of deep roots in lianas is not measured but assumed as a premise to explain increases in liana's abundance in tropical forests. Hence, we need to recognize that there are often multiple traits that generate the patterns we observe and that they may vary among liana species. We advocate that the main task should determine the relative importance of each mechanism in different

ecological contexts. We revisit this “paradigm” by showing that root depth cannot be considered the main explanation for liana abundance, and other traits and strategies may be equally reliable and plausible for explaining the observed pattern. Although it has been shown that the assumption of deep roots in lianas is not a general rule (Carvalho et al. 2016, Ewers et al. 2015), we aim to strengthen this reasoning by focusing on the evidence from studies challenging this assumption indicating alternative mechanisms behind liana abundance. Our intention is not to debunk the hypothesis that lianas have deep roots (Schnitzer 2005), but to show that there are certainly many mutually compatible causes, that may vary among species, for the relative success of lianas in seasonal tropical forests.

1.3 Lacking of evidence of deep roots in lianas

We investigated how the hypothesis of deeper roots in lianas has been evaluated in literature. Our procedure consisted in initially accessing the paper the first proposed the hypothesis of deep roots (Schnitzer 2005), here after named as Mechanistic Explanation for Liana Global Abundance (MELGA, termed here) and search for the references that mentioned the paper. To date, (September 2017) the paper was cited in 183 studies. Firstly, we checked whether a given paper mentioned the assumption of higher values of maximum root depth of lianas compared to trees. We verified if it was demonstrated that lianas possess higher maximum root depth compared to trees. Secondly, among the papers which mentioned the MELGA, we recorded how many aimed to test assumption. Finally, among those papers which tested MELGA, how many corroborated or rejected it. From the 183 papers, only 58 studies mention the MELGA. From these 58 articles, only two tested the assumption of deep roots but only one of them confirmed that lianas do have deep roots. Our findings showed that even though there is a considerable acceptance of the proposition of MELGA regarding liana root depth, to date, there is a lack of empirical evidence to consider the functional trait "maximum root depth" as the main mechanism to explain the advantage of lianas compared to trees in seasonal tropical forests. Amongst the studies supporting MELGA, only one clearly measured root length, however sampling only a single liana species and without not making comparisons with tree species (Restom and Nepstad 2004). At the same location, another study evaluating soil water uptake patterns of different growth forms (herbs, shrubs, lianas, and trees) found that trees tapped deeper water as compared to lianas (Moreira et al. 2000). Similarly, Andrade et al. (2005) found that their data “do not support the common assumptions that lianas rely primarily on deep soil water”. In this sense, Ewers et al. (2015) have argued that root depth is not a

consistent trait for distinguishing lianas and trees by their ability to tap water from soil due to a lack of empirical support and given that, until now, root depth and ability to uptake soil water has been found to vary depending on region and season rather than growth form.

Moreover, a recent model for predicting root penetration in soil depth showed that for a given soil bulk, a penetrometer resistance > 2.5 MPa imposes a limit on root growth (Gao et al. 2016). Consequently, as a rule, root growth under increasing soil resistance would be restricted to already existing pores (Gao et al. 2016). Thus, deep roots should be a trait more associated with the responses of individual species than a “typical” trait representing a given functional group i.e. lianas (Gao et al. 2016, Pierret et al. 2016). In another study, Chen et al. (2015) compared tree and liana water use in three Chinese tropical forests differing in drought season length and water availability (flood plain forest, FPF; tropical seasonal forest, TSF; karst forest, KF). By comparing the hydrogen isotope composition (deuterium) of water tapped by roots in three soil intervals (0–60 cm, 61–150 cm, 151–250 cm) with the proportion of deuterium in xylem of trees and lianas, they concluded that lianas tend to, proportionally, show more water uptake from deeper soil layers only during the dry season and in two – the driest - forests types (TSF and KF). The authors considered these findings a support for MELGA; however, the estimates of proportional water acquisition from different depths is crude once deuterium isotopes do not provide enough information to estimate three proportions and the problem remains undetermined. Moreover, Chen et al (2015) also assume that the lower pre-dawn water potential (more negative) in trees in comparison for lianas indicates that the surrounding soil for roots of trees has lower moisture, however, such assessment is impaired by the fact that nighttime transpiration is one the mechanisms by which pre-dawn water potential cannot be used to infer of root depth (Dawson et al. 2007; Donovan et al. 2001).

In a large in situ drought-induced experiment, Nepstad et al. (2007) showed a further lack of empirical evidence supporting MELGA by demonstrating that lianas in a tropical rainforest had higher mortality than trees and palms independent of stem size. Similarly, lianas were more drought-prone and showed low abundance in a semiarid climate due to a lower resistance to cavitation, shallow roots and leaf deciduousness (Carvalho et al. 2016). Importantly, not only access to water may be the reason for the liana abundance in seasonal forests. MELGA also considers the importance of enhanced levels of atmospheric CO₂ emissions as an alternative explanation for increased liana abundance. Due to the increment of atmospheric carbon, lianas could experience an increasing of their growth rates, favoring their competitive ability (Schnitzer 2005). However, an experiment comparing growth of lianas and trees under elevated atmospheric CO₂ concentration showed lianas had no advantage over trees, and that both were

equally favored by elevated concentrations of CO₂ (Marvin et al. 2015). Our concern on the single view in favor to deep roots in lianas is reinforced by the fact that the concept of deep roots remains unclear and ill-defined. The lack of appropriate methodology for measuring them limits our ability to further understand the factors affecting deep rooting and its role in plant performance and ecological processes (Pierret et al. 2016). Moreover, defining deep rooting is complicated by the difficulties of measuring maximum root depth and depending on the environment/study site, measuring maximum root depth may be technically impossible, and only a small proportion of studies have successfully used root profiles to detect maximum root depth (Pierret et al. 2016). In this sense, deep rooting is not a trait restricted to a specific group of plants but is observed across a wide variety of plants species and functional groups in different climates (Pierret et al. 2016). Conversely, soil properties such as soil penetrometer resistance and existence of a pore network seem to be significant factors allowing deep rooting to develop irrespective of plant species (Gao et al. 2016). This constraint in measuring and defining deep roots may underlie the evidence that lianas and tree saplings can compete intensely for belowground resources, affecting even aboveground biomass allocation in trees (Martínez-Izquierdo et al. 2016; Schnitzer et al. 2005), suggesting that if lianas always have deeper roots than trees we would expect a coexistence between these two life forms due to niche segregation for water resource belowground (Silvertown et al. 2004).

1.4 Looking ahead: additional functional hypothesis and necessary approaches to test them

Based on the previous studies cited above which indicate other mechanisms than deep roots to increases in liana abundance, we propose alternative hypotheses that should be addressed in future studies interested to explain liana success in seasonal tropical forests. Basically, the increase in liana abundance with drought may be caused by other traits than deep roots; and different combination of traits leading to the same final resultant. However, the identification on how traits are good proxies for fitness and able to describe environmental filtering is part of the foundation stones of plant functional ecology (Shipley et al. 2016) and we argue that MELGA and our additional hypothesis should be tested based on such identification. Such foundation stones are important assumptions that must be evaluated before one can drive conclusions on the functional meaning of traits such as deep roots (Shipley et al. 2016). Thus, for each hypothesis to be tested it is necessary (i) identifying whether deep roots, and additional traits, are proxies for increases in fitness/abundance. This should be done by evaluating

relationship between trait values of co-occurring liana species and their relative abundances to validate a trait (e.g., deep roots) as functional (Rosado et al. 2013; Shipley et al. 2016); (ii) whether such traits vary predictably along an environmental gradient (Shipley et al. 2016). Relationships environment-trait where, from wetter to drier sites for instance, it should be expected increases in trait values of deep roots (e.g., measured by community-averaged trait values; CWM) if they are functional (Shipley et al. 2016).

Following this reasoning, Asner and Martin (2012) reported that lianas show a set of trait values indicating an acquisitive resource syndrome and greater efficiency to use nutrients indicating an advantage, in comparison to trees, along a gradient of increasing irradiance and disturbance, what may be an additional factors leading to increase in liana abundance. Importantly, they evaluated differences in leaf chemical traits between lianas and trees and showed the average water-use efficiency (estimated based on $\delta^{13}\text{C}$) did not differ between lianas and trees. It was also remarkable that differences between lianas and trees was dependent on variation in precipitation and temperature leading to cases where both life-forms show trait convergence (Asner and Martin 2012). This last finding is in line with the fact that comparison between life-forms must also take into account phenology once lianas and deciduous trees may have similar water use strategies (Chen et al. 2017). Contrary to the wide accepted pattern, there are studies where the increases in species richness of lianas either present significant, or non-significant, relationship to decreases in dry season length and increases in mean annual precipitation, where the degree of disturbance is the main factor leading to higher liana abundance (Van Der Heijden & Phillips, 2008, 2009). Such reports reinforce that the search for mechanisms explaining liana abundance is not so simple to only rely on root depth and that testing relationships environment-trait and trait-abundance is essential to validating traits as functional.

1.5 Hydraulic redistribution and multifocal growth

Lianas can have very long stems, sometimes reaching lengths of up to 310 m (Sakai et al. 2002), which can frequently grow both upward to the canopy and downward (Schnitzer et al. 2008). These stems commonly root when touching the ground (Putz 1984), allowing the same individual to be rooted at many points in a landscape (Schnitzer et al. 2008). We hypothesize that this multifocal growing strategy of lianas may be one of the traits providing the ability to cope with drought conditions, by enabling the plant to uptake water and nutrients over a broader area (Tang et al. 2012). Shallow and lateral roots experiencing different patch resource

availability (soil water potential gradient to drive water flow), as observed in lianas, may promote water movement from wet to dry soil through the roots, the so-called hydraulic redistribution (HR) (Burgess and Bleby 2006; Neumann and Cardon 2012) HR is a widespread phenomenon (Neumann & Cardon 2012) that may provide several advantages for plants, such as increasing root life span (Bauerle et al. 2008) and root viability (Burgess et al. 1998), maintenance of leaf water content (Nardini and Pitt 1999), increase in nutrient uptake (Neumann & Cardon, 2012), and promotion of refilling in root-embolized xylem (McCully 1999). To our knowledge, although not measured in lianas, HR has been documented in other functional types (grasses, forbs, shrubs, and trees) and may potentially occur in every species and type of rooting patterns (Neumann & Cardon, 2012) and, should be an important focus of research in lianas (Powers, 2014). Under drought conditions, multifocal growing may benefit lianas in obtaining water and nutrients, allowing them to efficiently redistribute water from different microhabitats as well as store water. Therefore, our testable prediction is that a multifocal growing strategy may make lianas better on exploring soil resources at multiple sites leading to the higher abundance of lianas. Such strategy in turn may be considered an additional trait allowing them to cope with drought periods, as well as contribute to the forest water balance. We advocate that efforts should be made on describing HR (e.g. based on sapflow sensors such as heat ratio method that capture bi-directional fluxes, (Burgess et al. 1998) combined to mapping their spatial distribution to detect multifocal growth strategy. We expect that liana species having more rooting points (multifocal growth strategy) will have a greater magnitude of HR (in terms of frequency, intensity or duration) in response to a rainy event after a drought, and show a higher relative abundance. Once measurements of physiological traits such as sap flow might be time-consuming, register of multifocal growth (as proxy for HR), an additional prediction is that along a gradient of water availability, there will be an increase in the rooting points (multifocal growth).

1.6 Combining trade-offs to describe water use

Although the argument for deep roots in some lianas also comes from their low capacitance in comparison to trees (Chen et al. 2015, Chen et al. 2017, De Guzman et al. 2016), lianas species possess a greater to transport and store water compared to trees (Ewers et al. 2015), what could be an indicative of low investment in deep roots. These xylem traits, however, become a trade-off once lianas become more prone to cavitation/embolism (Chen et al. 2017, De Guzman et al. 2016, Ewers et al. 2015). A recent investigation may provide evidence of an

alternative mechanism to deal with drought, which can be applied to liana species. By comparing trait differences among tree species from three successional stages (early successional, mid-successional, and old-growth), Paz et al. (2015) demonstrated that early- and mid-successional tree species invested more in root depth elongation, while old-growth species were shallow-rooted but had higher storage capacity. This indicates that root depth may be more associated with trade-offs of storage capacity than plant type. Although Paz et al. (2015) did not have measure lianas, this trade-off gives an important insight for lianas' investment in root depth once the trait value can indicate shared relationships among traits for different life-forms (Wright et al. 2004, Reich 2014). Consistent to this possible trade-off (Paz et al. 2015), lianas are the functional group, after succulent plants, with the highest worldwide proportion of parenchyma in the secondary xylem (Morris et al. 2016). This result contradicts the view that deep roots are associated to a low capacitance indicating that deep roots in lianas are not mandatory (Schnitzer 2005, Chen et al. 2015). A second trade-off to explore is related to resistance/resilience to cavitation, which is mediated by wood density. Ogasa et al. (2013) detected a negative correlation between recovery performance in xylem hydraulic conductivity and cavitation resistance. In other words, cavitation resistance was an opposite strategy to xylem hydraulic conductivity recovery in coping with drought. The authors suggested that wood density, which is usually expected to be low in lianas (Ewers et al. 2015), is the trait mediating this trade-off. A low wood density is associated with a higher water/nutrient storage ability in parenchyma of secondary xylem (Ogasa et al. 2013). Additionally, xylem refilling after cavitation is associated with solute release, commonly hydrolized sugars from starch (Bucci et al. 2003), in the lumen of xylem vessels by the contact cells (Tyree et al. 1999); this generates an osmotic gradient allowing water acquisition. Hence, liana stems could have higher amounts of stored solute to promote vessel refilling due to their low wood density. By combining these two trade-offs (root depth and storage capacity or resistance recovery) based on the measurements of such traits, we hypothesize that (i) more abundant lianas could also present shallow roots associated to a higher capacitance conferring a high resilience to embolism/water storage to deal with drought.

1.7 Alternatives functional designs to explain higher abundance in lianas

Hypotheses to explain the higher abundance of lianas are not mutually exclusive once they may be combined due to the concept of alternative functional designs (Marks 2007, Marks and Lechowicz 2006). Based on the concept of hierarchy of traits, different trait arrays (multiple

phenotypes) may lead to the same integrative trait and, therefore, similar responses at whole plant level (Marks 2007, Rosado and de Mattos 2010, Rosado and de Mattos 2017). Different studies have confirmed the importance of evaluating the role of distinct trait combinations to describe response/ecological strategies of species (Kraft et al. 2015, Pivovarov et al. 2016, Rosado and de Mattos 2010, Rosado and de Mattos 2017). In this hierarchy of traits, organ-level traits may be more dependent of phylogeny while whole-plant traits are more responsive to the environment (Marks 2007). Thus, we propose that the reason why lianas thrive in seasonal forests is not an exclusive result of a single trait but different arrays of traits. A strategy that combines traits such as hydraulic redistribution, multifocal growing strategy, drought resilience, and higher water storage capacity may represent a combination of mechanisms that explains the higher abundance of lianas in seasonal forests. For instance, recent finding adds evidence that lianas are not as drought-resistant as previously thought and deep roots are not the only possible water source (Fu et al. 2015). The foliar water uptake (FWU) in lianas was greater than in tree species and higher than soil water uptake in a tropical seasonal forest (Fu et al. 2015). As pointed out by these authors, if lianas are able to access a deeper water supply in soil than are trees, they would require a lower proportional contribution of fog water. In fact, FWU is a widespread phenomenon (Burgess and Dawson 2004; Goldsmith et al. 2013) advocated as an important mechanism for plants confronted with water deficits, as it represents an additional water source for maintaining physiological processes and growth (Eller et al. 2013; Simonin et al. 2009). However, the ability for greater FWU is related to leaf permeability that may also promote greater water loss, and although this may alleviate water stress, species with greater FWU are also more susceptible to drought (Eller et al. 2016). Thus, it seems clear that increases in liana abundance under scenarios of water shortage, due to lianas' ability to cope with environment, may be the result of multiple combinations of functional traits leading to the same final result, that is, alternative functional designs leading to similar positive water balance and increases in abundance. In this case, relationships environment-trait and trait-abundance should not focus only on organ-level traits (more dependent of phylogeny) but on traits at whole-plant level which may be more prone to describe the response of lianas to environment.

1.8 Conclusions

The commonly used hypothesis behind the global patterns of liana abundance (MELGA, Schnitzer 2005) is a valid and important mechanism but it is not the only one because other

findings indicate alternative strategies, even without a deep root system. We proposed a multi-trait approach to access the problem with the complexity it deserves. This has important implications because it may mislead our interpretation of community structure and processes involving lianas species and predictions of future scenarios, especially considering global climatic change. The hypothesis proposed here should, at least, raise further research on the mechanisms driving the success of lianas in tropical forests.

1.9 Acknowledgements

This paper is part of T.A. Amorim' PhD thesis. We thank the team of Plant Ecology Lab (UERJ) for comments and suggestions on this study. TAA was supported by CAPES (88881.135051/2016-01) and BHPR by grants from FAPERJ (E-26/110.985/2013 and E-26/111.208/2014) and Prociencia Scholarship.

Author contributions: T.A.A and B.H.P.R. conceived and designed the research. T.A.A. analyzed the data. T.A.A., A.F.N.F. and B.H.P.R. wrote the manuscript and all authors revised and approved it.

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2 HOW DOES CLIMATIC AND SPATIAL FACTORS INFLUENCE TAXONOMIC AND PHYLOGENETIC DIVERSITY OF CLIMBING PLANTS IN A REGIONAL SCALE?

2.1 Abstract

Climbing plants are one of the most typical plant functional group in tropical forests comprising about 25% of plant species richness in these ecosystems. Despite this higher richness in tropical forests, ecological knowledge relative to patterns of climbing plant diversity and community assembly in regional scale can be considered as “black boxes”. However, the popularization of scientific databases available on internet and the access of scientific literature are contributing to change this scenario, allowing to check the comprehensiveness of ecological theories. The aim of this study was to test the relative contribution of climatic and spatial variables over taxonomic and phylogenetic diversity of climbing plants. We hypothesized that climatic variables could play stronger influence on patterns of alpha and beta taxonomic and phylogenetic diversity. We gathered information about occurrence of climbing plants in 18 Protected Areas located in one of the world biodiversity hotspots (i.e. Atlantic Rainforest) in Rio de Janeiro State, Brazil. We found a higher contribution of spatial variables over taxonomic alpha diversity, while spatial and climatic variables had similar contribution on patterns of phylogenetic diversity. In terms of phylogenetic diversity, we found a stronger contribution of climatic variables than spatial variables over alpha diversity and only spatial variables influencing beta-diversity. Our finds shed light on important issues concerning the climbing plant assembly on regional scale, showing in general terms a coupled effect of niche and neutral process on patterns of climbing plant diversity.

Keywords: Woody-and-herbaceous-vines. Alpha-diversity. Beta-diversity. Atlantic-rainforest. Niche-theory. Neutral theory. Variance-partitioning.

2.2 Introduction

Climbing plants are one of the most typical plant functional group in tropical forests (Schnitzer and Bongers 2002), comprising about 25% of plant species richness (Gentry et al. 1991). Despite the higher species richness in tropical forests, ecological knowledge relative to patterns of climbing plant diversity and community assembly in regional scale can be considered as “black boxes” because only few studies addressed this topic (*e.g.* Gallagher et al. 2011, Durigon et al. 2014, Hu et al. 2010). However, the popularization of scientific databases available on internet and the access of scientific literature may contribute to change this scenario (Kattge et al. 2011).

Gathering scientific information of climbing plant across a given region can give us the tools needed to test and compare the range of current ecological theories and draw inferences about the possible fate of ecological communities concerning the influence of climatic global changing. For example, is known that climatic constraints are considered important drivers of plant diversity across broad scales. They are able to filter species distribution, influencing the local pool of species and the species turnover among sites (de Bello et al. 2013). Moreover, there are a lot of evidence demonstrating a huge contribution of spatial patterns, such as geographic distance across sites, area of a given site and range of altitude harbored within a site on shaping the patterns of plant diversity (Pescador et al. 2015). In this sense, the ability of plant dispersion and site size are the main drivers of species diversity. Hence, the patterns of plant regional diversity would be mainly a result of a balance between the relative contribution of these two drivers: climatic constraints such as mean annual precipitation, mean annual temperature - *i.e.* factors associated to species tolerances/requirements as expected by Niche Theory (Westoby and Wright 2006) and spatial patterns such as site area and distance among sites, more related to the Neutral approach (Hubell 2001).

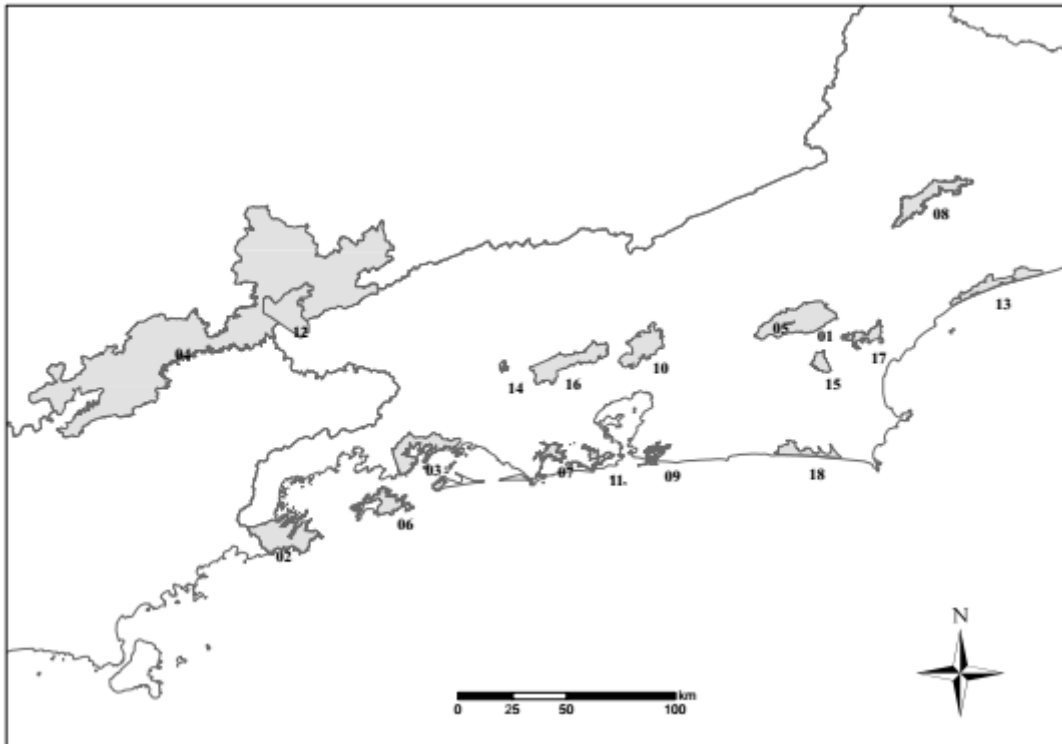
Investigations on the relative contribution of neutral and deterministic processes have been strengthened in last years (Pennington et al. 2006, Pennington and Lavin 2016). The aim of this study was to test the influence of climatic variables (as predicted by Niche Theory) and spatial variables (as predicted by Neutral Theory) on the taxonomic and phylogenetic diversity of climbing plants in a regional scale. We hypothesized climatic constraints will have a stronger contribution to explain the variation in taxonomic and phylogenetic diversity than spatial variables in a regional scale once climatic conditions usually are strong drivers of species distribution.

2.3 Methods

We selected 18 Protected Areas located in Rio de Janeiro State, Brazil (Figure 1). In fact, one of these areas was in the border of Rio de Janeiro State and São Paulo State, with the most part of PA within São Paulo, Serra da Mantiqueira Area of Environmental Preservation (SEMAT). We choose these PA according For each site, we searched for herbaceous and woody climber species occurrence available in literature (supporting information, Table S1) and also using voucher information from two virtual herbaria websites (“*JABOT*”:and “*INCT - Herbário Virtual da Flora e dos Fungos*”: <http://inct.splink.org.br/>). For two following sites: Ilha Grande State Park (PEIGR) and Curió Natural Municipal Park (PNMCU) (see Table 1) we also collected species samples in the field. We updated the taxonomic information, confirming the current species names spelling and looking for synonyms using the *The Plant List* website (www.theplantlist.org). We searched these nomenclatural issues using the package Taxonstand (Cayuela et al. 2012) in R program version 3.4.1, R (R Core Team 2017). The species number per plot was one of the response variables using to test our predictions. Only plants identified to species level were considered in our analysis. We did not consider infra-specific categories.

We gathered a set of climatic information for each site: mean annual temperature (MAT), mean annual precipitation (MAP), mean evapotranspiration (E), mean number of days of precipitation per year (NPY) and mean air relative humidity (RH) considered our climatic variables. For spatial variables, we measured site area (km²), site altitude (m) and its minimum distance from the ocean (MDO) and geographic coordinates of each site (decimal degrees). For geographic coordinates, we centered the latitude and longitude values. We performed principal coordinate neighboring matrices (PCNM) using Euclidean distance of the geographic coordinates of each site. This approach is commonly used to transform (spatial) distances to rectangular data that suitable for constrained ordination or regression (Borcard and Legendre 2002). Then we selected the first and second axis of PCNM because they are normally interpreted and used to represent large-scale patterns (Borcard and Legendre 2002).

Figure 1: Map of Rio de Janeiro State, Brazil, showing the location of the 18 sites.



Legend: 01 = Macaé de Cima Area of Environmental Preservation, 02 = Cairuçu Area of Environmental Preservation, 03 = Marambaia Area of Environmental Preservation, 04 = Serra da Mantiqueira Area of Environmental Preservation, 05 = Paraíso Ecological Station, 06 = Ilha Grande State Park, 07 = Pedra Branca State Park, 08 = Desengano State Park, 09 = Serra da Tiririca State Park, 10 = Serra dos Órgãos National Park, 11 = Tijuca National Park, 12 = Itatiaia National Park, 13 = Restinga de Jurubatiba National Park, 14 = Curió Natural Municipal Park, 15 = Poço das Antas Biological Reserve, 16 = Tinguá Biological Reserve, 17 = União Biological Reserve, 18 = Massambaba Ecological Reserve.

Source: The author, 2018.

Table 1: Values of species richness and phylogenetic indices of 18 sites along Rio de Janeiro State, Brazil.

Protected Area	Acronym	RICH	MPD	NRI	MNTD	NTI
Serra da Tiririca State Park	PESTI	213	247.46	1.10	58.44	-1.16
Serra dos Órgãos National Park	SEROR	164	258.88	-0.78	62.35	-1.01
Cairuçu Area of Environmental Preservation	APACU	151	239.50	1.86	50.93	1.45
Macaé de Cima Area of Environmental Preservation	MAECM	145	252.63	0.14	56.02	0.64
Massambaba Ecological Reserve	RESMA	141	234.19	2.36	55.05	0.91
Itatiaia National Park	PNITA	121	266.59	-1.47	61.19	0.13
Poço das Antas Biological Reserve	REBPA	106	258.69	-0.51	63.58	0.14
Ilha Grande State Park	PEIGR	105	241.35	1.31	61.18	0.57
Tijuca National Park	PARTJ	73	282.77	-2.53	67.60	0.58
Marambaia Area of Environmental Preservation	MARAM	71	229.72	2.11	50.80	2.43
Serra da Mantiqueira Area of Environmental Preservation	SEMAT	68	267.10	-1.09	70.83	0.39
Tinguá Biological Reserve	RBTIN	57	261.60	-0.57	92.71	-1.26
Curió Natural Municipal Park	PNMCU	57	211.19	3.13	57.72	1.94
União Biological Reserve	RBUNI	37	222.61	1.83	68.57	1.67
Restinga de jurubatiba National Park	RESJU	32	214.75	2.16	74.65	1.49
Desengano State Park	PEDES	28	286.66	-1.82	122.19	-1.00
Paraíso Ecological Station	EEPAS	24	251.88	0.10	97.95	0.67
Pedra Branca State Park	PEPEB	13	299.43	-1.57	189.54	-1.60

Legend: The sites are ranked from the highest to lowest species number (RICH). Bold number indicate the highest and lowest value per index amongst the sites. Mean pair-wised phylogenetic distance (MPD), mean nearest taxon phylogenetic distance (MNTD), net relatedness index (NRI) and net taxon index (NTI).

Source: The author, 2018.

2.3.1 Phylogenetic metrics

We constructed a single phylogenetic tree of species found across the sites using the R function “S.PhyloMaker” (Qian and Jin 2016). This function allowed us to construct a phylogenetic tree based on gene sequencing and fossil data available at Zanne et al. (2014) and Qian and Jin (2016). We calculated the following phylogenetic indices: mean pair-wise phylogenetic distance (MPD), mean nearest taxon phylogenetic distance (MNTD), net relatedness index (NRI) and net taxon index (NTI). MPD and NRI express the average phylogenetic distance of the overall phylogeny while, MNTD and NTI express the average distance among terminal (more related) taxa in a phylogeny. We also constructed a matrix of phylogenetic dissimilarity based on MPD. We calculated all metrics using the package *picante* (Kembel et al. 2010).

2.3.2 Data analysis

We applied the log transformation to achieve normal distribution. All variables were scaled into units of standard deviation – z-score – (Legendre and Legendre 2012). We ran a stepwise multiple regression based on the Akaike Information Criterion (AIC) for each group of variables (*i.e.* climatic and spatial) using the package *MASS* (Venables and Ripley 2002). This procedure allowed us to select which set of explanatory variables provided a best linear regression model for each response variable. After variable selection, we executed a variance partitioning among the climatic and spatial variables in order to check which set of variables best explained species richness per site and the indices of phylogenetic alpha diversity calculated. We performed the variance partitioning only when both groups of variables were significant. The variance partitioning analysis was performed using the package *vegan* (Oksanen et al. 2016).

To test how taxonomic and phylogenetic beta-diversity could be influenced by climatic variables, we performed a permutational analysis of variance based on a dissimilarity matrix (PERMANOVA) with 999 permutations. The dissimilarity of species richness was calculated using the Jaccard index, while phylogenetic dissimilarity was calculated based on MPD (see topic phylogenetic analysis). We performed a PERMANOVA of taxonomic diversity and phylogenetic diversity using all climatic variables together. In the case of spatial variables we just ran the PERMANOVA using site altitude and area as explanatory variables. For testing the effect of geographic distance on taxonomic and phylogenetic beta-diversity, we ran a Procrustes analysis. This analysis consists in rotating a configuration of a given ordination in order to find the maximum similarity with another configuration (*i.e.* another ordination). Hence, we fixed the geographic distance (dissimilarity matrix of geographic coordinates) and rotated taxonomic and phylogenetic beta-diversity. Finally, we tested the significance of the

correlation in Procrustes rotation by 999 permutations. We use Nonmetric Multidimensional Scaling (NMDS) in Procrustes analysis.

2.4 Results

2.4.1 Patterns of alpha-diversity

We found 694 climber species along the 18 sites (Table S1). The sites presented different patterns of phylogenetic under and overdispersion. All this information for each site is shown in Table 1. PESTI was the site with highest species richness (213), while PEPEB had respectively the highest values the values of MPD and MNTD (Table 1). In terms of phylogenetic structure, based on NRI, PARTJ showed the highest overdispersion (-2.53) and PNMCU highest underdispersion (3.13). Considering NTI, PEPEB showed the highest overdispersion and (-1.60) MARAM highest underdispersion (2.43).

Species Richness per site had E and NPY as climatic variables selected by stepwise procedure. However, the final model was not significant (Table 2). In terms of spatial variables, species richness was influenced by Altitude, MDO and PCNM1 (R^2 -adjusted = 0.33, $p = 0.03$). MPD had MAT, NPY and RH as explanatory climatic variables (R^2 -adjusted = 0.53, $p < 0.01$) and Altitude as spatial variable (R^2 -adjusted = 0.22, $p < 0.05$). MNTD had MAT, E, NPY and ARM as explanatory climatic variables (R^2 -adjusted = 0.36 $p = 0.04$) while none spatial variable was selected. NRI had MAP, MAT, NPY and RH as explanatory climatic variables (R^2 -adjusted = 0.62, $p = 0.003$). The spatial variable selected was Altitude (R^2 -adjusted = 0.32, $p < 0.001$). NTI was not related to NPY and RH. PCNM2 and Area were the spatial variables related to NTI. Yet, the results were non-significant (R^2 -adjusted = 0.10, $p = 0.18$). The results of each linear multiple regressions are summarized on Table 2 and Table 3.

Table 2: Linear regressions of the remaining climatic variables after the procedure of stepwise regression based on Akaike information Criterion.

Response		R ² -	p ($\alpha \leq$		
Variables	Climatic Variables	adjusted F	DF	0.05)	
RICH	E ^{-ns} , NPY ^{-ns}	0.14	2.4	15	0.12
MPD	MAT ^{-ns} , NPY ^{+*} , RH ^{**}	0.53	7.42	14	0.002
NRI	MAP ^{-ns} , MAT ^{+*} , NPY ^{-ns} , RH ^{+**}	0.62	7.8	13	0.003
MNTD	MAT ^{-*} , E ^{+ns} , NPY ^{+ns} , RH ^{-ns}	0.36	3.43	13	0.04
NTI	NPY ^{-ns} , RH ^{+ns}	0.21	3.24	15	0.07

Legend: RICH = species richness, MPD = mean pairwised phylogenetic distance, NRI = net relatedness index, MNTD = mean nearest taxon phylogenetic distance, NTI = net taxonomic index. E = mean evapotranspiration, NPY = number of days with precipitation per year, MAT = mean annual temperature, MAP = mean annual precipitation, RH = mean air relative humidity, ns = non-significant, * ≤ 0.05 , ** ≤ 0.01 , + = positive relation between explanatory and response variable, - = negative relation between explanatory and response variable.

Source: The author, 2018.

Table 3: Linear regressions of the remaining spatial variables after the procedure of stepwise regression based on Akaike information Criterion.

Response Variables	Spatial Variables	R ² - adjusted F	DF	p ($\alpha \leq 0.05$)	
RICH	PCNM1 ^{-ns} , Altitude ^{+*} , MDO ^{-**}	0.33	3.80	14	0.03
MPD	Altitude ^{+*}	0.22	5.71	16	0.03
NRI	Altitude ^{-*}	0.32	9.11	16	<0.001
MNTD	MDO ^{+ns}	0.08	2.40	16	0.14
NTI	PCNM2 ^{-ns} , Area ^{-ns}	0.10	1.94	15	0.18

Legend: RICH = species richness, MPD = mean pairwise phylogenetic distance, NRI = net relatedness index, MDO = minimum distance of the ocean, MNTD = mean nearest taxon phylogenetic distance, NTI = net taxonomic index. PCNM1 = scores of the first axis of principal neighboring matrices ordination, PCNM2 = scores of the second axis of principal coordinate neighboring matrices ordination, MDO = minimum distance from the ocean, ns = non-significant, * ≤ 0.05 , + = positive relation between explanatory and response variable, - = negative relation between explanatory and response variable.

Source: The author, 2018.

In variance partitioning, climatic variables had a stronger effect than spatial variables on MPD and NRI. The model including climatic plus spatial variables predicted 67 % of the variation across sites for MPD and 66 % for NRI (Table 4, Figures 2 and 3). The variance partitioning showed a non-significant effect of the spatial patterns when the effect of climatic variables was controlled.

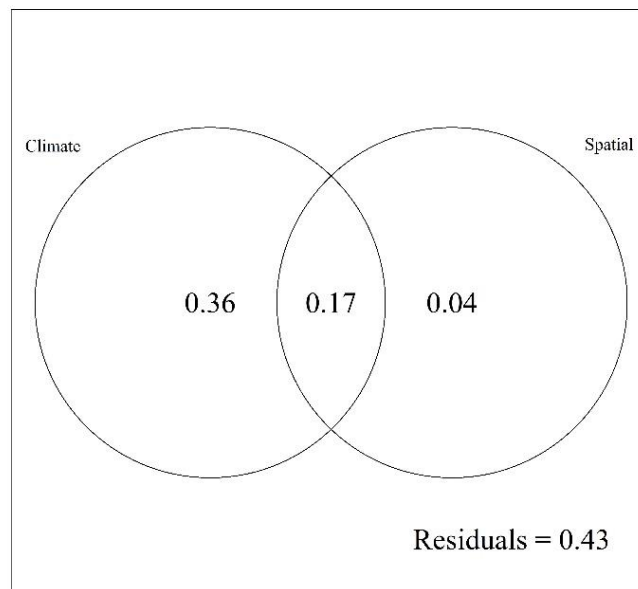
Table 4: Variance partitioning analysis of the 18 sites along Rio de Janeiro State, Brazil.

Response variable	C+S				C:S				S:C			
	R ² -adjusted	F	DF	p ($\alpha \leq 0.05$)	R ² -adjusted	F	DF	p ($\alpha \leq 0.05$)	R ² -adjusted	F	DF	p ($\alpha \leq 0.05$)
MPD	0.57	6.71	4	0.003	0.35	5.45	3	0.02	0.04	0.06	1	0.14
NRI	0.66	7.7	5	<0.001	0.34	5.05	4	0.01	0.05	2.87	1	0.13

Legend: Here are shown the variance explained by climatic and spatial variables together (C+S), the variance explained by environmental variables after controlling the effect of spatial variables (C:S) and the variance explained by spatial variables after controlling the effect of environmental variables (S:C). Response variables: MPD - mean pair-wised phylogenetic distance, distance, NRI - net relatedness index.

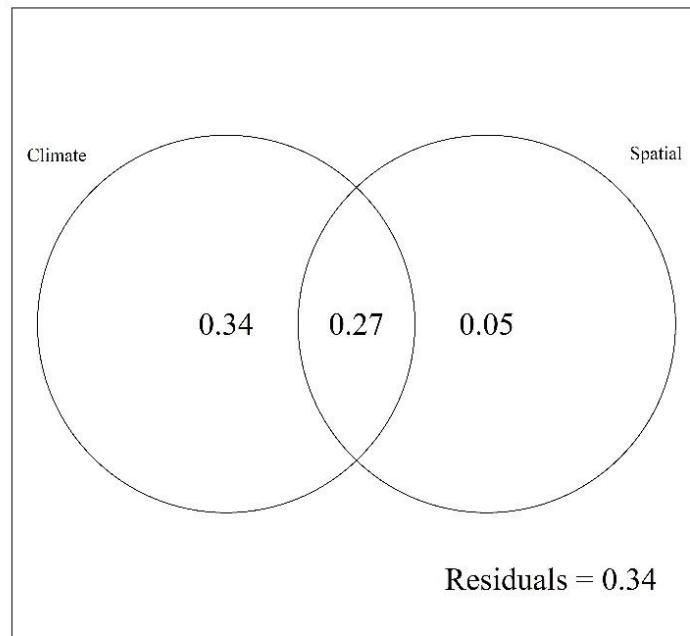
Source: The author, 2018.

Figure 2: Venn Diagram showing the relative contribution of the climatic and spatial variables over mean pair-wised phylogenetic distance (MPD). Climatic + Spatial variables = 0.57.



Source: The author, 2018.

Figure 3: Venn Diagram showing the relative contribution of the climatic and spatial variables over net relatedness index (NRI). Climatic + Spatial variables = 0.66.

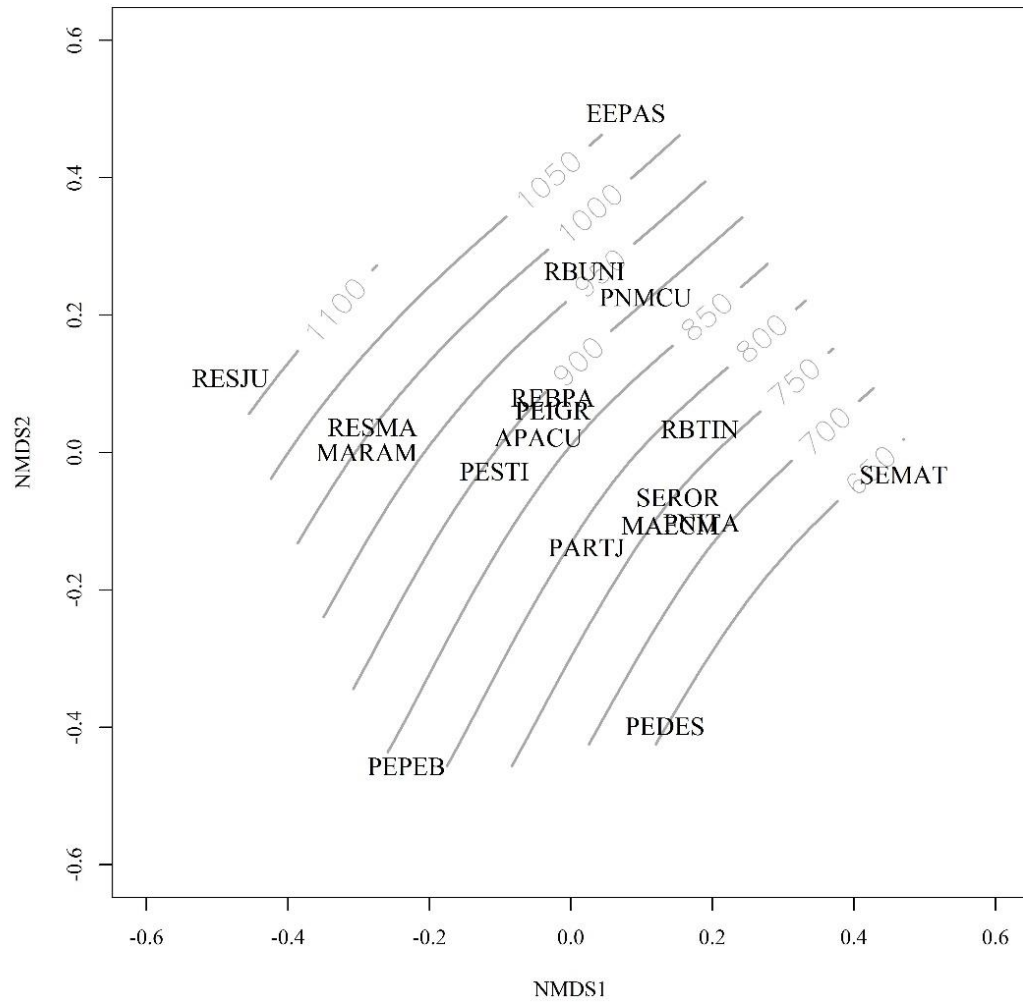


Source: The author, 2018.

2.4.2 Patterns of beta-diversity

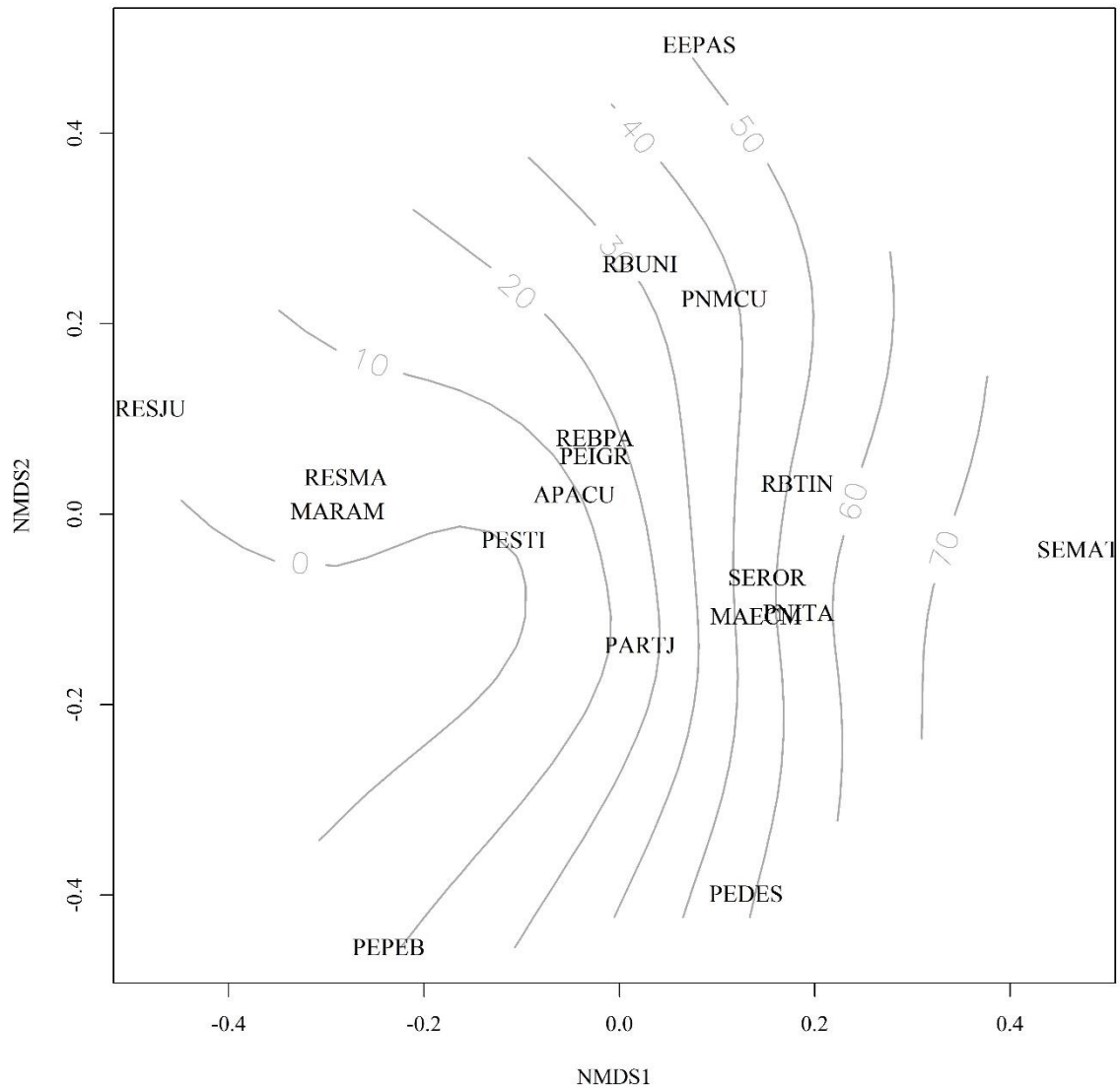
The PERMANOVA showed significant effect of only for E over taxonomic beta-diversity ($R^2 = 0.09$, $DF = 1$, $p = 0.02$, Figure 4) and a marginally significant effect of ARM ($R^2 = 0.08$, $DF = 1$, $p = 0.06$, Table 5). Altitude and Area did not affect the patterns of taxonomic beta diversity across the sites. In terms of phylogenetic diversity none of the variables were related to the patterns of phylogenetic diversity (Table 6). The results of Procrustes rotations showed a non-significant relationships between taxonomic beta-diversity and geographic distance across the sites ($r = 0.14$, $p = 0.93$). Similarly, phylogenetic beta-diversity was not related to geographic distance across the sites ($r = 0.12$, $p = 0.74$).

Figure 4: Nonmetric Multidimensional Scaling (NMDS) based on Jaccard index showing the patterns taxonomic similarity across the 18 sites in Rio de Janeiro State, Brazil. The grey lines are the values of mean evapotranspiration (mm). Stress = 0.15.



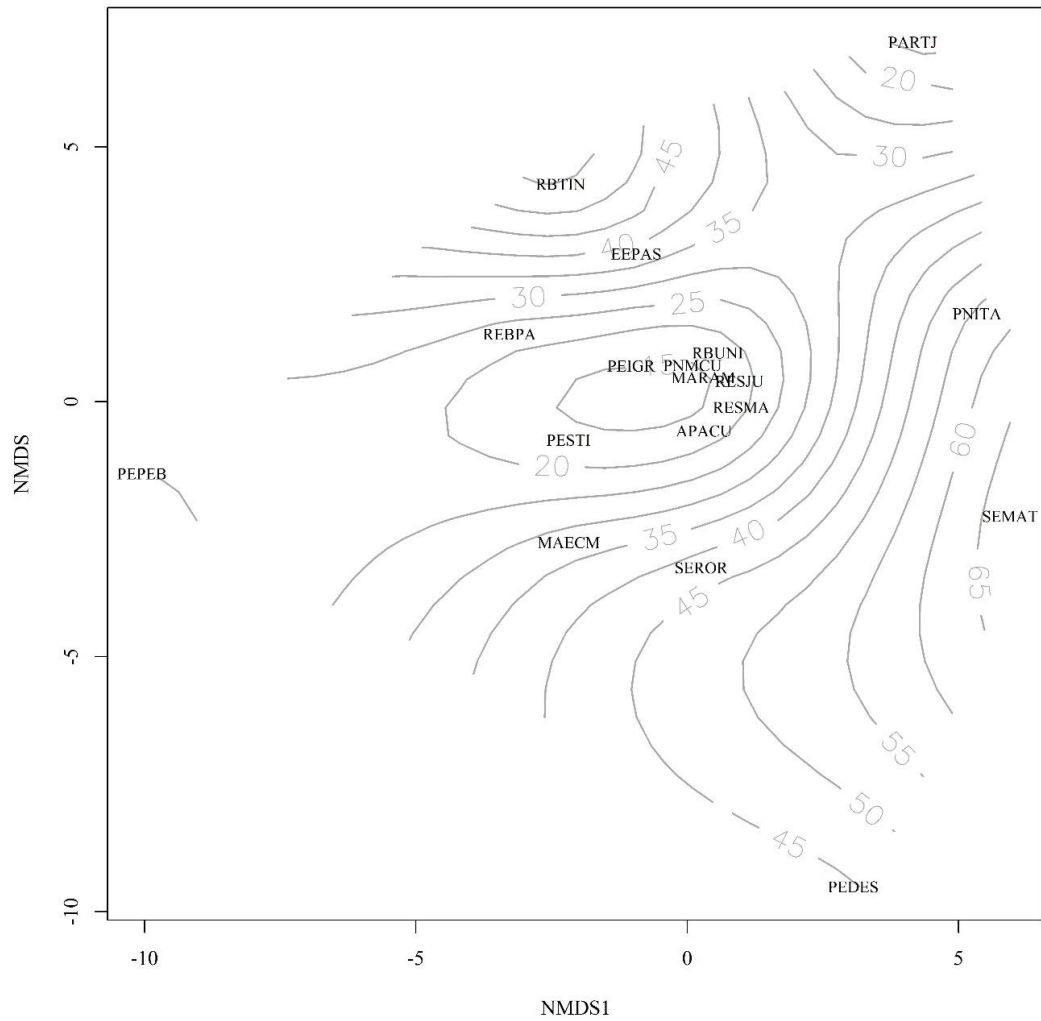
Source: The author, 2018.

Figure 5: Nonmetric Multidimensional Scaling (NMDS) based on Jaccard index showing the patterns taxonomic similarity across the 18 sites in Rio de Janeiro State, Brazil. The grey lines are the values of minimum distance from the ocean (km). Stress = 0.15.



Source: The author, 2018.

Figure 6: Nonmetric Multidimensional Scaling (NMDS) using phylogenetic beta diversity index based on mean phylogenetic pairwise distance (β -MPD). Here are shown the patterns phylogenetic similarity across the 18 sites in Rio de Janeiro State, Brazil. The grey lines indicates the values of minimum distance from the ocean (km). Stress = 0.18



Source: The author, 2018.

Table 5: Results of the permutational analysis of variance based on dissimilarity matrix (PERMANOVA) of involving climatic and spatial variables and the taxonomic beta-diversity.

Climatic									
Variables	DF	F	R ²	Pr(>F)	Spatial Variables	DF	F	R ²	Pr(>F)
RH	1	1.33	0.08	0.06	Altitude	1	0.91	0.05	0.67
E	1	1.52	0.09	0.02	Area	1	0.73	0.04	0.922
MAP	1	1.01	0.06	0.42	MDO	1	1.40	0.08	0.03
MAT	1	0.88	0.05	0.72	PCNM1	1	0.80	0.05	0.85
NPY	1	0.94	0.05	0.57	PCNM2	1	0.76	0.05	0.87

Legend: Significant results are bold. Mean annual temperature (MAT), mean annual precipitation (MAP), mean evapotranspiration (E), mean number of days of precipitation per year (NPY) and mean air relative moisture (RH), minimum distance of ocean (MDO, km). Number of permutations: 999

Source: The author, 2018.

Table 6: Results of the permutational analysis of variance based on dissimilarity matrix (PERMANOVA) of involving climatic and spatial variables and the phylogenetic beta-diversity.

Climatic									
Variables	DF	F	R ²	Pr(>F)	Spatial Variables	DF	F	R ²	Pr(>F)
RH	1	0.98	0.06	0.62	Altitude	1	1.03	0.06	0.23
EE	1	1.05	0.06	0.21	Area	1	1.02	0.06	0.30
MAP	1	0.94	0.06	0.97	MDO	1	1.08	0.06	0.01
MAT	1	1.00	0.06	0.52	PCNM1	1	1.01	0.06	0.30
NPY	1	0.93	0.06	0.87	PCNM2	1	0.93	0.05	0.94

Legend: Mean annual temperature (MAT), mean annual precipitation (MAP), mean evapotranspiration (E), mean number of days of precipitation per year (NPY) and mean air relative moisture (ARM). Number of permutations: 999.

Source: The author, 2018.

2.5 Discussion

2.5.1 Patterns of alpha-diversity

This study was the most comprehensive effort to gather information concerning climbing plants species in Brazilian territory. We found 694 climbing species across the 18 PA along Rio de Janeiro State. A study harboring 34 countries worldwide found 1092 climbing species (Gallagher et al. 2012). From these 1092, 490 species were located in Brazilian territory (Gallagher et al. 2012). However, none of studies cited by Gallagher et al. (2012) had sampling sites in Rio de Janeiro State. Yet, our study shared 167 species with Gallagher et al. (2012). It is about a quarter of species that we found in our study and around 15% of species richness found in Gallagher et al. (2012). Thus, our results highlight the importance of Atlantic Rain forest as a diversity hotspot (Mittermeier et al. 2005), showing that even these critically endangered area still possess a very high species diversity.

Our results revealed that species richness varied regardless of the influence of climate while spatial structure significantly influenced the species richness. This is different from what was found to vascular epiphytes in the same sites (Pantaleão et al. not published). Epiphytic richness was positively related to mean annual precipitation and negatively to mean annual temperature and non-related to spatial structure. Apparently, the differences of water availability across the sites did not influence their capacity to harbor climbing plant species. However, for larger geographic scales in tropical forests climatic variables such as dry season length (*i.e.* number of months of dry season) and mean annual precipitation can play respectively, a strong direct and negative effect and indirect and positive effect (Heijden and Phillips 2009, Hu et al. 2010). Moreover, the study of Heijden and Phillips (2009) encompassed a broader area in central and northwest region in South America and the south region of Central America.

Yet, contrary to our hypothesis, the spatial variables selected Altitude and MDO influenced the species richness. Atlantic forest that possesses one of the highest levels spatial heterogeneity (Scarano 2002), creating a patchy environment and highly variable in terms of resource. It can permit species with many different requirements to coexist in relatively small areas. On the other hand, as we get closer to the ocean we usually have a flat landscape with more sand, salt concentration and low fertility soils. The low fertility, salty and more flat topography may act reducing the species richness

As we hypothesized, all the results showed a stronger contribution of the climate on phylogenetic diversity than spatial variables. Thus, the sites with higher phylogenetic diversity were those with lower temperature, drier air but many days of precipitation which are conditions

usually found on seasonal forests (Tonhasca-Junior 2005). Additionally, it is known that seasonal forests are the tropical sites expected to possess the highest species abundance and basal area of lianas (Schnitzer 2005, DeWalt et al. 2010). Consequently, our results add evidence that seasonal forests can be considered as hotspots of climbing plant diversity within tropical forests. Moreover, seasonal forest may be an important pool of phylogenetic diversity harboring a higher amount of phylogenetic lineages. Our predictions however, should be considered with caution, once we had a limited number of sites located in seasonal forests in our survey (PEDES). Seasonal forests in Rio de Janeiro State are the most endangered forest type of the State, having only few and small fragments (Fidalgo et al. 2007). Our results highlight the importance of conservation of seasonal forests for the maintenance of diversity of phylogenetic lineages of climbing plants.

2.5.2 Patterns of beta-diversity

The results of taxonomic beta-diversity showed that climatic and spatial patterns had similar contribution for the species turnover across sites. Climatic variables were represented by E explaining about 9% of the turnover while spatial structure was represented by MDO, corresponding to 8% of the variation. Our results shed light on important theoretical issues concerning patterns of climbing plant diversity across distinct geographic scales. Although the number of species varied independently of climatic and spatial variables, the climatic variable E was able to influence the turnover of species along the sites. This may indicate that water availability, especially air humidity, may be an important mechanism in species filtering across fragments. In fact, climber species are known to use the atmospheric water as an alternative water source in a proportion up to 41% greater than the trees (Fu et al. 2016). Thus, sites with the highest floristic similarity may have in common the liana species with similar ability to use atmospheric water.

Considering the spatial variables, our results show that similarity was ordered according MDO (Figure 5). An exception to this rule is the PEIGR, which despite being an island, was in the middle of the ordination, indicating a flora with species that occur in places both near and more distant to the ocean. This discrepancy can be explained by the high heterogeneity among habitats, ranging from so-called marginal ecosystems such as *restingas* (sandy coastal lowland ecosystems, Assis et al. 2011), mangroves, tropical lowland forests to montane forests at about 1000 m.a.s.l. All of them, in general lines have distinct water availability. Yet regarding the gradient of proximity to the ocean, SEMAT was most distant (Figure 5) and consisted of one of the areas with the highest floristic distinction among the sites. This may reinforce the

importance of this gradient of proximity to the ocean. Moreover, it can indicate that, at least in terms of taxonomic diversity, Rio de Janeiro has a relatively distinct flora of climbing plants when compared with neighboring regions. In addition, it should be noted that this gradient of proximity to the ocean may be the factor that generated the E gradient since in general terms the areas closest to the ocean were the ones with the highest E.

Contrary to our hypothesis, phylogenetic beta-diversity had no relationship with climatic variables while spatial variables significantly explained around 6% of the beta-phylogenetic diversity. Similarly, to the case of beta-taxonomic diversity, again MDO was the predictor variable. We advocated that the reasons for these patterns are the same for what we showed to taxonomic beta-diversity. Despite their similar explanatory mechanisms, phylogenetic and taxonomic beta-diversity were not related each other (data not shown).

We found the most part of the sites mainly located in *restinga* areas were very similar to each other, forming a cluster in the ordination (Figure 6. *Restingas* are considered the youngest ecosystems in terms of their geological origin, about 6500 years ago (Roncarati and Menezes 2005). Hence, the arrival of species in this ecosystem occurred recently in the geological period and their species composition is expecting to be a subset of the neighbor forest (see Conde et al. and Menezes and Araujo 2005). However, in terms of phylogenetic diversity of climbing plants, *restingas* shelter particular evolutionary lineages, suggesting a rapid diversification of climbing plants in such ecosystem. Climbing habit is considered a key evolutionary innovation that permitted some plants to colonize “new environments” (Gianoli 2004). For example, climbing taxa are more diverse than its respective sister group (Gianoli 2004). Restingas are ecosystems subject harsh environmental conditions such high variation in temperature day long, high solar incidence, low fertility and salty soils. On the other hand, climbing plants have many functional strategies which in turn gave to this functional group success to colonize and hence success to diversify. When can elicit the combination of following strategies common in climbing plants which may have triggered the evolutionary diversification in *restingas*. Firstly, trait strategies linked to deal with drought: (i) high amount of parenchyma for water storage (Morris et al. 2016), (ii) high rates of water uptake from air moisture (Fu et al. 2016) and (iii) multifocal growth strategy (see chapter one). Secondly, traits linked to higher photosynthetic activity and foraging: (i) low SLA, (ii) higher concentration on foliar nitrogen, (iii) high concentration of foliar phosphorus and low root specific length (Asner and Martin 2012, Collins et al. 2016). These set of traits may have paved the way of phylogenetic diversification of climbing plants in *restingas*.

2.6 Conclusions

Here, we demonstrated that the information available on online scientific repositories provide important source of primary information allowing us to organize the most comprehensive survey of climbing plants in Brazil with 694 species. Moreover, this survey permitted allowed us to test important theories, which are attempts to explain how ecological communities are assembled. We found that in terms of taxonomic diversity spatial variables had a more important role over patterns of alpha diversity, while both climatic and spatial variables had equivalent strength to predict patterns taxonomic beta-diversity. Furthermore, we found that climatic variables were strong predictors of phylogenetic alpha diversity when compared to spatial variables, which in turn were not significant after variance partitioning. Conversely, phylogenetic beta-diversity was only related to spatial variables. Our finds shed light on important issues concerning the climbing plant assembly on regional scale, showing in general terms a coupled effect of niche and neutral process on patterns on climbing plant diversity. Finally, we highlight that our findings can provide a support for adopting practices of managing and conservation of the ecosystems within Atlantic domain.

2.7 References

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Table S1: List of species of vines found along the 18 Protected Areas in Rio de Janeiro State, Brazil. Species are ranked according its frequency across the 18 sites. Frequency refers the total times a given species was found along the Protected Areas. Freq = Frequency.

Family	Species	Freq
Fabaceae	<i>Dalbergia frutescens</i> (Vell.) Britton	13
Acanthaceae	<i>Mendoncia coccinea</i> Ruiz and Pav.	12
Malpighiaceae	<i>Niedenzuella acutifolia</i> (Cav.) W.R.Anderson	11
Bignoniaceae	<i>Lundia corymbifera</i> (Vahl) Sandwith	10
Dilleniaceae	<i>Davilla rugosa</i> Poir.	10
Fabaceae	<i>Senegalia martiusiana</i> (Steud.) Seigler and Ebinger	10
Sapindaceae	<i>Paullinia meliifolia</i> Juss.	10
Violaceae	<i>Anchietea pyrifolia</i> (Mart.) G.Don	10
Fabaceae	<i>Machaerium oblongifolium</i> Vogel	9
Malpighiaceae	<i>Heteropterys nitida</i> DC.	9
Menispermaceae	<i>Chondrodendron platyphyllum</i> (A.St.-Hil.) Miers	9
Rubiaceae	<i>Emmeorhiza umbellata</i> (Spreng.) K.Schum.	9
Fabaceae	<i>Bauhinia microstachya</i> (Raddi) J.F.Macbr.	8
Fabaceae	<i>Piptadenia adiantoides</i> (Spreng.) J.F.Macbr.	8
Malpighiaceae	<i>Tetrapterys phlomoides</i> (Spreng.) Nied.	8
Sapindaceae	<i>Paullinia carpopoda</i> Cambess.	8
Sapindaceae	<i>Serjania caracasana</i> (Jacq.) Willd.	8
Sapindaceae	<i>Serjania communis</i> Cambess.	8
Smilacaceae	<i>Smilax quinquenervia</i> Vell.	8
Lygodiaceae	<i>Lygodium volubile</i> Sw.	7
Malpighiaceae	<i>Heteropterys coleoptera</i> A.Juss.	7
Malpighiaceae	<i>Heteropterys patens</i> (Griseb.) A.Juss.	7
Passifloraceae	<i>Passiflora alata</i> Curtis	7
Passifloraceae	<i>Passiflora organensis</i> Gardner	7
Rosaceae	<i>Rubus rosifolius</i> Sm.	7
Smilacaceae	<i>Smilax elastica</i> Griseb.	7
Smilacaceae	<i>Smilax rufescens</i> Griseb.	7
Trigoniaceae	<i>Trigonia nivea</i> Cambess.	7

Apocynaceae	<i>Forsteronia pilosa</i> (Vell.) Müll.Arg.	6
Apocynaceae	<i>Oxypetalum banksii</i> R.Br. ex Schult.	6
Begoniaceae	<i>Begonia convolvulacea</i> (Klotzsch) A.DC.	6
Begoniaceae	<i>Begonia fruticosa</i> (Klotzsch) A.DC.	6
Bignoniaceae	<i>Amphilophium crucigerum</i> (L.) L.G.Lohmann	6
Convolvulaceae	<i>Ipomoea philomega</i> (Vell.) House	6
Cucurbitaceae	<i>Melothria cucumis</i> Vell.	6
Cucurbitaceae	<i>Wilbrandia verticillata</i> (Vell.) Cogn.	6
Fabaceae	<i>Machaerium cantarellianum</i> Hoehne	6
Malpighiaceae	<i>Heteropterys intermedia</i> (A.Juss.) Griseb.	6
Malpighiaceae	<i>Stigmaphyllon lalandianum</i> A.Juss.	6
Marcgraviaceae	<i>Schwartzia brasiliensis</i> (Choisy) Bedell ex Gir.-Cañas	6
Menispermaceae	<i>Cissampelos andromorpha</i> DC.	6
Passifloraceae	<i>Passiflora amethystina</i> J.C.Mikan	6
Sapindaceae	<i>Paullinia micrantha</i> Cambess.	6
Sapindaceae	<i>Paullinia racemosa</i> Wawra	6
Apocynaceae	<i>Forsteronia leptocarpa</i> (Hook. and Arn.) A.DC.	5
Bignoniaceae	<i>Anemopaegma chamberlaynii</i> (Sims) Bureau and K.Schum.	5
Bignoniaceae	<i>Dolichandra unguis-cati</i> (L.) L.G.Lohmann	5
Bignoniaceae	<i>Fridericia leucopogon</i> (Cham.) L.G.Lohmann	5
Bignoniaceae	<i>Mansoa difficilis</i> (Cham.) Bureau and K.Schum.	5
Bignoniaceae	<i>Stizophyllum perforatum</i> (Cham.) Miers	5
Celastraceae	<i>Salacia elliptica</i> (Mart.) G.Don	5
Celastraceae	<i>Tontelea miersii</i> (Peyr.) A.C. Sm.	5
Asteraceae	<i>Mikania glomerata</i> Spreng.	5
Asteraceae	<i>Mikania hirsutissima</i> Baker	5
Asteraceae	<i>Mikania micrantha</i> Kunth	5
Convolvulaceae	<i>Ipomoea ramosissima</i> (Poir.) Choisy	5
Convolvulaceae	<i>Jacquemontia holosericea</i> (Weinm.) O'Donnell	5
Cucurbitaceae	<i>Cayaponia tayuya</i> (Vell.) Cogn.	5
Cucurbitaceae	<i>Momordica charantia</i> L.	5
Euphorbiaceae	<i>Tragia volubilis</i> L.	5
Fabaceae	<i>Centrosema virginianum</i> (L.) Benth.	5

Fabaceae	<i>Machaerium aculeatum</i> Raddi	5
Fabaceae	<i>Machaerium debile</i> (Vell.) Stellfeld	5
Fabaceae	<i>Machaerium lanceolatum</i> (Vell.) J.F.Macbr.	5
Fabaceae	<i>Machaerium uncinatum</i> (Vell.) Benth.	5
Fabaceae	<i>Mucuna urens</i> (L.) Medik.	5
Fabaceae	<i>Senegalia lacerans</i> (Benth.) Seigler and Ebinger	5
Fabaceae	<i>Senegalia lowei</i> (L. Rico) Seigler and Ebinger	5
Fabaceae	<i>Senegalia tenuifolia</i> (L.) Britton and Rose	5
Menispermaceae	<i>Odontocarya vitis</i> Miers	5
Passifloraceae	<i>Passiflora edulis</i> Sims	5
Phyllanthaceae	<i>Phyllanthus submarginatus</i> Müll.Arg.	5
Phytolaccaceae	<i>Seguieria americana</i> L.	5
Poaceae	<i>Aulonemia amplissima</i> (Nees) McClure	5
Poaceae	<i>Guadua tagoara</i> (Nees) Kunth	5
Sapindaceae	<i>Paullinia coriacea</i> Casar.	5
Sapindaceae	<i>Paullinia trigonia</i> Vell.	5
Smilacaceae	<i>Smilax spicata</i> Vell.	5
Acanthaceae	<i>Mendoncia puberula</i> Mart.	4
Acanthaceae	<i>Thunbergia alata</i> Bojer ex Sims	4
Amaranthaceae	<i>Hebanthe eriantha</i> (Poir.) Pedersen	4
Amaranthaceae	<i>Hebanthe pulverulenta</i> Mart.	4
Apocynaceae	<i>Condylocarpon isthmicum</i> (Vell.) A.DC.	4
Apocynaceae	<i>Mandevilla funiformis</i> (Vell.) K.Schum.	4
Apocynaceae	<i>Mandevilla guanabarica</i> Casar. ex M.F.Sales, Kin.-Gouv. and A.O.Simões	4
Apocynaceae	<i>Oxypetalum alpinum</i> (Vell.) Fontella and E.A.Schwarz	4
Apocynaceae	<i>Oxypetalum pedicellatum</i> Decne.	4
Begoniaceae	<i>Begonia integerrima</i> Spreng.	4
Bignoniaceae	<i>Adenocalymma comosum</i> (Cham.) DC.	4
Bignoniaceae	<i>Adenocalymma marginatum</i> (Cham.) DC.	4
Bignoniaceae	<i>Adenocalymma ternatum</i> (Vell.) Mello ex Bureau and K.Schum.	4
Bignoniaceae	<i>Fridericia conjugata</i> (Vell.) L.G.Lohmann	4
Bignoniaceae	<i>Fridericia rego</i> (Vell.) L.G.Lohmann	4

Cactaceae	<i>Pereskia aculeata</i> Mill.	4
Celastraceae	<i>Elachyptera micrantha</i> (Cambess.) A.C.Sm.	4
Asteraceae	<i>Baccharis inamoena</i> Gardner	4
Asteraceae	<i>Mikania acuminata</i> DC.	4
Asteraceae	<i>Mikania trinervis</i> Hook. and Arn.	4
Asteraceae	<i>Piptocarpha quadrangularis</i> (Vell.) Baker	4
Convolvulaceae	<i>Ipomoea cairica</i> (L.) Sweet	4
Convolvulaceae	<i>Ipomoea imperati</i> (Vahl) Griseb.	4
Convolvulaceae	<i>Ipomoea pes-caprae</i> (L.) R. Br.	4
Convolvulaceae	<i>Merremia dissecta</i> (Jacq.) Hallier f.	4
Convolvulaceae	<i>Merremia macrocalyx</i> (Ruiz and Pav.) O'Donell	4
Cucurbitaceae	<i>Apodanthera argentea</i> Cogn.	4
Cucurbitaceae	<i>Cayaponia cabocla</i> (Vell.) Mart.	4
Cucurbitaceae	<i>Cayaponia martiana</i> (Cogn.) Cogn.	4
Cucurbitaceae	<i>Cayaponia pilosa</i> (Vell.) Cogn.	4
Cucurbitaceae	<i>Melothria pendula</i> L.	4
Dioscoreaceae	<i>Dioscorea ovata</i> Vell.	4
Euphorbiaceae	<i>Dalechampia ficifolia</i> Lam.	4
Fabaceae	<i>Canavalia parviflora</i> Benth.	4
Fabaceae	<i>Canavalia rosea</i> (Sw.) DC.	4
Fabaceae	<i>Collaea speciosa</i> (Loisel.) DC.	4
Fabaceae	<i>Dalbergia ecastaphyllum</i> (L.) Taub.	4
Fabaceae	<i>Dioclea wilsonii</i> Standl.	4
Fabaceae	<i>Machaerium brasiliense</i> Vogel	4
Fabaceae	<i>Machaerium declinatum</i> (Vell.) Stellfeld	4
Fabaceae	<i>Machaerium reticulatum</i> Pers.	4
Fabaceae	<i>Phanera angulosa</i> (Vogel) Vaz	4
Fabaceae	<i>Phanera radiata</i> (Vell.) Vaz	4
Icacinaceae	<i>Leretia cordata</i> Vell.	4
Loganiaceae	<i>Strychnos acuta</i> Progel	4
Loganiaceae	<i>Strychnos trinervis</i> (Vell.) Mart.	4
Malpighiaceae	<i>Heteropterys chrysophylla</i> (Lam.) Kunth	4
Malpighiaceae	<i>Heteropterys sericea</i> (Cav.) A.Juss.	4

Malpighiaceae	<i>Niedenzuella poeppigiana</i> (A.Juss.) W.R.Anderson	4
Malpighiaceae	<i>Tetrapteryx mucronata</i> Cav.	4
Marcgraviaceae	<i>Marcgravia polyantha</i> Delpino	4
Onagraceae	<i>Fuchsia regia</i> (Vand. ex Vell.) Munz	4
Passifloraceae	<i>Passiflora miersii</i> Mart.	4
Passifloraceae	<i>Passiflora mucronata</i> Lam.	4
Poaceae	<i>Chusquea meyeriana</i> Rupr. ex Döll	4
Rhamnaceae	<i>Reissekia smilacina</i> (Sm.) Steud.	4
Rubiaceae	<i>Chiococca alba</i> (L.) Hitchc.	4
Rubiaceae	<i>Manettia mitis</i> (Vell.) K.Schum.	4
Sapindaceae	<i>Serjania clematidifolia</i> Cambess.	4
Sapindaceae	<i>Serjania cuspidata</i> Cambess.	4
Sapindaceae	<i>Serjania elegans</i> Cambess.	4
Sapindaceae	<i>Serjania lethalis</i> A. St.-Hil.	4
Sapindaceae	<i>Urvillea rufescens</i> Cambess.	4
Vitaceae	<i>Cissus verticillata</i> (L.) Nicolson and C.E.Jarvis	4
Apocynaceae	<i>Condylocarpon intermedium</i> Müll.Arg.	3
Apocynaceae	<i>Forsteronia refracta</i> Müll.Arg.	3
Apocynaceae	<i>Mandevilla atrovioleacea</i> (Stadelm.) Woodson	3
Apocynaceae	<i>Mandevilla hirsuta</i> (Rich.) K.Schum.	3
Apocynaceae	<i>Mandevilla pendula</i> (Ule) Woodson	3
Apocynaceae	<i>Orthosia scoparia</i> (Nutt.) Liede and Meve	3
Apocynaceae	<i>Peltastes peltatus</i> (Vell.) Woodson	3
Apocynaceae	<i>Peplonia asteria</i> (Vell.) Fontella and E.A. Schwarz	3
Apocynaceae	<i>Peplonia axillaris</i> (Vell.) Fontella and Rapini	3
Aristolochiaceae	<i>Aristolochia cymbifera</i> Mart.	3
Bignoniaceae	<i>Adenocalymma bracteatum</i> (Cham.) DC.	3
Bignoniaceae	<i>Adenocalymma trifoliatum</i> (Vell.) R.C.Laroche	3
Bignoniaceae	<i>Bignonia binata</i> Thunb.	3
Bignoniaceae	<i>Lundia damazii</i> C.DC.	3
Bignoniaceae	<i>Mansoa hymenaea</i> (DC.) A.H.Gentry	3
Bignoniaceae	<i>Pyrostegia venusta</i> (Ker Gawl.) Miers	3
Bignoniaceae	<i>Tanaecium selloi</i> (Spreng.) L.G.Lohmann	3

Boraginaceae	<i>Tournefortia breviflora</i> DC.	3
Boraginaceae	<i>Tournefortia volubilis</i> L.	3
Celastraceae	<i>Hippocratea volubilis</i> L.	3
Commelinaceae	<i>Dichorisandra hexandra</i> (Aubl.) Standl.	3
Asteraceae	<i>Calea pinnatifida</i> (R.Br.) Banks ex Steud.	3
Asteraceae	<i>Dendrophorbium fruticosum</i> (Vell.) C.Jeffrey	3
Asteraceae	<i>Mikania cordifolia</i> (L.f.) Willd.	3
Asteraceae	<i>Mutisia speciosa</i> Aiton ex Hook.	3
Asteraceae	<i>Piptocarpha leprosa</i> (Less.) Baker	3
Convolvulaceae	<i>Merremia umbellata</i> (L.) Hallier f.	3
Cucurbitaceae	<i>Cayaponia trilobata</i> Cogn.	3
Cucurbitaceae	<i>Cayaponia villosissima</i> Cogn.	3
Dioscoreaceae	<i>Dioscorea altissima</i> Lam.	3
Dioscoreaceae	<i>Dioscorea cinnamomifolia</i> Hook.	3
Dioscoreaceae	<i>Dioscorea grisebachii</i> Kunth	3
Dioscoreaceae	<i>Dioscorea piperifolia</i> Humb. and Bonpl. ex Willd.	3
Dioscoreaceae	<i>Dioscorea sinuata</i> Vell.	3
Euphorbiaceae	<i>Dalechampia convolvuloides</i> Lam.	3
Fabaceae	<i>Dioclea violacea</i> Benth.	3
Fabaceae	<i>Machaerium ternatum</i> Kuhl. and Hoehne	3
Fabaceae	<i>Senegalia grandistipula</i> (Benth.) Seigler and Ebinger	3
Fabaceae	<i>Vigna luteola</i> (Jacq.) Benth.	3
Malpighiaceae	<i>Niedenzuella lucida</i> (A. Juss.) W.R. Anderson	3
Malpighiaceae	<i>Peixotoa hispidula</i> A.Juss.	3
Malpighiaceae	<i>Stigmaphyllon gayanum</i> A.Juss.	3
Malpighiaceae	<i>Stigmaphyllon paralias</i> A.Juss.	3
Malpighiaceae	<i>Thryallis brachystachys</i> Lindl.	3
Menispermaceae	<i>Disciphania hernandia</i> (Vell.) Barneby	3
Menispermaceae	<i>Hyperbaena domingensis</i> (DC.) Benth.	3
Menispermaceae	<i>Orthomene schomburgkii</i> (Miers) Barneby and Krukoff	3
Nyctaginaceae	<i>Bougainvillea spectabilis</i> Willd.	3
Nyctaginaceae	<i>Leucaster caniflorus</i> Choisy	3
Passifloraceae	<i>Passiflora alliacea</i> Barb. Rodr.	3

Passifloraceae	<i>Passiflora vellozii</i> Gardner	3
Poaceae	<i>Chusquea anelytroides</i> Rupr. ex Döll	3
Poaceae	<i>Chusquea bambusoides</i> (Raddi) Hack.	3
Poaceae	<i>Chusquea oligophylla</i> Rupr.	3
Polygalaceae	<i>Diclidanthera laurifolia</i> Mart.	3
Polygalaceae	<i>Securidaca lanceolata</i> A.St.-Hil.	3
Ranunculaceae	<i>Clematis dioica</i> L.	3
Rosaceae	<i>Rubus urticifolius</i> Poir.	3
Sapindaceae	<i>Cardiospermum corindum</i> L.	3
Sapindaceae	<i>Paullinia weinmannifolia</i> A.Gray	3
Sapindaceae	<i>Serjania piscatoria</i> Radlk.	3
Sapindaceae	<i>Thinouia scandens</i> (Cambess.) Triana and Planch.	3
Sapindaceae	<i>Urvillea triphylla</i> (Vell.) Radlk.	3
Smilacaceae	<i>Smilax japicanga</i> Griseb.	3
Smilacaceae	<i>Smilax subsessiliflora</i> Duhamel	3
Solanaceae	<i>Solanum odoriferum</i> Vell.	3
Trigoniaceae	<i>Trigonia villosa</i> Aubl.	3
Vitaceae	<i>Cissus erosa</i> Rich.	3
Vitaceae	<i>Cissus paullinifolia</i> Vell.	3
Vitaceae	<i>Cissus stipulata</i> Vell.	3
Apocynaceae	<i>Ditassa banksii</i> Schult.	2
Apocynaceae	<i>Ditassa conceptionis</i> Fontella	2
Apocynaceae	<i>Ditassa nitida</i> E.Fourn.	2
Apocynaceae	<i>Forsteronia cordata</i> (Müll.Arg.) Woodson	2
Apocynaceae	<i>Forsteronia thyrsoides</i> (Vell.) Müll.Arg.	2
Apocynaceae	<i>Jobinia connivens</i> (Hook. and Arn.) Malme	2
Apocynaceae	<i>Mandevilla crassinoda</i> (Gardner) Woodson	2
Apocynaceae	<i>Mandevilla moricandiana</i> (A.DC.) Woodson	2
Apocynaceae	<i>Marsdenia dorotheae</i> Fontella and Morillo	2
Apocynaceae	<i>Mateleia maritima</i> (Jacq.) Woodson	2
Apocynaceae	<i>Metastelma burchellii</i> (Hook. and Arn.) Rapini	2
Apocynaceae	<i>Orthosia arenosa</i> Decne.	2
Apocynaceae	<i>Orthosia itatiaiensis</i> Malme	2

Apocynaceae	<i>Oxypetalum glaziovii</i> (E.Fourn.) Fontella and Marquete	2
Apocynaceae	<i>Oxypetalum lanatum</i> Decne. ex E. Fourn.	2
Apocynaceae	<i>Oxypetalum regnellii</i> (Malme) Malme	2
Apocynaceae	<i>Peplonia organensis</i> (E.Fourn.) Fontella and Rapini	2
Apocynaceae	<i>Prestonia coalita</i> (Vell.) Woodson	2
Apocynaceae	<i>Sarcostemma clausum</i> (Jacq.) Schult.	2
Apocynaceae	<i>Temnadenia odorifera</i> (Vell.) J.F.Morales	2
Arecaceae	<i>Desmoncus polyacanthos</i> Mart.	2
Begoniaceae	<i>Begonia solananthera</i> A.DC.	2
Bignoniaceae	<i>Adenocalymma cymbalum</i> (Cham.) Bureau and K.Schum.	2
Bignoniaceae	<i>Adenocalymma subsessilifolium</i> DC.	2
Bignoniaceae	<i>Anemopaegma prostratum</i> DC.	2
Bignoniaceae	<i>Dolichandra unguiculata</i> (Vell.) L.G.Lohmann	2
Bignoniaceae	<i>Fridericia bracteolata</i> (DC.) L.G.Lohmann	2
Bignoniaceae	<i>Fridericia speciosa</i> Mart.	2
Bignoniaceae	<i>Mansoa lanceolata</i> (DC.) A.H.Gentry	2
Boraginaceae	<i>Tournefortia bicolor</i> Sw.	2
Boraginaceae	<i>Tournefortia gardneri</i> A.DC.	2
Campanulaceae	<i>Centropogon cornutus</i> (L.) Druce	2
Campanulaceae	<i>Siphocampylus duploserratus</i> Pohl	2
Cannabaceae	<i>Celtis iguanaea</i> (Jacq.) Sarg.	2
Capparaceae	<i>Capparis lineata</i> Dombey ex Pers.	2
Celastraceae	<i>Peritassa laevigata</i> (Hoffmanns. ex Link) A.C.Sm.	2
Celastraceae	<i>Tontelea leptophylla</i> A.C. Sm.	2
Celastraceae	<i>Tontelea passiflora</i> (Vell.) Lombardi	2
Celastraceae	<i>Tontelea tenuicula</i> (Miers) A.C. Sm.	2
Combretaceae	<i>Combretum fruticosum</i> (Loefl.) Stuntz	2
Asteraceae	<i>Cyrtocymura scorpioides</i> (Lam.) H.Rob.	2
Asteraceae	<i>Dasyphyllum flagellare</i> (Casar.) Cabrera	2
Asteraceae	<i>Mikania argyreia</i> DC.	2
Asteraceae	<i>Mikania biformis</i> DC.	2
Asteraceae	<i>Mikania lindbergii</i> Baker	2
Asteraceae	<i>Mikania lundiana</i> DC.	2

Asteraceae	<i>Mikania nigricans</i> Gardner	2
Asteraceae	<i>Mikania rufescens</i> Sch.Bip. ex Baker	2
Asteraceae	<i>Mikania vauthieriana</i> Baker	2
Asteraceae	<i>Pentacalia desiderabilis</i> Cuatrec.	2
Asteraceae	<i>Piptocarpha brasiliiana</i> Cass.	2
Connaraceae	<i>Connarus rostratus</i> (Vell.) L.B.Sm.	2
Convolvulaceae	<i>Ipomoea indica</i> (Burm.) Merr.	2
Convolvulaceae	<i>Ipomoea regnellii</i> Meisn.	2
Convolvulaceae	<i>Ipomoea tiliacea</i> (Willd.) Choisy	2
Convolvulaceae	<i>Jacquemontia velutina</i> Choisy	2
Convolvulaceae	<i>Operculina macrocarpa</i> (L.) Urb.	2
Cucurbitaceae	<i>Fevillea trilobata</i> L.	2
Cucurbitaceae	<i>Wilbrandia ebracteata</i> Cogn.	2
Dioscoreaceae	<i>Dioscorea dodecaneura</i> Vell.	2
Dioscoreaceae	<i>Dioscorea glandulosa</i> (Griseb.) Klotzsch ex Kunth	2
Dioscoreaceae	<i>Dioscorea laxiflora</i> Mart. ex Griseb.	2
Dioscoreaceae	<i>Dioscorea mollis</i> Kunth	2
Dioscoreaceae	<i>Dioscorea multiflora</i> Mart. ex Griseb.	2
Dioscoreaceae	<i>Dioscorea perdicum</i> Taub.	2
Dioscoreaceae	<i>Dioscorea regnellii</i> Uline ex R.Knuth	2
Dioscoreaceae	<i>Dioscorea therezopolensis</i> Uline ex R.Knuth	2
Euphorbiaceae	<i>Dalechampia micromeria</i> Baill.	2
Euphorbiaceae	<i>Dalechampia pentaphylla</i> Lam.	2
Euphorbiaceae	<i>Dalechampia triphylla</i> Lam.	2
Euphorbiaceae	<i>Plukenetia serrata</i> (Vell.) L.J.Gillespie	2
Euphorbiaceae	<i>Romanoa tamnoides</i> (A.Juss.) Radcl.-Sm.	2
Fabaceae	<i>Abrus precatorius</i> L.	2
Fabaceae	<i>Caesalpinia bonduc</i> (L.) Roxb.	2
Fabaceae	<i>Camptosema isopetalum</i> (Lam.) Taub.	2
Fabaceae	<i>Camptosema scarlatinum</i> (Benth.) Burkart	2
Fabaceae	<i>Centrosema brasilianum</i> (L.) Benth.	2
Fabaceae	<i>Cleobulia multiflora</i> Benth.	2
Fabaceae	<i>Clitoria laurifolia</i> Poir.	2

Fabaceae	<i>Dalbergia lateriflora</i> Benth.	2
Fabaceae	<i>Dioclea schottii</i> Benth.	2
Fabaceae	<i>Machaerium glabrum</i> Vogel	2
Fabaceae	<i>Machaerium gracile</i> Benth.	2
Fabaceae	<i>Piptadenia micracantha</i> Benth.	2
Fabaceae	<i>Piptadenia trisperma</i> (Vell.) Benth.	2
Fabaceae	<i>Senegalia mikanii</i> (Benth.) Seigler and Ebinger	2
Fabaceae	<i>Senegalia pedicellata</i> (Benth.) Seigler and Ebinger	2
Fabaceae	<i>Senegalia pteridifolia</i> (Benth.) Seigler and Ebinger	2
Loganiaceae	<i>Strychnos brasiliensis</i> (Spreng.) Mart.	2
Malpighiaceae	<i>Banisteriopsis sellowiana</i> (A.Juss.) B.Gates	2
Malpighiaceae	<i>Heteropterys crinigera</i> Griseb.	2
Malpighiaceae	<i>Heteropterys fluminensis</i> (Griseb.) W.R.Anderson	2
Malpighiaceae	<i>Heteropterys fragilis</i> Amorim	2
Malpighiaceae	<i>Heteropterys leschenaultiana</i> A.Juss.	2
Malpighiaceae	<i>Heteropterys lindleyana</i> A.Juss.	2
Malpighiaceae	<i>Heteropterys pauciflora</i> (A.Juss.) A.Juss.	2
Malpighiaceae	<i>Niedenzuella glabra</i> (Spreng.) W.R. Anderson	2
Malpighiaceae	<i>Niedenzuella sericea</i> (A. Juss.) W.R. Anderson	2
Malpighiaceae	<i>Stigmaphyllon alternifolium</i> A. Juss.	2
Malpighiaceae	<i>Stigmaphyllon auriculatum</i> (Cav.) A.Juss.	2
Malpighiaceae	<i>Stigmaphyllon tomentosum</i> A.Juss.	2
Marcgraviaceae	<i>Marcgraviastrum cuneifolium</i> (Gardner) Bedell	2
Menispermaceae	<i>Abuta rufescens</i> Aubl.	2
Menispermaceae	<i>Abuta selleana</i> Eichler	2
Menispermaceae	<i>Anomospermum reticulatum</i> (Mart.) Eichler	2
Onagraceae	<i>Fuchsia glazioviana</i> Taub.	2
Passifloraceae	<i>Passiflora actinia</i> Hook.	2
Passifloraceae	<i>Passiflora capsularis</i> L.	2
Passifloraceae	<i>Passiflora farneyi</i> Pessoa and Cervi	2
Passifloraceae	<i>Passiflora imbeana</i> Sacco	2
Passifloraceae	<i>Passiflora kermesina</i> Link and Otto	2
Passifloraceae	<i>Passiflora misera</i> Kunth	2

Passifloraceae	<i>Passiflora pentagona</i> Mast.	2
Passifloraceae	<i>Passiflora racemosa</i> Brot.	2
Passifloraceae	<i>Passiflora rhamnifolia</i> Mast.	2
Passifloraceae	<i>Passiflora setacea</i> DC.	2
Passifloraceae	<i>Passiflora suberosa</i> L.	2
Poaceae	<i>Chusquea capitata</i> Nees	2
Poaceae	<i>Chusquea capituliflora</i> Trin.	2
Poaceae	<i>Chusquea urelytra</i> Hack.	2
Poaceae	<i>Lasiacis ligulata</i> Hitchc. and Chase	2
Poaceae	<i>Merostachys burmanii</i> Send.	2
Poaceae	<i>Merostachys fischeriana</i> Rupr. ex Döll	2
Poaceae	<i>Merostachys petiolata</i> Döll	2
Poaceae	<i>Merostachys pluriflora</i> Munro ex E.G.Camus	2
Polygalaceae	<i>Securidaca macrocarpa</i> A.W. Benn.	2
Polygonaceae	<i>Coccoloba salicifolia</i> Wedd.	2
Rosaceae	<i>Rubus erythroclados</i> Mart. ex Hook.f.	2
Rubiaceae	<i>Manettia beyrichiana</i> K.Schum.	2
Rubiaceae	<i>Manettia congesta</i> (Vell.) K.Schum.	2
Rubiaceae	<i>Manettia glaziovii</i> Wernham	2
Rubiaceae	<i>Sabicea cinerea</i> Aubl.	2
Rubiaceae	<i>Sabicea grisea</i> Cham. and Schltldl.	2
Sapindaceae	<i>Cardiospermum grandiflorum</i> Sw.	2
Sapindaceae	<i>Paullinia bicorniculata</i> Somner	2
Sapindaceae	<i>Paullinia fusiformis</i> Radlk.	2
Sapindaceae	<i>Serjania corrugata</i> Radlk.	2
Sapindaceae	<i>Serjania deflexa</i> Gardner	2
Sapindaceae	<i>Serjania dentata</i> (Vell.) Radlk.	2
Sapindaceae	<i>Serjania ichthyctona</i> Radlk.	2
Sapindaceae	<i>Serjania laruotteana</i> Cambess.	2
Sapindaceae	<i>Urvillea glabra</i> Cambess.	2
Smilacaceae	<i>Smilax domingensis</i> Willd.	2
Smilacaceae	<i>Smilax hilariana</i> A.DC.	2
Smilacaceae	<i>Smilax remotinervis</i> Hand.-Mazz.	2

Solanaceae	<i>Solanum alternatopinnatum</i> Steud.	2
Solanaceae	<i>Solanum didymum</i> Dunal	2
Trigoniaceae	<i>Trigonia eriosperma</i> (Lam.) Fromm and E.Santos	2
Vitaceae	<i>Cissus serroniana</i> (Glaz.) Lombardi	2
Vitaceae	<i>Cissus striata</i> Ruiz and Pav.	2
Vitaceae	<i>Cissus sulcicaulis</i> (Baker) Planch.	2
Acanthaceae	<i>Clistax brasiliensis</i> Mart.	1
Alstroemeriaceae	<i>Bomarea edulis</i> (Tussac) Herb.	1
Amaranthaceae	<i>Alternanthera brasiliana</i> (L.) Kuntze	1
Amaranthaceae	<i>Chamissoa altissima</i> (Jacq.) Kunth	1
Amaranthaceae	<i>Gomphrena vaga</i> Mart.	1
Apocynaceae	<i>Araujia sericifera</i> Brot.	1
Apocynaceae	<i>Ditassa gracilis</i> Hand.-Mazz.	1
Apocynaceae	<i>Ditassa hispida</i> (Vell.) Fontella	1
Apocynaceae	<i>Ditassa maricaensis</i> Fontella and E.A.Schwarz	1
Apocynaceae	<i>Ditassa mucronata</i> Mart.	1
Apocynaceae	<i>Ditassa tomentosa</i> (Decne.) Fontella	1
Apocynaceae	<i>Forsteronia australis</i> Müll.Arg.	1
Apocynaceae	<i>Forsteronia brevifolia</i> Markgr.	1
Apocynaceae	<i>Forsteronia pubescens</i> A.DC.	1
Apocynaceae	<i>Forsteronia rufa</i> Müll.Arg.	1
Apocynaceae	<i>Forsteronia vellozoana</i> (A.DC.) Woodson	1
Apocynaceae	<i>Gonolobus dorothyanus</i> Fontella and E.A.Schwarz	1
Apocynaceae	<i>Jobinia hatschbachii</i> Fontella and E.A.Schwarz	1
Apocynaceae	<i>Jobinia lindbergii</i> E.Fourn.	1
Apocynaceae	<i>Jobinia paranaensis</i> Fontella and C. Valente	1
Apocynaceae	<i>Macroditassa grandiflora</i> (E.Fourn.) Malme	1
Apocynaceae	<i>Macroditassa laxa</i> (Malme) Fontella and E. Herrera	1
Apocynaceae	<i>Macroditassa mantiqueirae</i> Matoz. and T.U.P.Konno	1
Apocynaceae	<i>Mandevilla emarginata</i> (Vell.) C.Ezcurra	1
Apocynaceae	<i>Mandevilla fragrans</i> (Stadelm.) Woodson	1
Apocynaceae	<i>Mandevilla splendens</i> (Hook.f.) Woodson	1
Apocynaceae	<i>Mandevilla urceolata</i> Markgr.	1

Apocynaceae	<i>Mandevilla urophylla</i> (Hook.) Woodson	1
Apocynaceae	<i>Marsdenia fontellana</i> Morillo and Carnevali	1
Apocynaceae	<i>Marsdenia hilariana</i> E.Fourn.	1
Apocynaceae	<i>Marsdenia loniceroides</i> E.Fourn.	1
Apocynaceae	<i>Marsdenia suberosa</i> (E.Fourn.) Malme	1
Apocynaceae	<i>Matelea ganglinosa</i> (Vell.) Rapini	1
Apocynaceae	<i>Orthosia urceolata</i> E. Fourn.	1
Apocynaceae	<i>Oxypetalum appendiculatum</i> Mart.	1
Apocynaceae	<i>Oxypetalum costae</i> Occhioni	1
Apocynaceae	<i>Oxypetalum glabrum</i> (Decne.) Malme	1
Apocynaceae	<i>Peplonia hatschbachii</i> (Fontella and de Lamare) Fontella and Rapini	1
Apocynaceae	<i>Peplonia macrophylla</i> (Malme) U.C.S.Silva and Rapini	1
Apocynaceae	<i>Peplonia riedelii</i> (E.Fourn.) Fontella and Rapini	1
Apocynaceae	<i>Prestonia denticulata</i> (Vell.) Woodson	1
Apocynaceae	<i>Prestonia didyma</i> (Vell.) Woodson	1
Apocynaceae	<i>Prestonia dusenii</i> (Malme) Woodson	1
Apocynaceae	<i>Rhabdadenia madida</i> (Vell.) Miers	1
Apocynaceae	<i>Secondatia floribunda</i> A.DC.	1
Apocynaceae	<i>Skytanthus hancorniiifolius</i> (A.DC.) Miers	1
Apocynaceae	<i>Tassadia obovata</i> Decne.	1
Aristolochiaceae	<i>Aristolochia labiata</i> Willd.	1
Aristolochiaceae	<i>Aristolochia odora</i> Steud.	1
Aristolochiaceae	<i>Aristolochia pubescens</i> Willd. ex Duch.	1
Aristolochiaceae	<i>Aristolochia raja</i> Mart.	1
Aristolochiaceae	<i>Aristolochia rugosa</i> Lam.	1
Aristolochiaceae	<i>Euglypha rojasiana</i> Chodat and Hassl.	1
Asparagaceae	<i>Herreria glaziovii</i> Lecomte	1
Asparagaceae	<i>Herreria salsaparilha</i> Mart.	1
Basellaceae	<i>Anredera tucumanensis</i> (Lillo and Hauman) Sperling	1
Begoniaceae	<i>Begonia radicans</i> Vell.	1
Bignoniaceae	<i>Adenocalymma bracteolatum</i> DC.	1
Bignoniaceae	<i>Adenocalymma dusenii</i> Kraenzl.	1
Bignoniaceae	<i>Adenocalymma hirtum</i> (Mart. ex DC.) Bureau and K.Schum.	1

Bignoniaceae	<i>Adenocalymma paulistarum</i> Bureau and K.Schum.	1
Bignoniaceae	<i>Amphilophium bauhinioides</i> (Bureau ex Baill.) L.G.Lohmann	1
Bignoniaceae	<i>Amphilophium bracteatum</i> (Cham.) L.G.Lohmann	1
Bignoniaceae	<i>Amphilophium falcatum</i> (Vell.) L.G.Lohmann	1
Bignoniaceae	<i>Amphilophium frutescens</i> (DC.) L.G.Lohmann	1
Bignoniaceae	<i>Amphilophium neoglaziovii</i> L.G. Lohmann	1
Bignoniaceae	<i>Amphilophium paniculatum</i> (L.) Kunth	1
Bignoniaceae	<i>Anemopaegma oligoneuron</i> (Sprague and Sandwith) A.H.Gentry	1
Bignoniaceae	<i>Bignonia corymbosa</i> (Vent.) L.G.Lohmann	1
Bignoniaceae	<i>Bignonia sciuripabula</i> (K.Schum.) L.G.Lohmann	1
Bignoniaceae	<i>Callichlamys latifolia</i> (Rich.) K. Schum.	1
Bignoniaceae	<i>Cuspidaria floribunda</i> (DC.) A.H.Gentry	1
Bignoniaceae	<i>Cuspidaria octoptera</i> A.H.Gentry	1
Bignoniaceae	<i>Fridericia formosa</i> (Bureau) L.G.Lohmann	1
Bignoniaceae	<i>Fridericia pulchella</i> (Cham.) L.G.Lohmann	1
Bignoniaceae	<i>Fridericia samydoides</i> (Cham.) L.G.Lohmann	1
Bignoniaceae	<i>Fridericia subincana</i> (Mart.) L.G.Lohmann	1
Bignoniaceae	<i>Lundia obliqua</i> Sond.	1
Bignoniaceae	<i>Martinella obovata</i> (Kunth) Bureau and K.Schum.	1
Bignoniaceae	<i>Pleonotoma tetraquetra</i> (Cham.) Bureau	1
Bignoniaceae	<i>Stizophyllum inaequilaterum</i> Bureau and K.Schum.	1
Bignoniaceae	<i>Tynanthus cognatus</i> (Cham.) Miers	1
Bignoniaceae	<i>Tynanthus micranthus</i> Corr.Méllo ex K.Schum.	1
Bignoniaceae	<i>Xylophragma myrianthum</i> (Cham.) Sprague	1
Bignoniaceae	<i>Xylophragma pratense</i> (Bureau and K.Schum.) Sprague	1
Boraginaceae	<i>Tournefortia villosa</i> Salzm. ex DC.	1
Campanulaceae	<i>Siphocampylus convolvulaceus</i> (Cham.) G.Don	1
Campanulaceae	<i>Siphocampylus fimbriatus</i> Regel	1
Campanulaceae	<i>Siphocampylus fluminensis</i> (Vell.) E.Wimm.	1
Caprifoliaceae	<i>Valeriana scandens</i> L.	1
Celastraceae	<i>Anthodon decussatum</i> Ruiz and Pav.	1
Celastraceae	<i>Peritassa calypsoides</i> (Cambess.) A.C. Sm.	1
Celastraceae	<i>Pristimera nervosa</i> (Miers) A.C.Sm.	1

Celastraceae	<i>Salacia grandifolia</i> (Mart.) G. Don	1
Celastraceae	<i>Tontelea corcovadensis</i> A.C. Sm.	1
Celastraceae	<i>Tontelea lanceolata</i> (Miers) A.C. Sm.	1
Celastraceae	<i>Tontelea martiana</i> (Miers) A.C. Sm.	1
Asteraceae	<i>Baccharis rufidula</i> (Spreng.) Joch.Müll.	1
Asteraceae	<i>Calea serrata</i> Less.	1
Asteraceae	<i>Dasycondylus resinosus</i> (Spreng.) R.M.King and H.Rob.	1
Asteraceae	<i>Dasyphyllum brasiliense</i> (Spreng.) Cabrera	1
Asteraceae	<i>Dendrophorbium brachycodon</i> (Baker) C.Jeffrey	1
Asteraceae	<i>Dendrophorbium bradei</i> (Cabrera) C.Jeffrey	1
Asteraceae	<i>Heterocondylus vitalbae</i> (DC.) R.M.King and H.Rob.	1
Asteraceae	<i>Koanophyllon tinctorium</i> Arruda	1
Asteraceae	<i>Mikania banisteriae</i> DC.	1
Asteraceae	<i>Mikania buddleiaefolia</i> DC.	1
Asteraceae	<i>Mikania cabrerai</i> G.M.Barroso	1
Asteraceae	<i>Mikania campos-portoana</i> G.M.Barroso	1
Asteraceae	<i>Mikania conferta</i> Gardner	1
Asteraceae	<i>Mikania confertissima</i> Sch.Bip. ex Baker	1
Asteraceae	<i>Mikania glaziovii</i> Baker	1
Asteraceae	<i>Mikania hastifolia</i> Baker	1
Asteraceae	<i>Mikania hoehnei</i> B.L.Rob.	1
Asteraceae	<i>Mikania lasiandrae</i> DC.	1
Asteraceae	<i>Mikania macedoi</i> G.M.Barroso	1
Asteraceae	<i>Mikania microdonta</i> DC.	1
Asteraceae	<i>Mikania microlepis</i> Baker	1
Asteraceae	<i>Mikania oblongifolia</i> DC.	1
Asteraceae	<i>Mikania stipulacea</i> (Vahl) Willd.	1
Asteraceae	<i>Mikania vitifolia</i> DC.	1
Asteraceae	<i>Mutisia campanulata</i> Less.	1
Asteraceae	<i>Piptocarpha lundiana</i> (Less.) Baker	1
Asteraceae	<i>Piptocarpha notata</i> (Less.) Baker	1
Asteraceae	<i>Piptocarpha oblonga</i> (Gardner) Baker	1
Asteraceae	<i>Piptocarpha pyrifolia</i> (DC.) Baker	1

Asteraceae	<i>Steyermarkina pyrifolia</i> (DC.) R.M.King and H.Rob.	1
Asteraceae	<i>Trixis antimenorrhoea</i> (Schrank) Mart. ex Baker	1
Asteraceae	<i>Trixis glaziovii</i> Baker	1
Connaraceae	<i>Bernardinia fluminensis</i> (Gardner) Planch.	1
Connaraceae	<i>Connarus nodosus</i> Baker	1
Convolvulaceae	<i>Bonamia agrostopolis</i> (Vell.) Hallier f.	1
Convolvulaceae	<i>Convolvulus nodiflorus</i> Desr.	1
Convolvulaceae	<i>Evolvulus glomeratus</i> Nees and C. Mart.	1
Convolvulaceae	<i>Evolvulus pusillus</i> Choisy	1
Convolvulaceae	<i>Ipomoea alba</i> L.	1
Convolvulaceae	<i>Ipomoea cynanchifolia</i> Meisn.	1
Convolvulaceae	<i>Ipomoea purpurea</i> (L.) Roth	1
Convolvulaceae	<i>Ipomoea saopaulista</i> O'Donell	1
Convolvulaceae	<i>Jacquemontia blanchetii</i> Moric.	1
Convolvulaceae	<i>Jacquemontia ferruginea</i> Choisy	1
Convolvulaceae	<i>Jacquemontia glaucescens</i> Choisy	1
Convolvulaceae	<i>Jacquemontia martii</i> Meisn.	1
Convolvulaceae	<i>Jacquemontia mucronifera</i> Hallier	1
Convolvulaceae	<i>Merremia cissoides</i> (Lam.) Hallier f.	1
Convolvulaceae	<i>Merremia tuberosa</i> (L.) Rendle	1
Cucurbitaceae	<i>Cayaponia diversifolia</i> (Cogn.) Cogn.	1
Cucurbitaceae	<i>Cayaponia fluminensis</i> (Vell.) Cogn.	1
Cucurbitaceae	<i>Cayaponia longifolia</i> Cogn.	1
Cucurbitaceae	<i>Cayaponia ternata</i> (Vell.) Cogn.	1
Cucurbitaceae	<i>Cayaponia trifoliolata</i> (Cogn.) Cogn.	1
Cucurbitaceae	<i>Cyclanthera tenuifolia</i> Cogn.	1
Cucurbitaceae	<i>Fevillea passiflora</i> Vell.	1
Cucurbitaceae	<i>Gurania lobata</i> (L.) Pruski	1
Cucurbitaceae	<i>Gurania subumbellata</i> (Miq.) Cogn.	1
Cucurbitaceae	<i>Luffa cylindrica</i> (L.) M.Roem.	1
Cucurbitaceae	<i>Melothria trilobata</i> Cogn.	1
Cucurbitaceae	<i>Melothrianthus smilacifolius</i> (Cogn.) Mart.Crov.	1
Cucurbitaceae	<i>Wilbrandia glaziovii</i> Cogn.	1

Cucurbitaceae	<i>Wilbrandia hibiscoides</i> Silva Manso	1
Dilleniaceae	<i>Davilla grandifolia</i> Moric. ex Eichler	1
Dilleniaceae	<i>Tetracera breyniana</i> Schltdl.	1
Dilleniaceae	<i>Tetracera lasiocarpa</i> Eichler	1
Dioscoreaceae	<i>Dioscorea bradei</i> R.Knuth	1
Dioscoreaceae	<i>Dioscorea campestris</i> Griseb.	1
Dioscoreaceae	<i>Dioscorea campos-portoi</i> R.Knuth	1
Dioscoreaceae	<i>Dioscorea coronata</i> Hauman	1
Dioscoreaceae	<i>Dioscorea de-mourae</i> Uline ex R.Knuth	1
Dioscoreaceae	<i>Dioscorea furcata</i> Griseb.	1
Dioscoreaceae	<i>Dioscorea glomerulata</i> Hauman	1
Dioscoreaceae	<i>Dioscorea loefgrenii</i> R.Knuth	1
Dioscoreaceae	<i>Dioscorea mantigueirensis</i> R.Knuth	1
Dioscoreaceae	<i>Dioscorea margarethia</i> G.M.Barroso, E.F.Guim. and Sucre	1
Dioscoreaceae	<i>Dioscorea martiana</i> Griseb.	1
Dioscoreaceae	<i>Dioscorea pseudomacrocapsa</i> G.M.Barroso, E.F.Guim. and Sucre	1
Dioscoreaceae	<i>Dioscorea scabra</i> Humb. and Bonpl. ex Willd.	1
Dioscoreaceae	<i>Dioscorea stegelmanniana</i> R.Knuth	1
Dioscoreaceae	<i>Dioscorea subhastata</i> Vell.	1
Dryopteridaceae	<i>Polybotrya cylindrica</i> Kaulf.	1
Euphorbiaceae	<i>Dalechampia alata</i> Klotzsch ex Baill.	1
Euphorbiaceae	<i>Dalechampia brasiliensis</i> Lam.	1
Euphorbiaceae	<i>Dalechampia leandrii</i> Baill.	1
Euphorbiaceae	<i>Dalechampia olfersiana</i> Müll.Arg.	1
Fabaceae	<i>Bauhinia smilacina</i> (Schott) Steud.	1
Fabaceae	<i>Camptosema spectabile</i> (Tul.) Burkart	1
Fabaceae	<i>Centrosema arenarium</i> Benth.	1
Fabaceae	<i>Centrosema dasyanthum</i> Benth.	1
Fabaceae	<i>Centrosema grandiflorum</i> Benth.	1
Fabaceae	<i>Centrosema plumieri</i> (Pers.) Benth.	1
Fabaceae	<i>Centrosema pubescens</i> Benth.	1
Fabaceae	<i>Centrosema sagittatum</i> (Willd.) L.Riley	1
Fabaceae	<i>Chaetocalyx scandens</i> (L.) Urb.	1

Fabaceae	<i>Cochliasanthus caracalla</i> (L.) Trew	1
Fabaceae	<i>Cratylia hypargyrea</i> Benth.	1
Fabaceae	<i>Dalbergia brasiliensis</i> Vogel	1
Fabaceae	<i>Dalbergia sampaioana</i> Kuhlm. and Hoehne	1
Fabaceae	<i>Desmodium axillare</i> (Sw.) DC.	1
Fabaceae	<i>Dioclea virgata</i> (Rich.) Amshoff	1
Fabaceae	<i>Galactia striata</i> (Jacq.) Urb.	1
Fabaceae	<i>Leptospron adenanthum</i> (G. Mey.) A. Delgado	1
Fabaceae	<i>Machaerium punctatum</i> Pers.	1
Fabaceae	<i>Macroptilium gracile</i> (Benth.) Urb.	1
Fabaceae	<i>Mimosa extensa</i> Benth.	1
Fabaceae	<i>Mucuna japira</i> A.M.G.Azevedo, K.Agostini and Sazima	1
Fabaceae	<i>Rhynchosia phaseoloides</i> (Sw.) DC.	1
Fabaceae	<i>Senegalia recurva</i> (Benth.) Seigler and Ebinger	1
Fabaceae	<i>Senegalia velutina</i> (DC.) Seigler and Ebinger	1
Fabaceae	<i>Sigmoidotropis speciosa</i> (Kunth) A. Delgado	1
Fabaceae	<i>Teramnus volubilis</i> Sw.	1
Hernandiaceae	<i>Sparattanthelium botocudorum</i> Mart.	1
Hernandiaceae	<i>Sparattanthelium tupiniquinorum</i> Mart.	1
Lauraceae	<i>Cassytha filiformis</i> L.	1
Loganiaceae	<i>Strychnos gardneri</i> A.DC.	1
Malpighiaceae	<i>Amorimia maritima</i> (A.Juss.) W.R.Anderson	1
Malpighiaceae	<i>Amorimia rigida</i> (A.Juss.) W.R.Anderson	1
Malpighiaceae	<i>Banisteriopsis argyrophylla</i> (A.Juss.) B.Gates	1
Malpighiaceae	<i>Banisteriopsis martiniana</i> (A.Juss.) Cuatrec.	1
Malpighiaceae	<i>Banisteriopsis membranifolia</i> (A.Juss.) B.Gates	1
Malpighiaceae	<i>Banisteriopsis muricata</i> (Cav.) Cuatrec.	1
Malpighiaceae	<i>Banisteriopsis nummifera</i> (A.Juss.) B.Gates	1
Malpighiaceae	<i>Banisteriopsis oxyclada</i> (A.Juss.) B.Gates	1
Malpighiaceae	<i>Carolus renidens</i> (A.Juss.) W.R.Anderson	1
Malpighiaceae	<i>Diplopterys nigrescens</i> (A.Juss.) W.R.Anderson and C.Davis	1
Malpighiaceae	<i>Heteropterys alternifolia</i> W.R. Anderson	1
Malpighiaceae	<i>Heteropterys bicolor</i> A.Juss.	1

Malpighiaceae	<i>Heteropterys campestris</i> A.Juss.	1
Malpighiaceae	<i>Heteropterys ternstroemiifolia</i> A.Juss.	1
Malpighiaceae	<i>Heteropterys thyrsoidea</i> A. Juss.	1
Malpighiaceae	<i>Heteropterys tomentosa</i> A.Juss.	1
Malpighiaceae	<i>Heteropterys trigoniifolia</i> A. Juss.	1
Malpighiaceae	<i>Hiraea fagifolia</i> (DC.) A.Juss.	1
Malpighiaceae	<i>Hiraea gaudichaudiana</i> A.Juss.	1
Malpighiaceae	<i>Mascagnia sepium</i> (A.Juss.) Griseb.	1
Malpighiaceae	<i>Stigmaphyllon affine</i> A. Juss.	1
Malpighiaceae	<i>Stigmaphyllon angustilobum</i> A. Juss.	1
Malpighiaceae	<i>Stigmaphyllon ciliatum</i> (Lam.) A.Juss.	1
Malpighiaceae	<i>Stigmaphyllon rotundifolium</i> A. Juss.	1
Malpighiaceae	<i>Stigmaphyllon vitifolium</i> A.Juss.	1
Malpighiaceae	<i>Tetrapteryx discolor</i> (G.Mey.) DC.	1
Malpighiaceae	<i>Tetrapteryx styloptera</i> A.Juss.	1
Marcgraviaceae	<i>Marcgravia comosa</i> C. Presl	1
Melastomataceae	<i>Clidemia fluminensis</i> Baumgratz and D'El Rei Souza	1
Melastomataceae	<i>Leandra therezopolitana</i> Cogn.	1
Menispermaceae	<i>Cissampelos glaberrima</i> A.St.-Hil.	1
Menispermaceae	<i>Hyperbaena oblongifolia</i> (Eichler) Chodat and Hassl.	1
Menispermaceae	<i>Odontocarya acuparata</i> Miers	1
Menispermaceae	<i>Ungulipetalum filipendulum</i> (Mart.) Moldenke	1
Passifloraceae	<i>Passiflora campanulata</i> Mast.	1
Passifloraceae	<i>Passiflora deidamioides</i> Harms	1
Passifloraceae	<i>Passiflora galbana</i> Mast.	1
Passifloraceae	<i>Passiflora haematostigma</i> Mart. ex Mast.	1
Passifloraceae	<i>Passiflora jilekii</i> Wawra	1
Passifloraceae	<i>Passiflora mansoi</i> (Mart.) Mast.	1
Passifloraceae	<i>Passiflora marginata</i> Mast.	1
Passifloraceae	<i>Passiflora odontophylla</i> Harms ex Glaz.	1
Passifloraceae	<i>Passiflora ovalis</i> Vell. ex M. Roem.	1
Passifloraceae	<i>Passiflora speciosa</i> Gardner	1
Passifloraceae	<i>Tetrastylis ovalis</i> (Vell. ex M. Roem.) Killip	1

Poaceae	<i>Aulonemia aristulata</i> (Döll) McClure	1
Poaceae	<i>Aulonemia goyazensis</i> (Hack.) McClure	1
Poaceae	<i>Chusquea anelythra</i> Nees	1
Poaceae	<i>Chusquea juergensii</i> Hack.	1
Poaceae	<i>Chusquea leptophylla</i> Nees	1
Poaceae	<i>Chusquea longispiculata</i> L.G.Clark	1
Poaceae	<i>Chusquea oxylepis</i> (Hack.) Ekman	1
Poaceae	<i>Chusquea pulchella</i> L.G.Clark	1
Poaceae	<i>Chusquea ramosissima</i> Lindm.	1
Poaceae	<i>Chusquea sellowii</i> Rupr.	1
Poaceae	<i>Guadua paraguayana</i> Döll	1
Poaceae	<i>Merostachys clausenii</i> Munro	1
Poaceae	<i>Merostachys multiramea</i> Hack.	1
Poaceae	<i>Merostachys neesii</i> Rupr.	1
Poaceae	<i>Merostachys skvortzovii</i> Send.	1
Poaceae	<i>Merostachys ternata</i> Nees	1
Polygalaceae	<i>Bredemeyera autranii</i> Chodat	1
Polygalaceae	<i>Bredemeyera hebeclada</i> (DC.) J.F.B. Pastore	1
Polygalaceae	<i>Securidaca bialata</i> Benth.	1
Polygalaceae	<i>Securidaca diversifolia</i> (L.) S.F.Blake	1
Polygalaceae	<i>Securidaca ovalifolia</i> A.St.-Hil.	1
Polygonaceae	<i>Coccoloba arborescens</i> (Vell.) R.A.Howard	1
Polygonaceae	<i>Coccoloba excelsa</i> Benth.	1
Polygonaceae	<i>Coccoloba striata</i> Benth.	1
Rhamnaceae	<i>Gouania blanchetiana</i> Miq.	1
Rhamnaceae	<i>Gouania latifolia</i> Reissek	1
Rubiaceae	<i>Denscantia cymosa</i> (Spreng.) E.L.Cabral and Bacigalupo	1
Rubiaceae	<i>Galium hypocarpium</i> (L.) Endl. ex Griseb.	1
Rubiaceae	<i>Malanea glabra</i> A.Rich.	1
Rubiaceae	<i>Manettia gracilis</i> Cham. and Schltldl.	1
Rubiaceae	<i>Manettia luteorubra</i> (Vell.) Benth.	1
Rubiaceae	<i>Manettia pauciflora</i> Dusén	1
Rubiaceae	<i>Manettia verticillata</i> Wernham	1

Rubiaceae	<i>Sabicea aspera</i> Aubl.	1
Rubiaceae	<i>Sabicea villosa</i> Willd. ex Schult.	1
Rubiaceae	<i>Spermacoce ocymifolia</i> Willd. ex Roem. and Schult.	1
Sapindaceae	<i>Paullinia ferruginea</i> Casar.	1
Sapindaceae	<i>Paullinia marginata</i> Casar.	1
Sapindaceae	<i>Paullinia seminuda</i> Radlk.	1
Sapindaceae	<i>Paullinia ternata</i> Radlk.	1
Sapindaceae	<i>Serjania comata</i> Radlk.	1
Sapindaceae	<i>Serjania eucardia</i> Radlk.	1
Sapindaceae	<i>Serjania fluminensis</i> Acev.-Rodr.	1
Sapindaceae	<i>Serjania fuscifolia</i> Radlk.	1
Sapindaceae	<i>Serjania gracilis</i> Radlk.	1
Sapindaceae	<i>Serjania hebecarpa</i> Benth.	1
Sapindaceae	<i>Serjania lamprophylla</i> Radlk.	1
Sapindaceae	<i>Serjania macrostachya</i> Radlk.	1
Sapindaceae	<i>Serjania orbicularis</i> Radlk.	1
Sapindaceae	<i>Serjania paleata</i> Radlk.	1
Sapindaceae	<i>Serjania reticulata</i> Cambess.	1
Sapindaceae	<i>Serjania salzmanniana</i> Schltdl.	1
Sapindaceae	<i>Serjania scopulifera</i> Radlk.	1
Sapindaceae	<i>Serjania tenuis</i> Radlk.	1
Sapindaceae	<i>Thinouia mucronata</i> Radlk.	1
Sapindaceae	<i>Urvillea laevis</i> Radlk.	1
Sapindaceae	<i>Urvillea stipitata</i> Radlk.	1
Schlegeliaceae	<i>Schlegelia parviflora</i> (Oerst.) Monach.	1
Smilacaceae	<i>Smilax brasiliensis</i> Spreng.	1
Smilacaceae	<i>Smilax campestris</i> Griseb.	1
Smilacaceae	<i>Smilax lappacea</i> Humb. and Bonpl. ex Willd.	1
Smilacaceae	<i>Smilax larvata</i> Griseb.	1
Smilacaceae	<i>Smilax lutescens</i> Vell.	1
Smilacaceae	<i>Smilax muscosa</i> Toledo	1
Smilacaceae	<i>Smilax stenophylla</i> A.DC.	1
Solanaceae	<i>Solanum inodorum</i> Vell.	1

Solanaceae	<i>Solanum lantana</i> Sendtn.	1
Trigoniaceae	<i>Trigonia paniculata</i> Warm.	1
Trigoniaceae	<i>Trigonia rotundifolia</i> Lleras	1
Verbenaceae	<i>Lantana fucata</i> Lindl.	1
Verbenaceae	<i>Lantana radula</i> Sw.	1
Vitaceae	<i>Cissus pulcherrima</i> Vell.	1
Vitaceae	<i>Cissus simsiana</i> Roem. and Schult.	1

3 PATTERNS OF LIANA COMMUNITY FUNCTIONAL STRUCTURE ARE RELATED TO ALTITUDINAL VARIATION.

3.1 Abstract

Altitudinal variations have been described as good experimental models for assessing species response to changes in climate due to a considerable environmental variation in a relative small scale. Due to changes in environmental and microclimatic conditions it is expected to find drier environments with altitudinal increases. Although there is a good knowledge of tree community response along altitudinal variation, indicating increases in conservative water use, the same knowledge is not available for lianas which are an important component in tropical forest structure and dynamics. The objective of this study was to test the influence of altitudinal variation on aspects of community functional structure of lianas in a tropical forest. We set up ten 0.1 ha plots along an altitudinal variation (100-700 m.a.s.l.). We measured a set of plant traits linked to resource use. We tested the influence of the altitude on trait value and the influence of altitude over the plant trait strategies differentiation within plots. We found a significant influence of the altitude the traits selected and a strong influence of altitude on the patterns of trait functional diversity across the altitude. Our results demonstrated how environmental/microclimatic conditions can play an important role on plant functional assembly. Our results contributed to add evidence that even in a relative low altitudinal variation in tropical forest water deficit can influence plant traits. We highlight the importance of our findings for understanding how liana community structure can respond to climatic changes in the context of global warming.

Keywords: Woody-vine. Air-evaporative-demand. Tropical-mountain. Functional-traits.

3.2 Introduction

Altitudinal variation have been described as good experimental models for assessing species response to changes in climate due to a considerable environmental variation in a relative small scale (Sundqvist et al. 2013, Körner 2007). As altitude increases, there is an increase in solar incidence and a decreasing in atmospheric air pressure which implies in an increasing of the air evaporative demand (Leuschner 2000). Consequently, environments at higher altitudes may be under drought in comparison to lower sites (Leuschner 2000, Rosado et al. 2016). Plant community which occurs across altitudinal variation are expected to respond to these differences in water availability from lower to higher altitudes, showing a variation in trait values associated to increases in conservative water use (Pescador et al. 2015).

Empirical evidence shows that plant communities in tropical forests tends to exhibit a functional response to water shortage linked environmental changing even a long narrow altitudinal variation, from 100 to 1000 meters above sea level (Rosado et al. 2016). An important finding reported by Rosado et al. (2016) was to point out that even tropical rain forests have water deficits intensified with altitude. However, this study focused only in tree species and to our knowledge there is no study which investigated how lianas cope with changes in water availability along altitudinal variations.

Taking into account that lianas are considered as species able to cope with drought by decoupling from environment due to water storage or ability to access deep water (Schnitzer 2005), it remains as an open question whether they respond to altitudinal variations like observed in trees. Thus, understanding how lianas respond to environmental variations is very important given the contribution of this component to the functioning of tropical forests, especially in a scenario of global climate change, where environments are expected to become drier, especially in mountain forests (Rosado et al. 2016, Oliveira et al. 2015).

The objective of this study was to test the influence of altitudinal variation on aspects of community functional structure of lianas in a tropical forest. We hypothesized that the climatic constraints along altitude will lead to a higher conservative water use. Additionally, we hypothesized that the patterns of species coexistence will change, from a divergent trait strategy in lower altitudes (due a higher water availability) to trait convergence in higher altitudes due to a lower water availability in higherg altitudes. Additionally, we accounted the intraspecific trait variation, which incorporates trait variation within a given species and, therefore, may better characterize how species cope with environmental filtering by not relying on average values that neglects variation (ITV, Siefert et al. 2015, Violle et al. 2012). Thus, there are a

series of evidence that the inclusion of ITV in trait based studies can be an helpful approach to clarify how communities are assembled (Pescador et al. 2015).

3.3 Methods

3.3.1 Study area

The study area is located in the municipality of Angra dos Reis, Ilha Grande State Park (IGSP), Brazil (Figure 1). IGSP is an island located in Southeastern coast (-23.152203° , -44.236504°). The area of the Island is around 19 Km², mainly composed by secondary old growth forest (Callado et al. 2009). The highest peak of the island reaches about 1000 m.a.s.l. The climate is classified as tropical Aw with precipitation over 2000 mm in rainy season and temperate over 20 °C in the coldest season (Peel et al. 2007).

3.3.2 Sampling

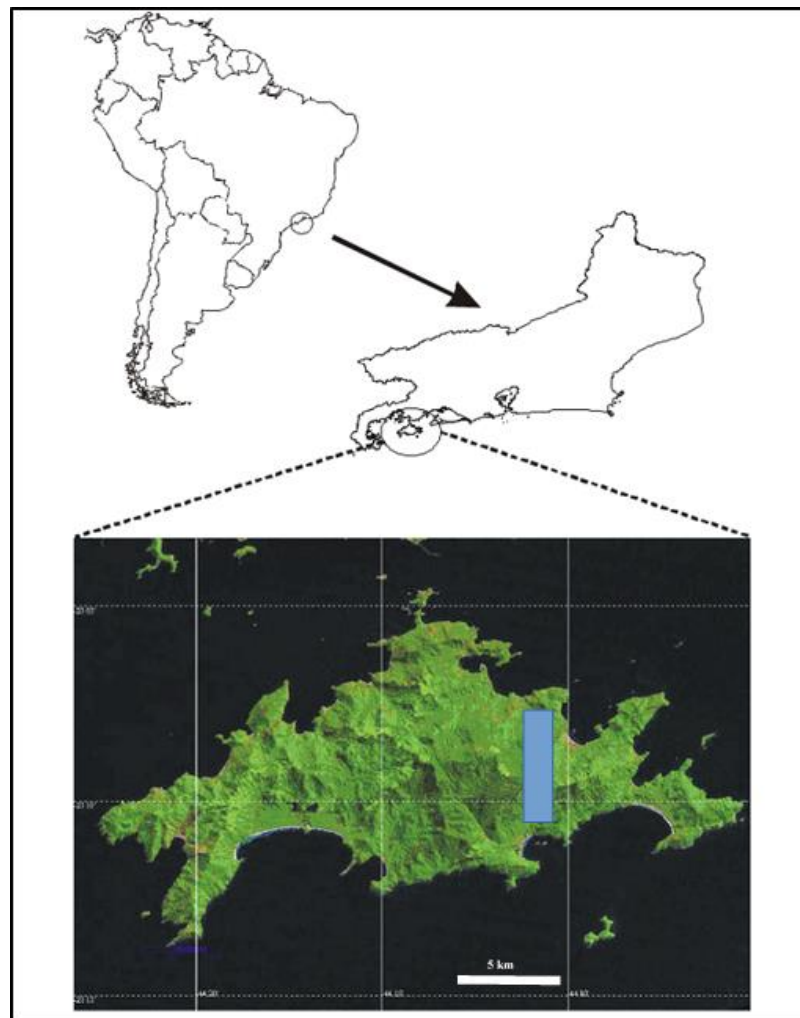
We conducted the sampling in ten permanent plots installed on the east side of the Island by the PPBio (Magnusson et al. 2005, Figure 1). Each plots comprised 250 meters in length and followed the contour of the landscape. The plot width for lianas sampling was 4 meters. All the lianas with stem diameter ≥ 1 cm at 1.3m length from rooting (hereafter dbh) were tagged and measured. We mapped the location of each specimen sampled within the plot based on the distance (in meters) from main plot axis (*i.e.* distance from the middle of the plot from 0 - 2 m, both in left and right side) and the location along the plot length (0 - 250 m). We collected samples to identify the species.

3.3.3 Trait measurements

For testing our first hypothesis we measured the following leaf traits: specific leaf area (SLA – cm²·g⁻¹), which is the leaf fresh area divided by leaf dried mass, blade thickness (BT – mm), which correspond the thickness of blade, measured avoiding primary and secondary veins, and leaf dry mass content (LDMC – g·g⁻¹), which the ratio of leaf dry mass by leaf fresh mass. SLA, BT, LDMC are classical traits used to describe many aspects of leaf economic spectrum, such as plant water use strategy (Wright et al. 2004, Díaz et al. 2015). Hence, our expectation is to find these set of leaf traits in a more conservative fashion (*i.e.* low SLA, high BT and high LDMC) in plots in higher altitudes. For woody traits, we measured wood density (g·cm⁻³). Woody density is linked to many plants strategy, including water uptake. Plants with higher hydraulic conductance usually have low wood density, because they normally invest in

wider xylem vessels (Chave et al. 2009). However, a trade-off of this higher conductance is a higher chance of embolism (Ewers et al. 2015), which can be critical in environments with lower water availability. Hence, we expected to find a higher woody density in higher altitudes. For each specimen per plot we had 1-5 leaf replicates and 1-3 wood replicates. For each species per plot we had 1-5 individuals' replicates both for leaf and wood traits. For our trait coexistence hypothesis, we also used a set of traits which are described more detailed in supplementary Table S1.

Figure 1: Map of Brazil showing the location of Ilha Grande in Rio de Janeiro State.



Legend: The blue bar on the east side of the Island shows the region where is located the 10 plots. Each plot was equally distant 1 km from the closest plot.

Source: Adapted from Nunes-Freitas, 2004

3.3.4 Data analysis

We conducted all the statistical analysis in R (R Core Team 2017). We calculated the community weighted mean (CWM) in two ways: weighting by species relative abundance and other weighting by species basal area. CWM is largely used to express the average trait value in functional ecology (Ricotta and Moretti 2011, Kraft et al. 2015). However, different weighting procedures might result in distinct values and thus, influence the interpretation of the community process. Additionally, we accounted for intraspecific variation (ITV). Firstly, we obtained species mean considering their occurrence across all plots, *i.e.* interspecific trait variation (STV). This approach gave us the contribution of species turnover. Secondly, using species average per plot, *i.e.* ITV (the contribution of species trait variation). Finally, we had four CWM values per plot: (i) CWM weighted by species abundance, using species mean across plot (CWM_{astv}), (ii) CWM weighted by species abundance, using species mean per plot (CWM_{aitv}), (iii) CWM weighted by species basal area, using species mean across plot (CWM_{bstv}) and (iv) CWM weighted by species basal area, using species mean per plot (CWM_{bitv}). We performed simple linear or quadratic regressions against the plot altitude ($\alpha \leq 0.05$). We opted for linear or quadratic regressions after a visual examining the scatterplots of each trait used. We validated this visual procedure testing the fitness the both linear and quadratic models and comparing the values obtained by Akaike Information Criterion (AIC). When a trait had two or more significant linear regressions, we compared the regressions slopes in order to check which kind of CWM type had a stronger relationship with altitude. We compared the regressions slopes using the package “smatr” in R (Warton et al. 2012). When a given trait showed both a linear and quadratic regression of significant for distinct CWM types, we compared the residuals of these regressions using a paired t-test. As the value of residuals indicates the degree of deviation of a given data from the theoretical regression line, we used the absolute values of the residuals to express the magnitude of the residuals.

In order to decouple the influence of STV and ITV operating on liana functional structure, we proceeded the trait flex analysis (Lepš, et al. 2011). This analysis is analogue to variance partitioning. We inform the CWM_{stv} and CWM_{itv} and the predictor variable (which can be continuous or categorical). The output informs us the relative contribution of both CWM, the covariation among them and the total contribution. The analysis was performed using the function “trait.flex.anova” (Lepš, et al. 2011).

To test our second hypothesis, we constructed a dissimilarity matrix based on Euclidean distance of specimens' relative position within each plot separately. To create a dissimilarity matrix based on trait values we used the trait overlap approach (de Bello et al. 2013). This

approach allowed us account trait intraspecific trait variation, using traits mean per plot per species and their respective standard deviation in the calculation. When a given species had only one specimen per plot we used the average standard deviation of the species across the plots. When a given species had just one individual across all plots we used the average standard deviation of the plot in which the species occurred. We calculated this trait dissimilarity using the function “trova” (de Bello et al. 2013). After creating these trait dissimilarity matrices per plot, we ran a multiple regression based on distance matrices for each plot using the package *ecodist* (Goslee and Urban 2007). Then we took the regression scores and regressed against the altitude of the plots. We transformed all the data that did not meet the assumption of normal distribution using log transformation.

3.4 Results

This study encompassed 90 species and 813 individuals. 17 individuals were undetermined to species level. We measured trait value on 88% of species found and 45% of individuals sampled. The comparison among linear and quadratic regressions models yielded in only two models best explained by quadratic regressions than their respective linear regression: LDMC (CWM_{stva}) and WD (CWM_{stva}) (Table 1). Additionally, the models with significant relationships were: BT (CWM_{stva} and CWM_{stvb}), LDMC (CWM_{stva} and CWM_{stvb}), SLA (CWM_{stva}) and WD (CWM_{stva}), Table 2, Figure 1.

Table 1: Results of analysis of variance comparing model fit for linear and quadratic regressions for the functional traits measured in lianas species across ten permanent plots located in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.

Trait	Calc	Weight	df	F	p	AIC.lin	AIC.quad
BT	ITV	Abd	1	0.21	0.66	-48.59	-46.88
		BA	1	0.81	0.40	-35.36	-34.45
	STV	Abd	1	1.28	0.30	-47.44	-47.12
		BA	1	2.52	0.16	-38.95	-40.02
LDMC	ITV	Abd	1	0.17	0.69	-40.06	-38.30
		BA	1	0.30	0.60	-37.02	-35.45
	STV	Abd	1	5.83	0.05	-54.04	-58.09
		BA	1	0.00	0.98	-51.82	-49.82
SLA	ITV	Abd	1	0.36	0.57	100.20	101.70
		BA	1	0.01	0.93	98.45	100.43
	STV	Abd	1	0.47	0.52	84.73	86.08
		BA	1	0.08	0.79	94.25	96.14
WD	ITV	Abd	1	0.64	0.45	-31.72	-30.60
		BA	1	0.81	0.40	-28.61	-27.71
	STV	Abd	1	8.53	0.02	-39.66	-45.62
		BA	1	3.92	0.09	-42.14	-44.58

Legend: Significant results indicate that quadratic regressions provided a best fit than linear regressions. Calc = Calculation method. Indicates whether the species mean were calculated using species traits values across plots (STV) or per plot (ITV). BT = Blade thickness (mm). LDMC = Leaf dried mass content (g.g-1). SLA = Specific leaf area (cm².g-1). WD = Wood density (g.cm-3). Weight = Indicates how the community weighted mean was weighted, using species abundance (Abd), or species basal area (BA). AIC.lin = results of Akaike information criterion for linear models. AIC.quad = results of Akaike information criterion for quadratic models. Significant results are bold highlighted.

Source: The author, 2018.

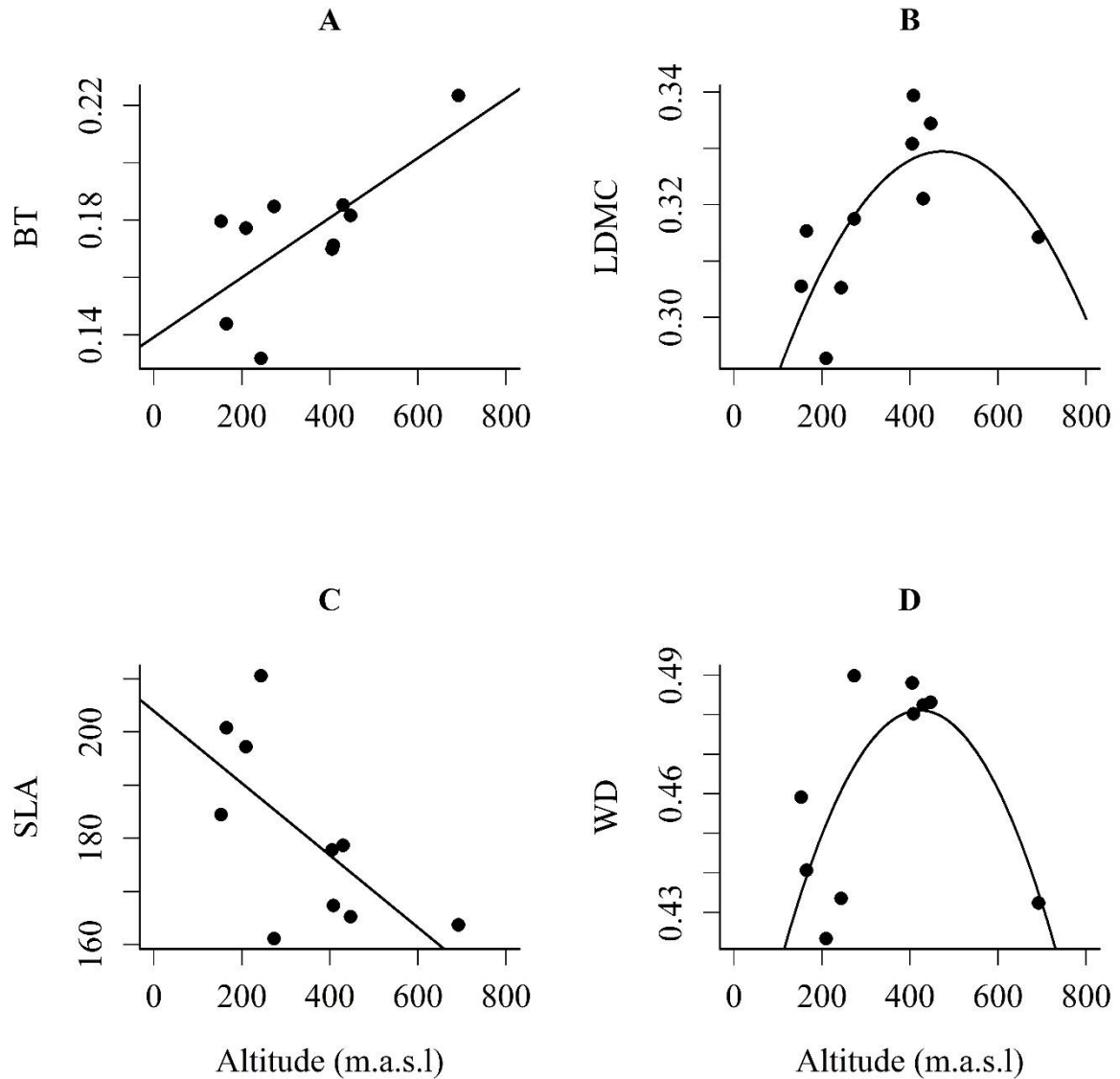
Table 2: Result of the regressions for the functional traits measured in lianas species across ten permanent plots located in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.

Type	Trait	Calc	Weight	R ²	F	p	df	Estimate
Linear	BT	ITV	Abd	0.21	2.15	0.18	8	+
Linear			BA	0.29	3.35	0.10	8	+
Linear		STV	Abd	0.49	7.74	0.02	8	+
Linear			BA	0.49	7.59	0.02	8	+
Linear	LDMC	ITV	Abd	0.02	0.20	0.66	8	+
Linear			BA	0.00	0.03	0.88	8	+
Quadratic		STV	Abd	0.58	4.83	0.05	7	+/-
Linear			BA	0.46	6.87	0.03	8	+
Linear	SLA	ITV	Abd	0.03	0.22	0.65	8	+
Linear			BA	0.03	0.23	0.65	8	-
Linear		STV	Abd	0.43	5.95	0.04	8	-
Linear			BA	0.28	3.13	0.11	8	-
Linear	WD	ITV	Abd	0.03	0.23	0.65	8	+
Linear			BA	0.01	0.06	0.81	8	+
Quadratic		STV	Abd	0.56	4.50	0.05	7	+/-
Linear			BA	0.05	0.42	0.54	8	+

Legend: Calc = Calculation method. Indicates whether the species means were calculated using species traits values across plots (STV) or per plot (ITV). BT = Blade thickness (mm). LDMC = Leaf dried mass content (g.g⁻¹). SLA = Specific leaf area (cm².g⁻¹). WD = Wood density (g.cm⁻³). Weight = Indicates how the community weighted mean was weighted, using species abundance (Abd), or species basal area (BA). Estimate indicate whether the relationship is positive (+) or negative (-). When the estimate is equal to “+/-”, it means that the relationship is quadratic and the first term is positive and the second term is negative related. Significant results are bold highlighted.

Source: The author, 2018.

Figure 1: Community weighted mean (CWM – weighted by species abundance) of species traits along altitudinal variation in ten permanent plots in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.

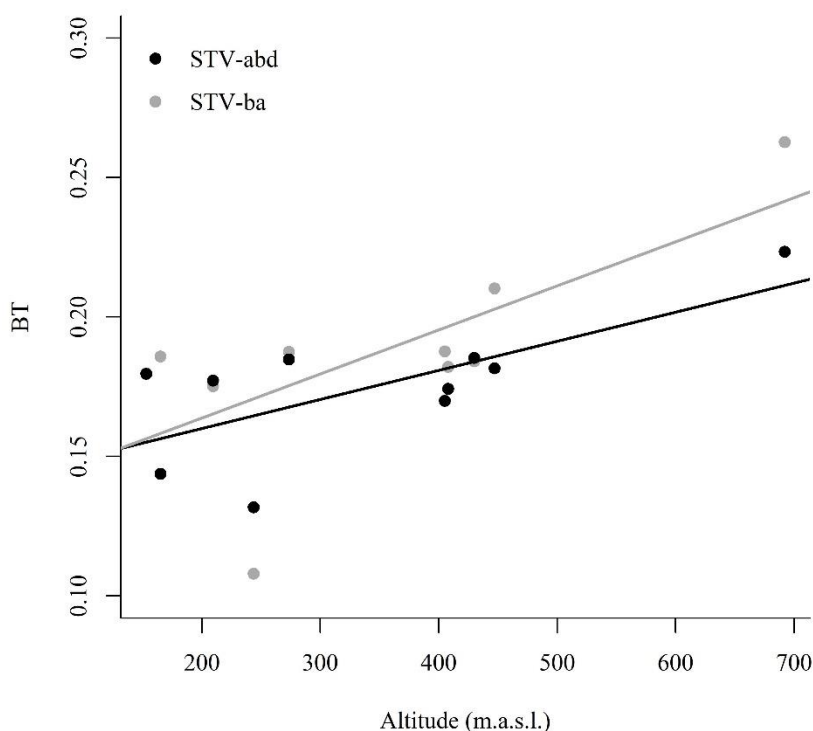


Legend: CWM weighted by species abundance, based on average traits per species. A- Blade thickness (BT – mm, $R^2 = 0.49$, $F = 7.73$, $DF = 8$, $p = 0.02$), B - Leaf dry mass content (LDMC – $g \cdot g^{-1}$, $R^2 = 0.60$, $F = 4.83$, $DF = 7$, $p = 0.05$), C- Specific leaf area (SLA – $cm^2 \cdot g^{-1}$, $R^2 = 0.42$, $F = 5.95$, $DF = 8$, $p = 0.04$) and D - Wood density ($g \cdot cm^{-3}$, $R^2 = 0.56$, $F = 4.50$, $DF = 7$, $p = 0.05$).

Source: The author, 2018.

We were able to compare the regressions slopes only for linear BT CWM_{stva} ($R^2 = 0.49$, $F = 7.74$, $DF = 8$, $p = 0.02$) and linear BT CWM_{stvb} ($R^2 = 0.49$, $F = 7.59$, $DF = 8$, $p = 0.02$), because only this trait had simultaneously two significant linear regressions. The results of comparison of regressions slopes showed a non-significant difference among regressions CWM_{stva} and CWM_{stvb} (Likelihood = 1.26, $df=1$, $p = 0.26$; Figure 2).

Figure 2: Comparisons of regressions slopes between the two significant CWM types for blade thickness (BT, mm) traits along altitudinal variation in ten permanent plots located in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.

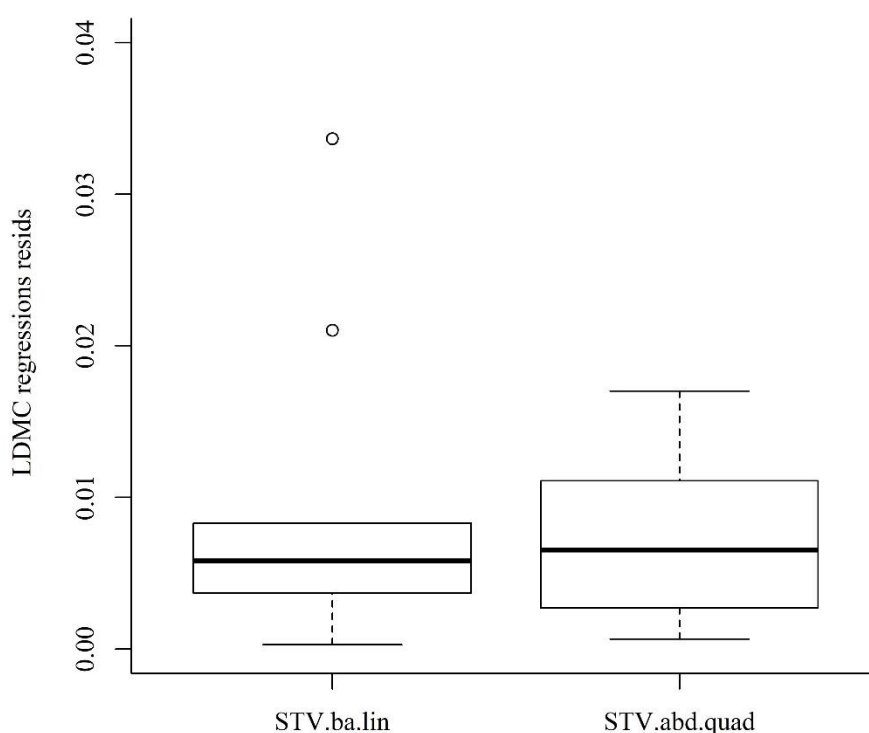


Legend: STV-abd, $R^2 = 0.49$, $F = 7.74$, $DF = 8$, $p = 0.02$. STV-ba, $R^2 = 0.49$, $F = 7.59$, $DF = 8$, $p = 0.02$. STV-abd is the linear regression represented by grey circles and lines. STV-ba is the regressions linear regressions represented by black circles and lines. STV-abd = Community weighted mean calculated using interspecific trait mean and weighted by species abundance. STV-ba = Community weighted mean calculated using interspecific trait mean and weighted by species basal area.

Source: The author, 2018.

LDMC was the only trait which had both a linear and a quadratic regression for two to CWM types: quadratic CWM_{stva} ($R^2 = 0.58$, $F = 4.53$, $DF = 7$, $p = 0.05$) and linear CWM_{stvb} ($R^2 = 0.46$, $F = 6.87$, $DF = 8$, $p = 0.03$) as significant. Comparing the regressions residuals we found no significant difference ($t = 0.58$, $df = 9$, $p = 0.58$), Figure 3.

Figure 3: Box-plot of the residuals of regressions of the trait leaf dried mass content (LDMC, $g \cdot g^{-1}$) and altitude across ten permanent plots located in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil ($t = 0.58$, $df = 9$, $p = 0.58$).



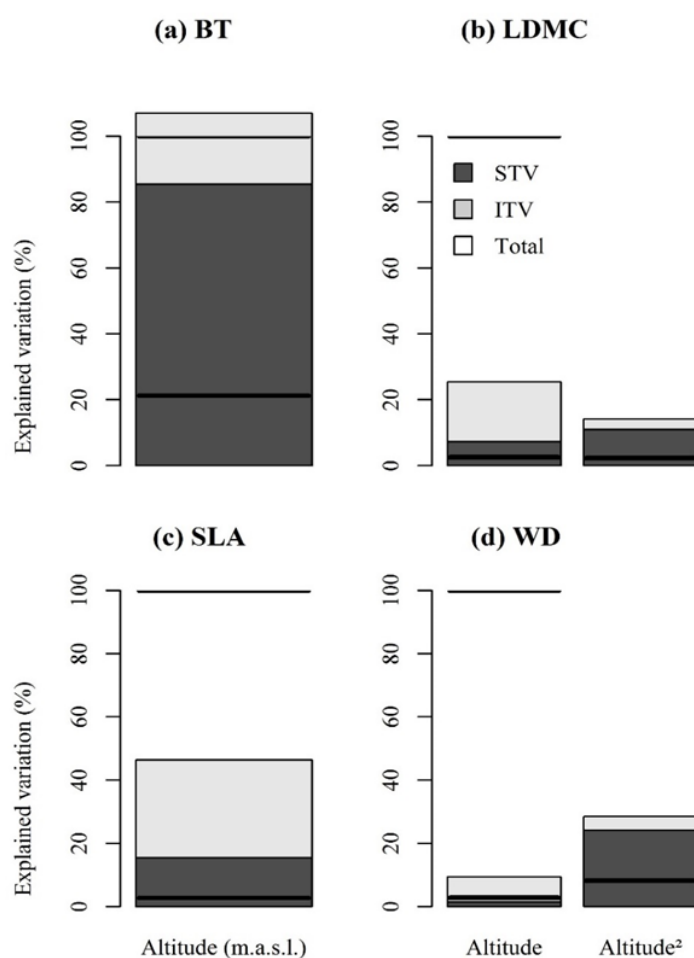
Legend: STV.ba.lin = Residuals of linear regression of LDMC and altitude using community weighted mean calculated with interspecific trait mean and weighted by species basal area. STV.abd.quad = Residuals of quadratic regression of LDMC and altitude using community weighted mean calculated with interspecific trait mean and weighted by species basal area.

Source: The author, 2018.

The results of trait flex analysis showed a higher contribution of STV than ITV in all traits measured. Only CWM_{stv} traits were significant (Table 3). In general CWM weighted by species abundance tended to explain a higher proportion of variance than CWM weighted by species

basal area, except in case of SLA (Figures 4 and 5). Even non-significant, the most part of covariations showed a negative correlation between STV and ITV.

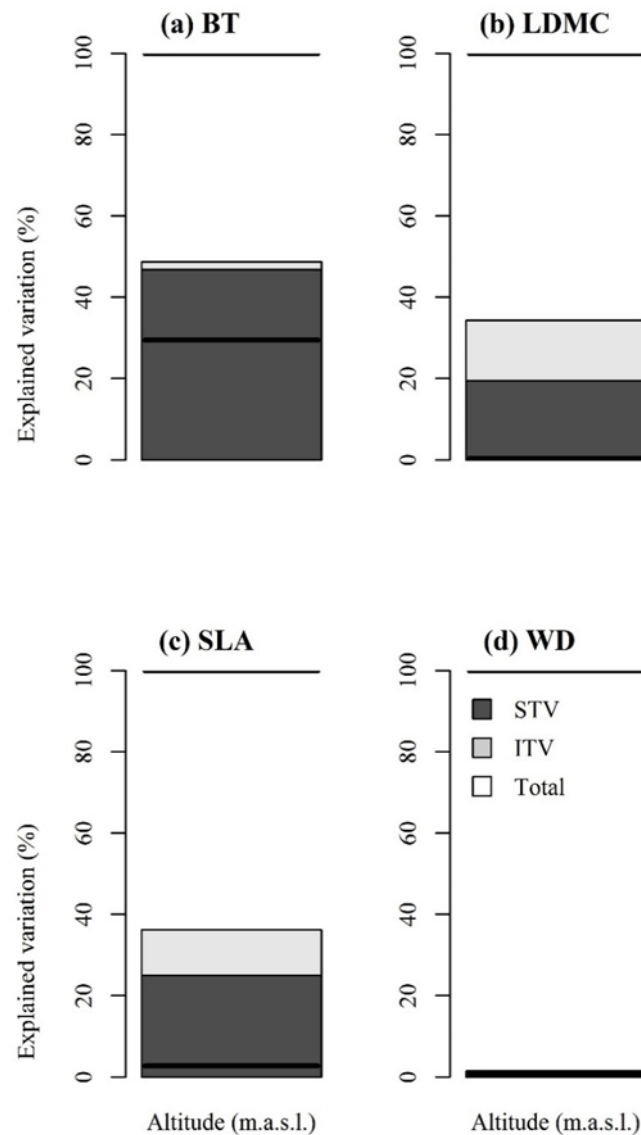
Figure 4: Relative contribution of the interspecific trait variation approach (STV) and intraspecific trait variation approach (ITV) of species traits along altitudinal variation in ten permanent plots in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.



Legend: Here the in community weighted mean (CWM) is weighted by species abundance. Traits measured were: (a) - Blade thickness (BT – mm), (b) - Leaf dried mass content (LDMC – $\text{g} \cdot \text{g}^{-1}$), (c)- Specific leaf area (SLA – $\text{cm}^2 \cdot \text{g}^{-1}$) and (d) - Wood density (WD, $\text{g} \cdot \text{cm}^{-3}$). LDMC and WD are quadratic regressions and thus, are represented by the first and second order of predictor variable (Altitude and Altitude²). Solid dark grey bars represent STV and solid light grey bars represent ITV. White and open bars limited by the black bars are the total variation is the variation in STV+ITV – Covariation among STV and ITV.

Source: The author, 2018.

Figure 5: Relative contribution of the interspecific trait variation approach (STV) and intraspecific trait variation approach (ITV) of species traits along altitudinal variation in ten permanent plots in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.



Legend: Here the in community weighted mean (CWM) is weighted by species basal area. Traits measured were: (a) - Blade thickness (BT – mm), (b) - Leaf dried mass content (LDMC – $\text{g} \cdot \text{g}^{-1}$), (c)- Specific leaf area (SLA – $\text{cm}^2 \cdot \text{g}^{-1}$) and (d) - Wood density (WD, $\text{g} \cdot \text{cm}^{-3}$). Solid dark grey bars represent STV and solid light grey bars represent ITV. White and open bars limited by the black bars are the total variation is the variation in $\text{STV} + \text{ITV} - \text{Covariation among STV and ITV}$.

Source: The author, 2018.

Table 3: Results of the comparison between the relative contribution of the interspecific trait variation approach (STV) and intraspecific trait variation approach (ITV) along altitudinal variation in ten permanent plots in Ilha Grande State Park, Angra dos Reis, Rio de Janeiro, Brazil.

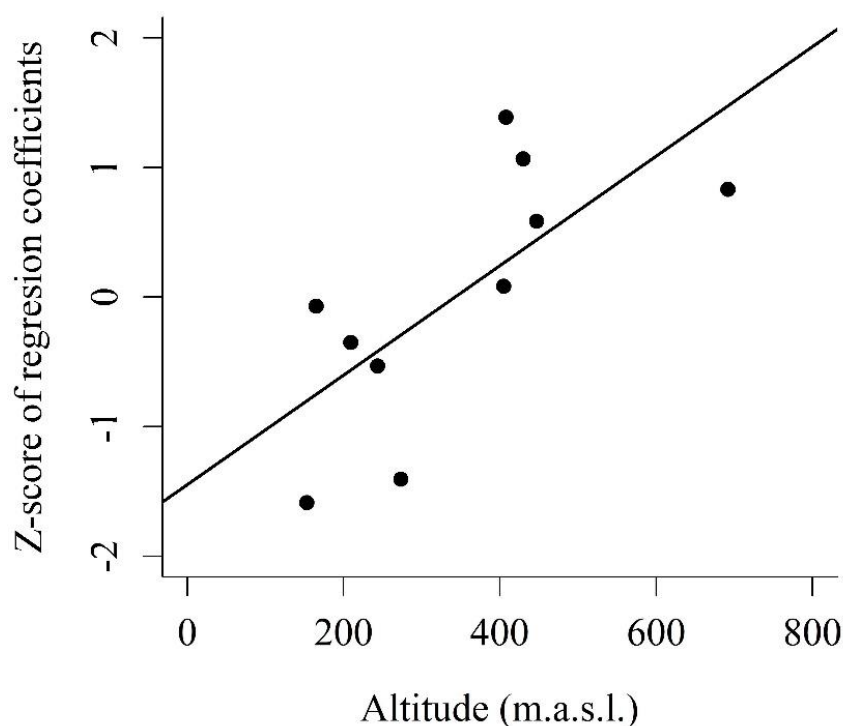
Trait	Weight	Variable	STV	ITV	Cov	Total
BT		Altitude	0.85 *	0.22 ^{ns}	-0.86 ^{ns}	0.21 ^{ns}
	Abd	Residuals	0.88 ^{ns}	0.64 ^{ns}	-0.73 ^{ns}	0.79 ^{ns}
		Total	1.74 ^{ns}	0.85 ^{ns}	-1.59 ^{ns}	1.00 ^{ns}
		Altitude	0.47 *	0.02 ^{ns}	-0.19 ^{ns}	0.29 ^{ns}
	BA	Residuals	0.49 ^{ns}	0.24 ^{ns}	-0.02 ^{ns}	0.71 ^{ns}
		Total	0.96 ^{ns}	0.26 ^{ns}	-0.22 ^{ns}	1.00 ^{ns}
LDMC		Altitude	0.07 ^{ns}	0.18 ^{ns}	-0.23 ^{ns}	0.02 ^{ns}
	Abd	Altitude²	0.11 *	0.03 ^{ns}	-0.12 ^{ns}	0.02 ^{ns}
		Residuals	0.13 ^{ns}	0.94 ^{ns}	-0.12 ^{ns}	0.95 ^{ns}
		Total	0.31 ^{ns}	1.16 ^{ns}	-0.47 ^{ns}	1.00 ^{ns}
	BA	Altitude	0.19 *	0.15 ^{ns}	-0.34 ^{ns}	0.00 ^{ns}
		Residuals	0.23 ^{ns}	0.55 ^{ns}	0.22 ^{ns}	1.00 ^{ns}
SLA		Total	0.42 ^{ns}	0.70 ^{ns}	-0.12 ^{ns}	1.00 ^{ns}
		Altitude	0.15 *	0.31 ^{ns}	-0.44 ^{ns}	0.03 ^{ns}
	Abd	Residuals	0.21 ^{ns}	0.63 ^{ns}	0.14 ^{ns}	0.97 ^{ns}
		Total	0.36 ^{ns}	0.94 ^{ns}	-0.30 ^{ns}	1.00 ^{ns}
		Altitude	0.25 ^{ns}	0.11 ^{ns}	-0.33 ^{ns}	0.03 ^{ns}
	BA	Residuals	0.64 ^{ns}	0.44 ^{ns}	-0.11 ^{ns}	0.97 ^{ns}
WD		Total	0.89 ^{ns}	0.56 ^{ns}	-0.44 ^{ns}	1.00 ^{ns}
		Altitude	0.01 ^{ns}	0.08 ^{ns}	-0.07 ^{ns}	0.03 ^{ns}
	Abd	Altitude ²	0.24 *	0.04 ^{ns}	-0.20 ^{ns}	0.08 ^{ns}
		Residuals	0.20 ^{ns}	0.50 ^{ns}	0.19 ^{ns}	0.89 ^{ns}
		Total	0.45 ^{ns}	0.63 ^{ns}	-0.08 ^{ns}	1.00 ^{ns}
		Altitude	0.01 ^{ns}	0.00 ^{ns}	-0.01 ^{ns}	0.01 ^{ns}
	BA	Residuals	0.26 ^{ns}	0.40 ^{ns}	0.34 ^{ns}	0.99 ^{ns}
	Total	0.27 ^{ns}	0.40 ^{ns}	0.33 ^{ns}	1.00 ^{ns}	

Legend: Traits measured were: Blade thickness (BT – mm), Leaf dried mass content (LDMC – $\text{g}\cdot\text{g}^{-1}$), Specific leaf area (SLA – $\text{cm}^2\cdot\text{g}^{-1}$) and Wood density (WD, $\text{g}\cdot\text{cm}^{-3}$). Weight represent if community weighted mean was weighted by species abundance (Abd) or by species basal area (BA). LDMC and WD are quadratic regressions and thus, are represented by the first and second order of predictor variable (Altitude and Altitude²). Cov = covariation. Total = total variation. Total variation is the variation in STV+ITV – covariation among STV and ITV. Significant results are bold highlighted. Probability values: $0.01 < * \leq 0.05$, ns = non-significant, > 0.05 .

Source: The author, 2018.

The results of our second hypothesis were according our expectation. We found a turnover in species functional trait strategies, from species traits divergence according individuals' proximity in lower altitudes to convergence of traits in higher altitudes ($R^2 = 0.49$, $F = 7.76$, $DF = 8$, $p = 0.02$), Figure 6.

Figure 6: Relationship between altitude and specimens' traits similarities according spatial proximity in ten permanent plots in Ilha Grande, Rio de Janeiro, Brazil.



Legend: Response variables are the regression coefficients (in units of standard deviation) from the multiple regression of matrices (specimens trait dissimilarity \times specimens pairwise spatial distance). Negative values represent divergent trait assembling while positive denotes convergence. ($R^2 = 0.49$, $F = 7.76$, $DF = 8$, $p = 0.02$). Z-score of regression coefficients = Regression coefficients converted to units of standard deviation.

Source: The author, 2018.

3.5 Discussion

As we expected, we found evidence of functional trait assembling according altitudinal variation. This influence however, was better detected using the approach calculating community weighted mean where species means refers to species trait value across the all plots together and weighting by species abundances (CWM_{stva}). Lianas are a functional group which tend to invest less in structural support (*i.e.* diametric growth) because they do not need to self-

supporting, but rely on other plants (Schnitzer 2005, Ewers et al. 2015). Consequently, the diametric increment tends to be in a slower rate when compared to other wood plant group, such as trees. In fact, this low investment in diametric increment can be detected in our data once the median of dbh was 2.1 cm. This characteristic of low investment in structural support may explain why the CWM weighted by basal area had lower explanatory power compared with CWM weighted by species abundance. Yet considering CWM_{stva} , our results showed that species turnover across plots explained the most part of trait variation. This finding may indicate that there is a set of exclusive species which can live under their optimized niche only in specific environmental/microclimatic conditions found within the plots where they occur.

We found a negative covariation among STV and ITV for the most part of traits evaluated in most part of CWM types. Even not significant, such trend of negative covariation deserves to be highlighted. This negative covariation indicates that trait value linked to STV operates towards a more conservative strategy as the altitude increases, as we hypothesized. On the other hand, trait value linked to ITV tended to shift to a more acquisitive strategy or vary irrespective to plots altitude. For example, *Diplopterys nigrescens* (A.Juss.) W.R.Anderson and C.Davis was the most abundant (99 individuals) and frequent (80% of plots) species in our study. However, their trait values per plot varied regardless altitudinal variation (data not shown). Thus, the ITV found in our study may indicate that most frequent/abundant species adopt a more generalist strategy. It can indicate a phenotypic variability among these species able to regulate their metabolic activity that they need not relying on morphological trait adjustment. Consequently, we did not find a relationship among the ITV of the traits measured and altitudinal variation.

Lianas are recognized as a functional group which usually possesses a faster acquisitive resources strategy when compared to other plant groups. This acquisitive strategy has been described for their morphological and physiological trait values (Asner and Martin 2012, Collins et al. 2016). However, we have strong evidence that occurs a functional trait adjustment in response to altitudinal variation. This finding may be critical to understand how lianas can be assembled in broader scale. The altitudinal variation usually emulates the climatic variation which occurs along latitudinal variation (Körner 2007). Thus, we can infer that liana species which occurs in more arid environments should present a more conservative strategy on morphological traits enabling them to deal with water deficit. In fact, there is evidence of this functional adjustment occurring at least to root traits (Carvalho et al. 2015, Carvalho et al. 2016). There is a large empirical evidence that global warming can alter forest structure and composition (Breshears et al. 2009, McDowell et al. 2011, Fauset et al. 2012). We have

evidence that climatic changes can select a given set of species which have given trait value suitable to a given environment. Nevertheless, our findings offer tools to demonstrate which species could be favored based on their trait value.

We found that liana community tend to shift their trait pattern, from divergent trait pattern when compared to their closest neighbors in lower altitudes, to a convergent trait pattern in higher altitudes. Our findings demonstrated that functional niche (*sensu* Carmona et al. 2016) of species tend to be more similar towards the highest altitude. As we included intraspecific trait variation in our analysis, we can assert that this trend remains strong even when the more abundant and frequent species which tend to vary their trait value regardless the variation in altitude (see the *Diplopterys nigrescens* example above) are present. Such functional convergence of trait strategy is usually viewed as consequence of environmental filtering acting on the pool of species which can thrive in a given locality (Rosado and de Mattos 2010, Bernard-Verdier et al. 2012, Sfair et al. 2016). Our data agree with this view. Functional convergence denotes a similar trait combination (Sosinski et al. 2013). In one hand it can buffer the community against potential problems concerning the loss of an important species which play or drive an important ecosystem process. On the other hand, the community tends to be less resilient when some disturbance occurs, once species tends to have a similar functional repertory to deal with the disturbance (Sosinski et al. 2013).

3.5.1 Possible implications of shift on leaf and wood traits for forest functioning

All leaf traits varied in the sense that the species tended to produce leaves with greater capacity to avoid the loss of water by evapotranspiration caused by tendency of aridity in higher altitudes (Leuschner 2000, Körner 2007). These variations in these traits are interpreted as investment in structures such as thicker and lignified cell walls, thicker cuticle, or even more trichomes (Wright et al 2004, John et al. 2017). Consequently, the leaves tend to be tougher. Tough and less palatable leaves usually require more time to be decomposed in the litter by both macro and microorganisms (Reich et al. 2014).

In addition to the measured leaf traits, the wood trait (wood density) indicates that there is a tendency to have denser wood as the altitude increases. This could be deduced even with the relationship between WD and altitude being presented as a second-order polynomial curve with the concavity facing downwards (Figure 1.d) because of the following factor. We remade the regression by taking away the plot, which presented the apparently discrepant data. As a result, the relationship remained significant linear and positive (data not shown). Thus, it is probable that this plot can be an outlier and WD obeys a positive relation with the altitude.

The values of leaves and wood traits toward to a more conservative spectrum can directly influence the cycling of nutrients in the forests, changing the dynamics of several organisms. Considering that branches and leaves of lianas they can contribute up to 40% of litter produced (Hora et al. 2008, Hegarty 1991) even though this functional group represents about 5% of the basal area in tropical forests (Schnitzer and Bongers 2011). It is reasonable to think that changes in the value of liana species traits can greatly affect the cycling dynamics of forest nutrients. Lianas are known to usually have leaves that provide the nutrients in the litter more quickly because they are more rapidly decomposed (Tang et al. 2012).

As we know there is a possibility that environments will become drier and hotter due to global climate change (Dai et al. 2013). These changes may favor species with tougher leaves and denser woods. This could trigger a profound change in nutrient dynamics in tropical forests causing a cascade of events affecting directly or indirectly different organisms. We detected that the lianas exhibited a functional response to this variation in water availability.

The total leaf area produced by a plant is directly related to the total sapwood area of their vessels (Medhurst and Beadle 2002). The reason behind this is to be able to satisfactorily supply water to the leaves during the photosynthetic process (Medhurst and Beadle 2002). Trees, for example, deal with this demand by investing in diametric growth in order to have a greater density of conducting vessels per area of wood (Medhurst and Beadle 2002). Lianas on the other hand, do not need to invest diametric growth because they grow supported in other plants. Nevertheless, lianas have large canopy areas with several leaves (Putz 1983). The evolutionary pathway found by this functional group was to invest in large vessels to maintain their crowns (Ewers et al. 2015). A scenario of increased drought can influence the size of the conductive vessels and consequently influence the amount of leaves that a liana produces. Thus, climatic changes can affect not only the quality, but also the quantity of leaves produced by lianas that are released in the litter.

3.6 Conclusions

We demonstrated that liana community tends to be functionally assembled according to the environmental/microclimatic variation which occurs across an altitudinal variation. We presented evidences that the threshold of altitudinal variation in which these functional adjustments occurs in plant communities is even smaller than that was reported on literature (Leuschner 2000, Pescador et al. 2015, Rosado et al. 2016). The approach adopted here allowed disentangling the role of altitude on assembling of ITV and STV. Furthermore, comparison

among distinct CWM types allowed us to better elucidate how altitudinal variation can shape the patterns of liana functional assembling. Nevertheless, given the importance of lianas on structure, process and dynamics of tropical forest (Schnitzer and Bongers 2002) we highlight that future climatic changes on such type of environment towards a dryer conditions may contribute to functional homogenization of liana communities compromising ecological process on tropical forest. Moreover, we expect a loss of species if the climate follows this trend given some liana species apparently were particular of specific altitudes. We emphasize that our finds should be considered for predicting the response of lianas to predict future scenarios global warming.

3.7 References

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Table S1: Relation of the traits used in calculation of trait dissimilarity, based on trait overlap approach (de Bello et al. 2012) for the lianas surveyed in Ilha Grande State Park, Angra do Reis, Rio de Janeiro Brazil.

Trait	Acronym	Description	Unit	\bar{Y}	σ
Blade area	AREA	Area of fresh leaf blade	cm ²	77.26	59.06
Blade fresh mass	BFM	Fresh mass of leaf blade	g	1.60	1.56
Petiole fresh mass	PFM	Fresh mass of leaf petiole	g	0.15	0.32
Internode fresh mass	IFM	Fresh mass of internode	g	0.60	1.38
Blade dry mass	BDM	Leaf blade mass after oven-dried	g	0.51	0.51
Petiole dry mass	PDM	Leaf petiole mass after oven-dried	g	0.03	0.04
Internode dry mass	IDM	mass mass after oven-dried	g	0.18	0.26
Metamer dry mass	MM	Metamer mass after oven-dried	g	0.57	0.60
Wood dry mass	WDM	A wood mass section after oven-dried	g	2.33	2.29
Wood volume	WV	Volume occupied of a given fresh wood section	cm ³	5.20	4.99
Petiole length	PL	Petiole length	mm	21.34	19.77
Internode length	IL	Internode length	mm	58.49	39.26
Blade thickness	BT	Blade thickness	mm	0.16	0.07

Petiole specific length	PSL	Petiole length per unit of petiole dried mass	cm.g ⁻¹	142.89	245.83
Internode specific length	ISL	Internode length per unit of internode dried mass	cm.g ⁻¹	24.86	20.30
Internode length per leaf area	ILLA	Internode length per unit of blade fresh area	cm.cm ⁻²	0.11	0.13
Petiole length per leaf area	PLLA	Petiole length per unit of blade fresh area	cm.cm ⁻²	0.04	0.04
Internode mass per leaf area	IMLA	Internode dried mass per unit of blade fresh area	g.m ⁻²	26.74	36.72
Petiole mass per leaf area	PMLA	Petiole dried mass per unit of blade fresh area	g.m ⁻²	3.72	2.33
Metamer mass per leaf area	MMLA	Metamer dried mass per unit of blade fresh area	g.m ⁻²	92.28	45.42
Leaf area per metamer mass	LAMM	Blade fresh area per unit of metamer dried mass	cm ² .g ⁻¹	130.25	52.15
Blade dry mass fraction	LMF	Blade dried mass per unit of metamer dried mass	%	72.84	17.11

Petiole dry mass fraction	PMF	Petiole dried mass per unit of metamer dried mass	%	4.21	2.22
Internode dry mass fraction	IMF	Internode dried mass per unit of metamer dried mass	%	23.27	17.24
Specific leaf area	SLA	Blade fresh area per unit of blade dried mass	cm ² .g ⁻¹	185.75	73.60
Leaf mass	LMA	Blade dried mass per unit blade fresh area	g.m ⁻²	62.49	23.43
Leaf volume	LVOL	Volume occupied of of a given fresh blade.	cm ³	1.39	1.41
Leaf density	LD	The amount blade dried mass content of a given blade fresh volume	g.cm ⁻³	0.42	0.23
Leaf area ratio	LAR	The amount metamer dried mass content of a given blade fresh area	g.m ⁻²	92.28	45.42
Leaf mass ratio	LMR	The amount of blade fresh area per unit of metamer dried mass	cm ² .g ⁻¹	130.25	52.15

Leaf dried mass content	LDMC	The proportion of leaf blade dried mass per leaf blade fresh mass	g.g^{-1}	0.32	0.08
Petiole dried mass content	PDMC	The proportion between petiole dried mass and petiole fresh mass	g.g^{-1}	0.28	0.11
Internode dried mass content	IDMC	The proportion between leaf blade dried mass and leaf blade fresh mass	g.g^{-1}	0.36	0.09
Metamer dried mass content	MDMC	The proportion between metamer dried mass and metamer fresh mass	g.g^{-1}	0.33	0.07
Wood density	WD	The amount wood dried mass content of a given wood fresh volume	g.cm^{-3}	0.47	0.11

Legend: In this table is given a brief description of the traits, their mean (\bar{Y}) and standard deviation (σ) considering all the plots together.

Source: The author, 2018

4 TESTING THE RELATIVE CONTRIBUTION OF SPATIAL AND ENVIRONMENTAL VARIABLES ON PHYLOGENETIC DIVERSITY OF TREE AND LIANAS IN A TROPICAL RAIN FOREST

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4.1 Abstract

Understanding the mechanisms shaping community assemblies belongs to some of the main fundamental questions in ecology. Recently, phylogenetic approach has been increasing in its appliance on ecological approach. Despite the widespread use of phylogenetic approach to improve the understanding on plant assembly and responses to environmental changes there is a current debate on the validity of patterns of phylogenetic under and overdispersion as proxies to assembly rules. Notwithstanding this debate, phylogenetic approach can be a promising approach when correctly applied. From our knowledge there is no initiative which addressed how co-occurring species belonging to different life-forms respond in terms phylogenetic diversity. The aim of this study was to investigate and compare the relative contribution of environmental and spatial variables over patterns of phylogenetic assembly in co-occurring trees and lianas. We found that lianas phylogenetic assembly responded mainly to spatial patterns while trees had a contribution more or less equivalent of environmental and spatial patterns. We considered that the distinct growth strategies and colonization of the growth forms may be the explanation behind the differences found. Moreover, we highlight the importance of our findings to implement conservation and management practices once these two functional groups can respond distinctly to practices implemented.

Keywords: Climbing-plants. Self-supporting-plants. Phylogenetic-approach. Functional groups. Tropical-forest. Environmental-structure. Spatial structure.

4.2 Introduction

Understanding the mechanisms shaping community assemblies belongs to some of the main fundamental questions in ecology (Sutherland et al. 2013). Traditionally, patterns of convergence and divergence in traits of coexistent species have been accounted as the result of environmental filtering and competition, respectively (Webb et al. 2002). In this sense, a common view is that phylogenetic diversity (PD), a measurement of biological diversity accounting the evolutionary differences among species (Faith 1992), could be used as proxy for community assembly (Webb et al. 2002). The reasoning for this assumption is that, assuming trait conservatism, convergence could be the result of more phylogenetically related species (*i.e.*, phylogenetic underdispersion) able to cope with environmental filtering (Webb et al. 2002), on the other hand the co-occurrence of less phylogenetic related species (*i.e.* overdispersion) would reflect the importance of competition (Webb et al. 2002). Thus, when trait information is lacking, an approach commonly used to elucidate how communities are assembled is to access phylogenetic diversity of communities (Swenson 2013, De Bello et al. 2016)

Despite the widespread use of PD to enhance the understanding on plant assembly and responses to environmental changes (Cavender-Bares et al. 2009, Winter et al. 2012, Kraft Ackerly 2010, Tucker et al. 2017), there is a current debate on the validity of patterns of phylogenetic under and overdispersion as proxies to assembly rules (Swenson 2013, Gerhold et al. 2015, de Bello et al. 2015, Rosado et al. 2016). It has been advocated that the direct relationship between an ecological force (*e.g.*, filtering and competition) and a community pattern (*e.g.*, trait convergence and phylogenetic underdispersion) is no longer correct because either factor, which are not mutually exclusive - environmental filtering, competition and disturbance - may lead to any functional and phylogenetic pattern (Gerhold et al. 2015). Moreover, beyond the fact that phylogenetic patterns differs from local to regional scales (from over to underdispersion, respectively, Swenson et al. 2006), any given phylogenetic pattern in a community may show different trait patterns (*i.e.*, convergence or divergence) depending on the traits measured (Swenson 2013, Rosado et al. 2017).

Following this claim for a more parsimonious interpretation of PD patterns, from our knowledge there was any initiative to evaluate how co-occurring species belonging to different life-forms may add more complexity when interpreting PD to infer processes behind community assembly. In this sense, it is not clear the interplay between environmental variables

and spatial autocorrelation related to PD of lianas and trees. Both are the most conspicuous plant functional groups in tropical forests (Schnitzer and Bongers 2002, ter Steege et al. 2013) and due to their hyperdiversity in tropical forests, they play an important role on whole forest structure (Tang et al. 2012, Fauset et al. 2015). In spite of lianas and trees being two important functional groups, some mechanisms underlying the phylogenetic diversity of lianas and trees are still beginning to be investigated. Some studies have already addressed the contribution of anthropogenic disturbance and environmental drivers such soil fertility respectively for phylogenetic diversity of trees (Santos et al. 2010) and lianas (Roeder et al. 2015). Lianas and trees would respond distinctly due their different strategies to occupy the environment and to resource use. In the case of trees, as their individuals are generally fixed (rooted) in a single point of a given environment they would be constrained to the resources of a unique place. In contrast, a single liana individual can be rooted in many points in a given landscape or/and may have compound crowns for each point where it is ascending upwards the canopy (Schnitzer et al. 2008). Therefore, lianas would not be constrained to the resources of a unique place as tree usually would. Besides this foraging advantage, this multifocal growth strategy (*sensu* Amorim et al. unpublished) may act as a dispersion structure as well. As a consequence, liana species would be more evenly distributed along the landscape and the effect of environmental filtering would be attenuated. Thus, due to the distinct growth strategies between lianas and trees we expected distinct drivers would play a major role on the PD. To our knowledge, these two functional groups were not investigated together and their response in terms of community phylogenetics were not compared neither. The importance of investigate co-occurring distinct life-forms can reveal distinct relationships between PD for both trees and lianas and spatial and environmental variables. It can help us to predict how changing environment in a tropical forest site may affect these two important woody life-forms.

The aim of this study was to investigate what are the drivers of community phylogenetics for lianas and trees. We hypothesized that tree PD would be shaped mainly by environmental variables such as soil fertility. Conversely, liana PD would be assembled mainly by spatial factors (*i.e.* proximity of sites) due to their rooting strategies.

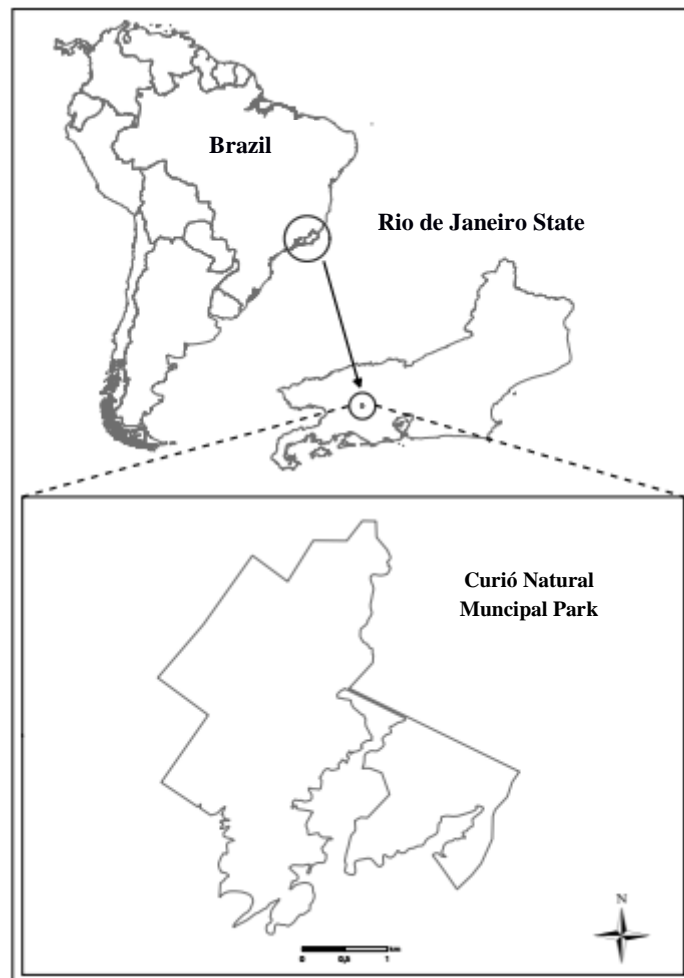
4.3 Methods

4.3.1 Study area

We conducted the study at Curió Natural Municipal Park (CNMP). The study site is a protected Atlantic Rain Forest remnant located in southeastern Brazil (22°35'14" S,

43°42'07"W, Figure 1). CNMP has 914 ha area and altitude ranging from 53-672 m.a.s.l. The average temperature is 22.4°C, the total+6 rainfall is 1260.8 mm and the mean air moisture is 75.3%. CNMP is mainly composed by a secondary forest (Cysneiros et al. 2015, Cysneiros et al. 2017).

Figure 1: Map showing the location of Curió Natural Muncipal Park (CNMP). CNMP is forest remnant located in southeastern Brazil.



Source: The author, 2018

We installed thirty 100 m² plots (2 X 50 m) distant at least 50 meters from each other. In each plot, we sampled all rooted lianas with stem diameter ≥ 1.0 cm (henceforth dbh) at 1.30 m from the rooting point (Schnitzer et al. 2008). Trees ≥ 5 cm dbh were sampled. We collected lianas and tree individuals for further identification. We collected soil samples (0-20cm depth) in the center and in the ends of the plot. We mixed each single sample of soil of each plot and obtained a compound sample. From these samples we obtained the following soil chemical and physical elements: pH (in water), the ions, hydrogen (H^+ , cmolc.dm⁻³), aluminum (Al^{3+} , C cmolc.dm⁻³), calcium (Ca^{2+} , cmolc.dm⁻³), magnesium (Mg^{2+} , cmolc.dm⁻³), potassium (K^+ , cmolc.dm⁻³), phosphorus (P^{3+} , cmolc.dm⁻³) organic carbon (C, g.kg⁻¹) and clay (%), silt (%) and sand (%). We also measured canopy openness (Open), by taking pictures of the canopy at 1.5 m from the ground with a hemispherical lens. We treated at Gap Light Analyzer 2.0 (Frazer *et al.* 1999). Using this software, we calculated the percentage of sky not covered by the canopy. It was interpreted as an indirect measurement of light entrance inside the forest. We measure the slope of the plot (%) using a digital clinometer at the same points of soil sampling. We considered soil, canopy and slope as the set of environmental variables. For lianas, we also considered as environmental variables the number of trees dbh ≥ 5 cm per plot (NT) and basal area (BA) of trees ≥ 5 cm dbh per plot. As surrogate of spatial variables, we used the geographic coordinates from the middle of each plot.

4.3.2 Phylogenetic analysis

We constructed a phylogenetic tree for each growth form. Species were classified by genus and family to use the PHYLOMATIC function of Phylocom 4.2 to assemble the species list into a phylogeny. We calibrated the age of the branches and the tips of phylogenetic trees using the maximum ages in the 95% highest confidence interval in the Bayesian Analysis estimated in Magallón et al. (2015). These authors did not estimate the ages for two families (Phytolaccaceae and Olacaceae). Hence, we used the estimated ages, (maximum Lognormal distribution values), from Bell et al. (2010). We calculated the mean pairwised phylogenetic distance (MPD), mean nearest taxon phylogenetic distance (MNTD), net related index (NRI), and nearest taxon index (NTI). MPD is the average phylogenetic distance among two random individuals in a sample and MNTD is the distance measured to the closest relative. NRI and NTI are standardized metrics of MPD and MNTD, respectively (Webb et al. 2002). We used the COMSTRUCT function to calculate the phylogenetic diversity metrics for each sample after constructing the time-calibrated phylogeny of our study area. We generate null communities from the phylogeny pool and after computing observed and expected MPD and MNTD for each

plot, we calculated the Net relatedness index (NRI) and nearest taxon index (NTI) metrics from 999 null communities. NRI indicates the overall clustering of taxa on phylogeny and NTI indicates terminal clustering (Webb et al. 2002). For both metrics, values of ≤ -1.96 indicates significantly overdispersion and $\geq +1.96$ indicates underdispersion (Vamosi et al. 2009). We calculated all metrics using phylocom software version 4.2 (Webb et al. 2008). Undetermined individuals (12) were excluded from our analysis.

4.3.3 Data analysis

We checked normality for all phylogenetic metrics and environmental variables. We did not check for spatial variables. We log-transformed (Logn) variables when they did not meet the assumption of normality. We also scaled all variables to units of standard deviation (z-score). For geographic coordinates, we centered the latitude and longitude values. We performed a principal coordinate neighboring matrices (PCNM) using Euclidian distance of the geographic coordinates of each plot. This approach is commonly used to transform (spatial) distances to rectangular data that is suitable for constrained ordination or regression (Boccard and Legendre 2002). Then, we retained the axes with positive values and interpreted them as spatial variables (Boccard and Legendre 2002).

Due to a huge number of environmental and spatial variables, we ran a forward selection (Blanchet et al. 2008, Dray et al. 2013) for each set of variables (environmental and spatial) in order to depict the most relevant variables influencing the phylogenetic diversity. This stepwise procedure consisted to perform a multiple regression between a given phylogenetic metric (MPD, MNTD, NRI, NTI) and each set variables and use the r-squared (r^2) and adjusted r-squared (r^2 -adj) values of each regression as a criterion for a variable selection. Then, we ran again the multiple regressions, this time informing the thresholds of r^2 and r^2 -adj and a level of significance as threshold ($\alpha \leq 0.1$). We did not adopt a so conservative α . Forward selection was also useful to avoid use variables highly correlated which could bias our results. The procedure stopped after to retain all the variables within the level of significance. The level of significance was calculated using 999 resampling. After variables selection, we ran a multiple regression among response variables and each remnant variables (both for liana and trees separately). The remaining variables after the procedure of variable selection for each phylogenetic index according the growth form are summarized on Table 1. In order to test what component had the highest relative contribution for the phylogenetic metrics, we partitioned-out the variance of environmental and spatial variables. We performed the variance partitioning only when the data purely environmental (PURE E) or purely spatial (PURE S) were

significant. The variance partitioning permitted us to calculate the proportion of variance of explained by environmental and spatial variables together (E+S), the proportion of variance explained by environmental variables after controlling the effect of spatial variables (E:S) and the proportion of variance explained by spatial variables after controlling the effect environmental variables (S:E). Every time a regression involving liana phylogenetic indices selected BA or NT (both tree features) we also checked whether BA or NT was correlated to some tree phylogenetic indices using Pearson simple correlation ($\alpha \leq 0.05$). We adopted this procedure in order to check if BA or NT could be linked to tree phylogenetic diversity. All the statistical analyses were performed in R (R Core Team 2015) using the packages “packfor” (Dray et al. 2013) and “vegan” (Oksanen et al. 2013) respectively for forward selection and PCNM and variance partition and procedures. For the sake of the clarity, we made a table with all the abbreviations used in this article but the chemical elements (Table S1, supporting information).

4.4 Results

Slope and Sand were the most common variables selected as explanatory variables in the regressions, both for liana and tree phylogenetic indexes (Table 1). For Trees, only Slope explained the variation in MPD ($R^2\text{-adj} = 0.17$, $F = 7.24$, $df = 28$, $P < 0.05$). Tree NRI PURE E regression was represented by pH, Slope and Sand. These variables together were strongly and positively related to tree NRI ($R^2\text{-adj} = 0.59$, $F = 14.77$, $df = 26$, $p < 8.2 \cdot 10^{-6}$). The relationship between MPD X PURE S was not significant. For Lianas, the relationship MPD X PURE E, and NRI X PURE E were not significant and thus, not accounted for variance partitioning (Table 1).

Table 1: Results of multiple regressions for lianas and trees from Parque Natural Municipal do Curió de Paracambi.

Growth form	response variable	PURE E	R ² adj	F	df	P-value	PURE S	R ² adj	F	df	P-value
Tree	MPD	Slope [*]	0.17	7.24	28	*	PCNM4 ^{+ns}	0.08	3.67	28	ns
	NRI	pH ^{+**} +Slope ^{+**}	0.59	14.77	26	****	PCNM3 ^{-*} +PCNM2 ^{+ns}	0.24	5.59	27	**
		+Sand ^{+*}									
	MNTD	Slope ^{***}	0.32	14.39	28	***	PCNM2 ^{-**} +PCNM13 ^{-*} +PCNM17 ^{-*} +PCNM9 ^{+*} +PCNM5 ^{-*}	0.53	7.54	24	***
NTI	Slope ^{+**}	0.23	9.46	28	**	PCNM2 ^{+*} +PCNM1 ^{-*} +PCNM13 ^{+ns}	0.31	5.42	26	**	
Liana	MPD	Mg ^{+*} +Slope ^{-ns}	0.13	3.1	27	ns	PCNM5 ^{-*}	0.16	6.68	28	*
	NRI	BA ^{+ns}	0.05	2.53	28	ns	PCNM17 ^{+*} +PCNM14 ^{-*}	0.22	3.95	27	*
	MNTD	NT ^{-**}	0.22	8.96	28	**	PCNM11 ^{-*} +PCNM10 ^{+*} +PCNM7 ^{-ns} +PCNM13 ^{+ns}	0.31	4.28	25	**
	NTI	NT ^{+**}	0.10	4.24	28	*	PCNM3 ^{+*} +PCNM18 ^{-*}	0.20	4.73	27	*

Legend: Here are showed the environmental (Pure E) and spatial (Pure S) variables obtained from variable selection procedure. Environmental variables: BA - Basal area of trees per plot, Mg - magnesium, NT - number of trees dbh \geq 5cm per plot, Sand - soil sand content, Slope - plot slope. Spatial variables: PCNM - principal coordinate neighboring matrices axis. Response variables: MPD - mean pair-wised phylogenetic distance, MNTD - mean nearest taxon phylogenetic distance, NRI - net relatedness index, NTI - net taxon index. Upperscore minus signal (-) indicates negative correlation between response and predictor variables, upperscore plus signal (+) indicates positive correlation between response and predictor variables. P-value codes: ns= non significant, * = P < 0.05, ** = P < 0.01, *** = P < 0.001, **** = P < 0.0001

Source: The author, 2018

Tree NRI PURE S showed an increasing of phylogenetic clustering with increasing of spatial distance (Table 1, supporting information). In tree MNTD and NTI, Slope was the only environmental explanatory variable. Moreover, in general terms, the increasing of spatial distance promoted a decreasing of phylogenetic divergence (MNTD values) and increasing of phylogenetic clustering (NTI values) (Table 1, supporting information). For lianas, all phylogenetic indices but MNTD and NTI had among the explanatory variables BA, NT, which were features of tree stand. Yet for lianas, regressions MPD X PURE E and NRI X PURE E had no significant effect (Table 1). In liana MNTD and NTI only NT represented PURE E component. Spatial variables played a major role of phylogenetic diversity of lianas. Similarly, to trees, the general trend was the decreasing of phylogenetic divergence with the increasing of spatial distance and the increasing of phylogenetic clustering with increasing spatial distance (Table S2 supporting information).

The variance partitioning for trees showed NRI E:S remained significant. Although, tree NRI S:E was not significant (Table 2). Tree MNTD and NTI both E:S and S:E were significant. However, S:E explained higher proportion of variance in tree MNTD an NTI indexes. Similarly, in lianas, we had both E:S and S:E significant for MNTD and NTI indexes. Moreover, as we found for trees, in lianas S:E explained higher proportion of variance in MNTD an NTI indexes (Table 2).

Table 2: Variance partitioning analysis for lianas and trees from Parque Natural Municipal do Curió de Paracambi.

Growth form	response variable	E+S				E:S				S:E			
		R ² adj	F	df	P-value	R ² adj	F	df	P-value	R ² adj	F	df	P-value
Tree	NRI	0.58	9.00	24	****	0.34	8.3	24	***	0.01	0.8	24	ns
	MNTD	0.58	7.22	23	***	0.05	4.00	23	*	0.27	4.6	23	**
	NTI	0.45	6.09	25	***	0.14	7.4	25	*	0.22	4.8	25	*
Liana	MNTD	0.42	5.22	24	**	0.11	5.8	24	*	0.20	3.5	24	*
	NTI	0.30	5.18	26	**	0.10	4.8	26	*	0.20	5.1	26	*

Legend: Here are shown the variance explained by environmental and spatial variables together (E+S), the variance explained by environmental variables after controlling the effect of spatial variables (E:S) and the variance explained by spatial variables after controlling the effect of environmental variables (S:E). Response variables: MPD - mean pair-wised phylogenetic distance, MNTD - mean nearest taxon

phylogenetic distance, NRI - net relatedness index, NTI - net taxon index. Tree MPD was not shown because only environmental variables had a significant influence. Liana MPD and NRI were not shown because only spatial variables had a significant influence (see Table 1). P-value codes: ns= non-significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$.

Source: The author, 2018

The correlations between tree phylogenetic indices and BA and NT had only MNTD and NTI showing significant correlations (Table 3). Overall, tree MNTD was negatively correlated to NT and BA, while NTI was positively correlated.

Table 3: Correlations tests among tree phylogenetic indices and number of trees per plot (NT) with diameter at breast height (dbh) ≥ 5 cm and tree basal area (BA) in Parque Natural Municipal do Curió de Paracambi.

	BA	NT
MPD	-0.26	0.14
NRI	0.26	-0.001
MNTD	-0.45*	-0.43*
NTI	0.42*	0.13

Legend: The correlations values (r) followed by asterisks, denoted significant correlations ($P < 0.05$). MPD - mean pair-wised phylogenetic distance, MNTD - mean nearest taxon phylogenetic distance, NRI - net relatedness index, NTI - net taxon index.

Source: The author, 2018.

4.5 Discussion

4.5.1 Patterns of liana community phylogenetics

We found evidence supporting our hypothesis that phylogenetic pattern of liana community would be mainly driven by spatial variables and not by processes of environmental filtering. Our data indicated that lianas had only spatial variables explaining variation in MPD and NRI. Moreover, spatial variables explained a higher proportion of liana MNTD and NTI than environmental variables. The main driver of this pattern can be attributed to growing strategy of lianas, not the environmental factors commonly evoked in different studies on environmental filtering and community assembly (*e.g.* Lebrija-Trejos et al. 2010, Kraft et al. 2015, Ulrich et

al. 2017). This finding may be explained by the fact that one individual liana can be rooted at many points in the forest and also have more than one crown for each point where they reach the canopy (Gerwing et al 2006, Schnitzer et al. 2008). According to our predictions, phylogenetic diversity of trees would be explained by environmental variables. In terms of trends of environmental variables, pH was positively related to NRI, indicating that more acid soil contributed mainly to increase phylogenetic overdispersion.

Lianas have potentially the ability to elongate their stems and grow sometimes over one hundred meters (Ewers et al. 2015). This multifocal growing pattern may imply two important consequences explaining the results found: (i) lianas species could be more evenly distributed along the plots and (ii) as they are rooted at many points and can have crowns in many points, they can obtain resources from many points. Hence, the effect of environmental variables influencing liana diversity can be attenuated. Consequently, phylogenetic diversity could be more influenced by spatial autocorrelation, as we found.

Taking into account the environmental variables, they played a secondary role on the patterns of liana phylogenetic assembling. This secondary contribution, however, deserves attention once the unique variable that contributed was related to host tree features (number of tree per plot). Liana MNTD was negatively related to number of trees per plot (NT) while liana NTI was positively related to NT. These patterns indicate the importance of host tree availability for shaping liana phylogenetic diversity once an increase of phylogenetic clustering occurs at higher tree density. Apparently, this pattern is contradictory, once a higher tree density could provide a higher availability of support for lianas. However, in our study case, the increasing of tree density might have been accompanied by an increase in abundance of some tree species that have a set of traits which could avoid liana species to ascend on them. Consequently, it could decrease liana phylogenetic diversity. We have an evidence for this explanation since we found a negative correlation between tree MNTD and NT. This finding showed that an increasing of NT was correlated to decreasing of tree MNTD. It means that a higher number of trees per plot was accompanied by the increasing in abundance of few related tree species or increasing in abundance of a same species. Considering that MNTD (as well NTI) is a measure of phylogenetic diversity that accounts the mean distance to the more related species, it reveals that only the closest related tree species may be mediating the negative relationship between NT and liana MNTD and NTI.

Our findings are aligned to the findings by Roeder et al. (2015) where the increasing of tree basal area influenced positively liana NRI. Thus, plots with higher tree basal area tended to be

those where liana species were phylogenetic more clustered. Here, in spite of using BA as predictor variable (because this variable was not selected by forward selection procedure), we used number of trees per plot (NT). However, tree BA per plot is a product of both the sum of individual tree size and number of tree per plots *i.e.* tree basal area per plot usually is positively correlated with number of tree per plots (Pancel and Köhl 2016). It also important to highlight that besides the findings by Roeder et al. (2015) our results are the only study that demonstrated the importance of trees features as basal area and number of trees per plots for liana phylogenetic diversity. To sum up, spatial structure played a major role on patterns of liana community phylogenetics than environmental filtering. In other words, closest plots tended to show similar values of phylogenetic divergence and phylogenetic structure. Yet, having a minor importance on liana phylogenetic assembling, tree abundance per plot contributed for the pattern found, highlighting the importance of tree hosts for shaping liana assembling.

4.5.2 Patterns of tree community phylogenetics

The data confirmed our hypothesis that environmental variables would be more important do describe the variation in tree phylogenetic diversity was confirmed, at least for MPD. Tree MPD was negatively related to Slope. It indicates that the steepest plots tended to show closest lineages. A steeper terrain may limit the establishment of seeds that would be more prone to roll downward under such circumstances. Once seed mass and size are traits normally conserved in phylogeny (Kraft and Ackerly 2010), we can infer that related species which share a higher seed mass and size value would be less favored to occupy steep plots. For example, the site with the lowest MPD value (78.54) was compound only by two species – *Cupania racemosa* (Vell.) Radlk. (8 individuals) and *Myrcia splendens* (Sw.) DC (2 individuals). These species have small (respectively $2\text{--}2.8 \times 0.5\text{--}0.8$ cm and $0.5\text{--}0.6 \times 0.4\text{--}0.5$ cm) and light seeds (Rosa and Romero 2012, Frazão and Somner 2016). Moreover, a steeper site, due the action of gravity, is more susceptible to landslides or other disturbance generally facilitated by steep environments (Forbes and Broadhead 2011). Hence we could infer that only lineages sharing a set of traits (*e.g.* more resistant against breakage or sufficiently flexible, being strongly attached in the ground or having higher capacity to resprout after the landslide) that confer ability to deal with landslides would thrive in this scenario prone to disturbance. Consequently, trees species would be constrained in their phylogenetic diversity.

Environmental variables (represented by pH, Slope and Sand) explained a higher proportion of variation in NRI than spatial variables. Additionally, after controlling the effect

spatial variables, environmental variables still remained explaining the variation in NRI, though in a small proportion. However, the opposite was not true: after controlling the effect of environmental variables, spatial variables lost their power to predict any variation in tree NRI. Thus, probably the tolerance to acid soils is not a conserved trait to these tree species (Bernard-Verdier et al. 2012). Slope and Sand were also positive correlated to NRI. Yet, instead to contribute for overdispersion like pH, Slope and Sand tended to generate phylogenetic clustering. We argue that the mechanism that explains the influence of Slope over NRI is similar to what proposed to tree MPD. We additionally highlight the contribution of sandy soils to phylogenetic clustering by enhancing the effects of Slope, because soils with a higher content of sand tend to be more friable (Forbes and Broadhead 2011).

Contrary to our hypothesis, spatial variables determined a higher portion of variation for MNTD and NTI than environmental variables, even when the effect of environmental variables was controlled. Thus, we can infer that related species in the phylogeny of trees from CNMP are mainly constrained by dispersal limitation. This finding may indicate that these related-species have similar dispersal strategies. Considering the contribution of environmental variables, we had again Slope being the unique variable explaining the variation in tree MNTD and NTI. Slope was negatively related to MNTD and positively related to NTI. Hence, we consider the influence of Slope has similar applications to what was already discussed for MPD and NRI. Furthermore, we advocate that Slope influences tree phylogeny in CNMP in overall and terminal lineages. Thus, we can consider Slope as a potentially important environmental filter for phylogenetic diversity of trees in CNMP. In synthesis, environmental variables mainly determined the pattern of phylogenetic structure and divergence only when we consider the effect in the overall trend for the community (expressed by MPD and NRI). When we consider only related species (expressed by MNTD e NTI), we had the spatial structure of plots determining phylogenetic structure and divergence. Thus it may indicate evolutionary conservatism on related species concerning their dispersion ability.

4.6 Conclusions

As we expected, we found a higher contribution of spatial variables as main driver of phylogenetic diversity of lianas in CNMP. The probable explanation elicited were liana growth strategies which could reduce dispersal limitation. Thus lianas species would be more evenly distributed affecting directly their phylogenetic diversity. Furthermore, the negative

relationship between liana phylogenetic diversity and tree density per plot provided another new finding to literature evidencing the contribution of trees (i.e. host availability) to phylogenetic diversity of lianas. For trees, our expectations were partially confirmed. The overall trends in phylogeny (expressed by MPD and NRI) showed to be stronger influenced by environmental variables than spatial variables. Otherwise, phylogenetic diversity of trees concerning related species (MNTD and NTI) were mainly determined by spatial variables.

We showed that quantifying relative contribution of environmental and spatial variables may reveal important distinctions among plant functional groups. It has significant implications for predict changings in plant phylogenetic diversity in tropical forest because a same driver may play a distinct role or no role among growth forms. Here we demonstrated that distinct life-forms will respond distinctly to the environmental and spatial changes (*e.g.* promoted as consequence of the process of fragmentation) that may cause distinct patterns of phylogenetic assembling. Especially in a scenario of an intense fragmentation in all over tropical forests, we recommend that conservation studies involving PD should investigate or at least consider more than one plant functional group. Otherwise, by neglecting their distinct response we probably will be taking inefficient decisions concerning conservation strategies.

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Table S1: List of acronyms and the corresponding meanings for variables measured in Curió Natural Municipal Park (CNMP).

Acronym	Meaning
BA	Basal area of trees ≥ 5 cm dbh per plot
E:S	Proportion of variance explained by environmental variables after controlling the effect of spatial variables
E+S	Proportion of variance explained by environmental and spatial variables together
MNTD	Mean nearest taxon phylogenetic distance
MPD	Mean pairwise phylogenetic distance
NRI	Net related index
NT	Number of trees dbh ≥ 5 cm per plot
NTI	Nearest taxon index
PCNM	Principal coordinate neighboring matrices
PURE E	Environmental variables
PURE S	Spatial variables
S:E	Proportion of variance explained by spatial variables after controlling the effect environmental variables

GENERAL CONCLUSIONS

Our research on the patterns of climbing plant diversity at distinct geographic scales has yielded several important findings. Considering the aspects related to the current explanation of patterns of liana global abundance, our results showed how the combination of functional traits more focused on a resource acquisitive strategy and a multifocal growth strategy typical of this functional group may be mechanisms operating to determine ecological patterns of liana at different scales. Thus, the alternative proposition we present may point in a different direction to the current expected fate for climbing plants considering global climate change scenarios. This hypothesis still remain to be tested.

At regional scales, this study was the most exhaustive compilation of data on climbing plants for the Brazilian territory, resulting in 694 species. Using this information, we were able to demonstrate how climatic and spatial conditions can work together determining patterns of diversity. In addition, our results demonstrated that depending on the dimension of diversity (i.e. taxonomic or phylogenetic, alpha or beta), the variables that determine the patterns may alternate in magnitude or even do not influence. It is worth to highlight that geologically recent regions such as the restingas can already present a phylogenetic distinction when compared even with neighbor regions. We emphasize the relevance of the information resulting from this research to conservation strategies especially in the area of Rio de Janeiro State, where this study was carried out. The first study of this work on a local scale was basically aimed to test the relationship between the value of the functional traits related to water use and the altitudinal variation in the Ilha Grande State Park. The main differences between the study made here and the other studies that consider the altitude as a source of environmental / microclimatic variation was the incorporation of an approach that considered the intraspecific variation of functional traits, in addition to being made with lianas. This study was able to reveal how altitude can operate differently (or even not operate) on interspecific and intraspecific variation of functional characteristics. In addition, we were able to demonstrate how the predominant functional strategy among community plants can change (from trait divergence to trait convergence as the plants get spatially closer) given a relationship with the altitudinal variation. This study also showed that the threshold of altitudinal variation that impose functional variations in the plant community is lower than has been assumed in the literature for rainforest tropical forests, demonstrating that even such forest type may be subject to water deficit. We advocate that our

findings should be considered when simulating how plants community can cope with drought in tropical forest environments.

The second, local-scale study elucidated important topics on how distinct functional groups may respond to environmental and spatial gradient in terms of their phylogenetic component. Our results demonstrated that trees and lianas in general have distinct patterns of phylogenetic diversity in function of environmental and spatial variables. Distinct behavior concerning the gradients showed that these functional groups have clear differences between the patterns of phylogenetic alpha diversity and that these differences probably are linked to differences in colonization strategy and resources foraging. These differences point out that management methods and conservation of forest remnants should consider the differences in the responses of these functional groups in order to guarantee a more efficient intervention.

Collectively, our results revealed how environmental, spatial and climatic conditions can determine the patterns of different dimensions of the diversity of climbing plants at distinct geographic scales. In addition, we have gathered evidence (either through literature or data collected in the field) that demonstrated how the functional characteristics may be relevant to describe the variation in patterns of plant diversity. We emphasize that studies that incorporate various dimensions of diversity may be more appropriate ways of understanding how communities are assembled. We emphasize that functional approaches that consider intraspecific variation may actually allow for more detailed interpretations of how communities are structured. We understand that such approach requires more time in field sampling and more specialized analytical capacity and that it is not always possible to meet due to limitations imposed to studies intended to use such approach. However, we emphasize that investing in studies with such approach can provide better tools to understand how plant communities are structured. Finally, we emphasize that the findings of our studies put together in this thesis provided a portrait of community assembling of climbing plants. In a scenario of global climate change we emphasize that our results are important in decision-making to mitigate the negative effects on biological diversity in tropical forests.