UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
(BIOLOGIA VEGETAL)

Diversidade e estrutura arbórea ao longo de um gradiente altitudinal na Floresta Tropical Pluvial Atlântica

VITOR DE ANDRADE KAMIMURA

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutor em Ciências Biológicas (Biologia Vegetal).

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TÍTULO DA TESE: DIVERSIDADE E ESTRUTURA ARBÓREA AO LONGO DE UM GRADIENTE VERTICAL DE TEMPERATURA NA FLORESTA TROPICAL PLUVIAL ATLÂNTICA

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“A função primária da comunicação escrita foi facilitar a servidão.”

Claude Lévi-Strauss

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SUMÁRIO

APRESENTAÇÃO

Sobre o formato da tese

Esta tese foi estruturada em três capítulos, com uma Introdução Geral que apresenta, de forma simplificada, os conceitos básicos e o suporte teórico necessário para o entendimento de todos os capítulos que a compõe. Os capítulos são referentes a estudos realizados com diferentes abordagens sobre um grande conjunto de dados da comunidade arbórea da Floresta Atlântica, redigidos em inglês e no formato de manuscritos para apreciação em periódicos científicos. Ainda, estão inseridas as Considerações Finais, em que coloco pontos de vista, questões e compreensões pessoais sobre a temática desenvolvida e resultados encontrados.

Para facilitar o entendimento e a fluidez na leitura dos capítulos, as figuras e tabelas foram inseridas no corpo do texto, e os materiais suplementares de cada manuscrito estão ao final do capítulo correspondente.

A escolha do tema e a trajetória

A exuberância e encantos da Floresta Atlântica foram fatores determinantes na escolha de toda a minha carreira acadêmica até este ponto. Desde o Trabalho de Conclusão de Curso, passando ao Mestrado até culminar no Doutorado, a sua imensurável diversidade continua a me despertar extrema curiosidade e furor. Apesar de ser uma formação florestal com um número relativamente grande de estudos e sob diferentes abordagens, ainda nos resta muito a conhecer e tentar desvendar sobre tudo aquilo que concerne a sua riqueza de espécies e ecologia. As Florestas Tropicais, no geral, ainda apresentam muitas lacunas de conhecimento e possibilidades de novos estudos. Assim, qualquer proposta de trabalho envolvendo estes locais são inerentemente justificáveis e interessantes para o conhecimento científico e público.

Quando fui devidamente apresentado, em 2008, às imensas riquezas e poesia das diferentes formações florestais da Mata Atlântica, eu me vi tentado e impulsionado a compreender os eventos e processos que são capazes de promover tamanha co-ocorrência de espécies. Contando com a ajuda do meu ‘contínuo’ orientador, o Professor Marco Antonio Assis, iniciei minha trajetória no mundo do conhecimento botânico. Hoje, sei que este foi um primeiro passo fundamental na minha curta aventura acadêmica, culminando em uma publicação da pesquisa realizada no Trabalho de Conclusão de Curso (Kamimura, et al., 2008; “Floristic, structure and ecological groups of a tree community in the Atlantic Rainforest at Serra do Mar, SP, Brazil." - Nativa: Pesquisas Agrárias e Ambientais), e que me permite falar com um pouco mais de propriedade sobre tudo aquilo que pesquisei até hoje, embora tenha rumado mais a fundo para a área da Ecologia.

Este anfractuoso caminho teve um despertar na graduação, quando fui apresentado a Ecologia de Comunidades, por intermédio da Professora Leila Moura. Embora houvesse esse lado desperto, meu mestrado teve um caráter taxonômico como escopo inicial, no qual iniciamos com uma revisão das espécies da Família Lauraceae que ocorrem ao longo de um gradiente de elevação na Floresta Atlântica do sudeste brasileiro. Além disso, propusemos a produção de uma chave de identificação destas espécies, por meio de seus caracteres vegetativos. Contudo, na minha dissertação final e defesa, apresentei os padrões de variação da diversidade e estrutura dessa família ao longo da área estudada, nos quais encontramos uma novidade para as relações entre riqueza de espécies arbóreas e altitude, verificamos o aumento de espécies de Lauraceae conforme aumento da elevação. Como produto deste longo e gratificante trabalho, conseguimos uma publicação no tradicional periódico internacional “*Flora*” (Kamimura, et al., 2017; "Tree diversity and elevational gradient: The case of Lauraceae in the Atlantic Rainforest." - *Flora*)

Este fato, junto a tudo aquilo descrito anteriormente e a minha descoberta da Ecologia Funcional e Filogenética, me levaram a buscar compreender os processos e mecanismos que levam a arrebatadora diversidade arbórea da Floresta Atlântica. Estes quatro anos e meio de doutorado, além de me abastecerem com um enorme crescimento acadêmico, experiências na docência, saídas de campo inigualáveis, conhecer pessoas e lugares incríveis; me proporcionou uma das mais transformadoras oportunidades que tive em minha vida. No período de novembro de 2018 a outubro de 2019, fui contemplado com um bolsa de doutorado sanduíche (PDSE) da CAPES, por meio de uma aplicação individual. Esta oportunidade me possibilitou trabalhar junto a um incrível grupo de pesquisa e desenvolver com grande qualidade um dos capítulos desta tese. Trabalhei no Centro de Investigaciones sobre Desertificación (CIDE), Valência, Espanha, supervisionado pelo Dr. Francesco de Bello e com colaboração do Dr. Pavel Fibich do Departamento de Botânica, University of South Bohemia, České Budějovice, República Checa. A experiência de viver em outro país, beber de uma nova cultura, saborear novas conversas, e aprender com um dos mais renomados pesquisadores da área de Ecologia Funcional, e todos pesquisadores do CIDE, entre outros locais, é algo que não seria possível traduzir em palavras.

Porém, neste final de doutorado, me vejo impulsionado, novamente, a expandir minha área de trabalho e mantendo toda a gratidão pelo que essa jornada me trouxe de conhecimento, espero juntá-la a outras áreas de estudo, para poder ressignificar tudo isso, e lograr trazer um pouco de subjetividade a esta grande área do conhecimento. Por exemplo, inserido a Filosofia da Alteridade, tal como elucubrada por Emmanuel Lévinas, neste contexto das ciências biológicas e possibilitar, quiçá, uma maior comunicação entre a ecologia e outras áreas do conhecimento, bem como com pessoas que não estão dentro da academia.

RESUMO GERAL

A ecologia busca elucidar os processos e mecanismos responsáveis pelos padrões de diversidade, estrutura, montagem e funcionamento das comunidades. Neste trabalho, investigamos três questões fundamentais na ecologia de comunidades, utilizando um grande conjunto de dados da composição, demografia e atributos funcionais de comunidades arbóreas amostrados ao longo de um gradiente de elevação na Floresta Atlântica. No primeiro capítulo, utilizamos abordagens integrativas por meio de métricas da diversidade de espécies e filogenética sob diferentes arranjos de espécies (p.e. comunidade vs. famílias) para avaliar os processos ecológicos que conduzem as relações entre diversidade e elevação em florestas com mega diversidade. Encontramos um padrão de variação unimodal da diversidade da comunidade arbórea, emergindo da combinação dos diferentes padrões de diversidade de suas famílias com maior abundância. A diversidade filogenética local foi negativamente relacionada com a elevação e a diversidade regional (*turnover*) de espécies foi maior quanto maior a distância entre as comunidades. Estes resultados indicam a competição e a filtragem ambiental como principais processos nos mecanismos de montagem de comunidades ao longo de gradiente de elevação, e que a união das abordagens ecológica e evolutiva, sob diferentes arranjos de espécies, é fundamental para entender os processos que conduzem as relações entre diversidade e os gradientes ambientais. No segundo capítulo, além dos efeitos da variação de altitude, estudamos os efeitos da extração seletiva de madeira no padrão de diversidade e na estrutura filogenética de comunidades arbóreas, e avaliamos como a escala espacial pode alterar os resultados dessas análises. O corte seletivo e o filtro de altitude aumentaram a diversidade filogenética, apesar de conduzirem ao agrupamento filogenético. Os efeitos da altitude e da exploração madeireira foram mais fortes em larga escala, e os resultados foram alterados de acordo com os clados usados na análise. Dessa maneira, o filtro ambiental pode ofuscar o efeito da extração seletiva de madeira e, quando o filtro de elevação é excluído, os nichos abertos provavelmente por perturbações da exploração madeireira, levam a maior co-ocorrência de espécies filogeneticamente distantes. No terceiro capítulo, estudamos as relações entre os atributos funcionais e as taxas demográficas das espécies arbóreas considerando a importância de incluir interações entre os atributos, assim como o tipo florestal e o intervalo de tempo entre os censos (incluindo ou não um evento de seca), usando técnicas estatísticas inovadoras para melhorar o teste de premissas da análise funcional com um grande conjunto de dados. Aplicando o ‘aprendizado de máquina’ por meio de modelos de árvore de regressão impulsionados, descobrimos que a inclusão das interações entre atributos aumentou significativamente o poder dos modelos para prever as relações entre atributos e taxas demográficas, dependentes do tipo de vegetação e do intervalo de tempo. Assim, para avaliar a funcionalidade das comunidades vegetais, é importante considerar que pode haver múltiplos fenótipos com respostas demográficas semelhantes, resultados de interações entre atributos em diferentes habitats e intervalos de tempo. Concluindo, demonstramos que o uso de diferentes abordagens na ecologia de comunidades é fundamental para que possamos avaliar os processos ecológicos e mecanismos que conduzem a mega-diversidade de florestas tropicais e o funcionamento de suas comunidades.

Palavras-chave: Aprendizado de máquinas, árvores, corte seletivo de madeira, demografia, diversidade, ecologia de comunidades, ecologia evolutiva, ecologia funcional, diversidade, floresta atlântica, floresta tropical, gradiente de elevação.

ABSTRACT

A central point in ecology is to elucidate the processes and mechanisms responsible for the patterns of diversity, structure, assembly, and functioning of communities. Here, by using a large set of data on the composition, demography, and functional attributes of tree communities sampled along an elevation gradient in the Atlantic Forest, we investigated three fundamental questions across three chapters in the ecology of communities. In the first chapter, we used an integrated approach of species diversity and phylogenetic diversity under different species arrangements (e.g. community vs. families) to assess the ecological processes that drive the relationships between diversity and elevation in mega-diversity forests. We found a unimodal pattern of diversity variation for the tree community, emerging from the combination of different patterns of diversity of its most abundant families. The local phylogenetic diversity was negatively related to the elevation and the regional diversity (turnover) of species was greater as greater the elevation difference between communities. These results showed species competition and environmental filtering as the most important processes in the community's assembly mechanisms along an elevation gradient and that the union of ecological and evolutionary approaches, under different species arrangements, are fundamental to evaluate the processes that drive relationships between diversity and environmental gradients at each scale. In the second chapter, along with the effects of altitude variation, we studied the effects of selective logging on the diversity and phylogenetic structure of tree communities and evaluated how spatial scale change these results. Selective logging tends to increase phylogenetic diversity but leads to phylogenetic clustering. The effects of elevation and logging were stronger on large scale, and the results were changed according to the clades used in the analysis. Therefore, the environmental filter can overshadow the effects of selective logging, when the elevation-filter was excluded, it revealed open niche-spaces probably created by disturbance of logging, leading to the co-occurrences of distantly related species. In the third chapter, we studied the trait-demography rates relationships of tree species taking into account trait-interactions, forest type, time-interval between censuses (including or not a drought event) under robust statistical techniques to improve testing functional ecology assumptions by means of large datasets. Using machine learning through boosted regression tree models, we found that the inclusion of the trait-interactions significantly increased the power of the models to predict the trait-demography rates relationships and that trait-interactions were dependent on vegetation type and on time interval. Thus, to assess the functionality of the attributes, it is necessary to incorporate the concept of multiple phenotypes with similar demographic responses, resulting from various trait-interactions in different habitats and time intervals. To sum up, we demonstrate that the use of different approaches over community ecology is crucial for assessing the ecological processes and mechanisms that lead to a mega-diversity of tropical forests and the functioning of their communities.

Keywords: Atlantic forest; community ecology; demography; diversity; elevation gradient; evolutionary ecology, functional ecology, machine learning; selective logging; tree; tropical forest.

INTRODUÇÃO GERAL

Um dos principais e mais antigos objetivos da Ecologia é elucidar os processos ecológicos e mecanismos responsáveis pelos padrões de distribuição das espécies e funcionamento das comunidades (Pavoine & Bonsall 2011). Há séculos, os padrões de distribuição de espécies vegetais e a variação de diversidade são alvos de diversos estudos que foram baseados, inicialmente, em levantamentos florísticos (e.g. Wright 1878, Preston 1948, Whittaker 1960, Eiten 1972). Com o avanço e consolidação do conhecimento florístico, muitos trabalhos passaram a avaliar as mudanças de composição e riqueza de espécies entre diferentes comunidades (Gentry 1988, Lieberman *et al.* 2013), e buscaram explicar as causas da variação da diversidade vegetal ao longo de gradientes ambientais (Körner 2018, Laiolo *et al.* 2018). Somado a isto, o aprofundamento sobre abordagens filogenéticas e funcionais permitem outros entendimentos e possibilidades de análises acerca dos mecanismos e processos que atuam sobre a montagem e funcionamento das comunidades em diferentes contextos ambientais (Webb *et al.* 2002, Swenson *et al.* 2006, Worthy & Swenson 2019).

Os estudos das implicações da variação altitudinal sobre a riqueza de espécies estão entre os mais difundidos na literatura (McCain & Grytnes 2010). Porém, não há consenso sobre um padrão de alteração da distribuição e riqueza de espécies relacionado à variação altitudinal (McCain & Grytnes 2010, Graham *et al.* 2014). No geral, dois padrões são relatados para a variação de diversidade, um linear decrescente e outro unimodal-parabólico ou em forma de “sino” (e.g. Gentry 1988, Rahbek & Museum 1995, Kluge *et al.* 2006, McCain & Grytnes 2010, Khine *et al.* 2019). Nas Florestas Tropicais, estes dois padrões vêm sendo amplamente descritos ao longo de gradientes verticais de variação de riqueza de espécies, permanecendo uma falta de consenso dos principais fatores que poderiam conduzir a estas diferenças encontradas entre os estudos (Rahbek 2005, McCain & Grytnes 2010, Sanders & Rahbek 2012). Segundo Nogués-Bravo *et al.* (2008), a escala de estudo e os impactos por atividade humana seriam dois grandes fatores gerando diferenças entre padrões de variação de riqueza em gradientes altitudinais, no qual partindo de uma escala regional para escalas menores de estudo, o padrão linear ou monotônico de variação da diversidade se altera a um padrão unimodal-parabólico. Além da escala espacial, estas variações nos padrões de diversidade podem estar associadas às abundâncias relativas das famílias mais ricas em uma comunidade, que podem variar em curtas distâncias espaciais (e.g. Kamimura *et al.* 2017, Subedi *et al.* 2020). Embora estas mudanças incidam sobre os padrões de diversidade das comunidades como um todo (Peters *et al.* 2016, Descombes *et al.* 2017, Cirimwami *et al.* 2019), estudos de comunidades que enfoquem diferentes arranjos de espécies foram pouco explorados (Peters *et al.* 2016, Kamimura *et al.* 2017, Subedi *et al.* 2020). É essencial interpretar como os padrões de diversidade da comunidade podem emergir da combinação de diferentes padrões de suas famílias com maior contribuição na riqueza de espécies e abundância de indivíduos.

Contudo, para compreendermos a variação na distribuição e diversidade de espécie ao longo de gradientes abióticos, não basta usarmos as medidas tradicionais de diversidade, baseadas em unidades taxonômicas, mas também os índices de diversidade e abordagens filogenética e funcionais (Webb *et al.* 2002, Petchey *et al.* 2004, Hooper *et al.* 2005). Em linhas gerais, a diversidade filogenética é uma medida baseada nas idades de especiação (Faith 1992, Webb *et al.* 2002), enquanto a diversidade funcional é calculada por meio dos atributos das espécies relacionados ao funcionamento das comunidades (Petchey & Gaston 2006). Estes índices de diversidade melhoram a compreensão das possíveis respostas das comunidades às mudanças ambientais quando somadas as medidas tradicionais (Ricotta 2005, Gerhold *et al.* 2015).

Nas últimas décadas, foram desenvolvidos diferentes métodos de análises, índices e medidas de diversidade, que ponderam as diferenças entre as espécies dentro de um contexto filogenético e funcional (Webb *et al.* 2002, Petchey & Gaston 2006, Cadotte *et al.* 2009, 2012). As análises de diversidade funcional e filogenética, junto a abordagem de riqueza de espécies, possibilitam frentes de estudos inovadoras sobre as relações das espécies com o funcionamento e manutenção dos ecossistemas, e ajudam a predizer respostas das comunidades às variações geofísicas em gradientes ambientais (Petchey *et al.* 2004, Mason *et al.* 2005). Estas abordagens assistem a melhor compreensão da ecologia de comunidades e são essenciais para avaliar os processos ecológico e mecanismos que direcionam as relações de variação da diversidade e o funcionamento ecossistêmico com a variação altitudinal (Srivastava *et al.* 2012, Swenson 2013, Laiolo *et al.* 2018,).

No geral, os estudos da similaridade taxonômica, filogenética e funcional de espécies coocorrentes trazem informações-chaves para testar se processos ecológicos são determinísticos, como partição de nichos e filtragem ambiental, ou processos neutros (Hubbell 2001, Webb *et al.* 2002, Ackerly 2003, Swenson 2013, Laiolo *et al* 2018). Porém, os processos ecológicos podem ser melhor compreendidos ao analisar a diversidade em dois componentes, a diversidade *alpha*, em escala local, e a diversidade *beta*, em escala regional, comparando a variação da composição de espécies entre comunidades ou ao longo do tempo (Whittaker 1960, 1972, Graham & Fine 2008, Pavoine & Bonsall 2011, Legendre 2019). Estudar cada um dos componentes da diversidade, sob as diferentes perspectivas ecológicas, e compreender como estão conectados, é fundamental para testar hipóteses ecológicas sobre a montagem de comunidades (Pavoine & Bonsall 2011, Elliott & Davies 2019). Estas hipóteses são baseadas, principalmente, nos mecanismos que atuam na: (i) diferenciação na utilização de recursos em combinação com as diferentes interações entre espécies; (ii) restrição de distribuição das espécies relacionadas a condições ambientais mais severas; e (iii) limitação da capacidade dispersão das espécies ou recrutamento de maneira estocástica (Hubbell 2001, Graham & Fine 2008, Fitzpatrick *et al.* 2013, Ibanez *et al.* 2018).

Dentro destas frentes de estudos, os gradientes de elevação podem ser utilizados como “experimentos naturais” para testar respostas ecológicas e evolutivas das espécies sob a influência de variáveis ambientais (Graham *et al.* 2014, Körner 2018). Estes estudos são especialmente importantes em regiões com elevada diversidade, uma vez que estas regiões apresentam acelerada perda de habitats (Brooks *et al.* 2002, Mittermeier *et al.* 2011). Contudo, poucos estudos exploraram os efeitos do manejo florestal associado aos efeitos da variação altutidinal em comunidades arbóreas de Florestas Tropicais, sob uma abordagem que inclua a história evolutiva das espécies pesquisadas (Srivastava *et al.* 2012, Feng *et al.* 2014, Monge-González *et al.* 2020).

Além da compreensão dos fatores e mecanismo associados aos padrões de variação dos diferentes componentes da diversidade, novas abordagens e ferramentas estatísticas permitem avançar nos estudos dentro da ecologia funcional (Wiegand *et al.* 2017, Körner 2018, Pistón *et al.* 2019). Em relação a abordagem funcional, a aplicação de técnicas estatísticas inovadoras, como a aprendizagem de máquinas (ver Elith *et al.* 2008, Pistón *et al.* 2019), permitem revisitar questões fundamentais sobre a funcionalidade dos atributos (Yang *et al.* 2018, Worthy & Swenson 2019). A ecologia funcional é baseada no pressuposto de que os atributos das espécies determinam seu sucesso (Violle *et al.* 2007). Contudo, fortes relações entre atributos funcionais e aptidão (ou *fitness*) são pouco encontradas na literatura (Griffith *et al.* 2016, Worthy & Swenson 2019). Isto ocorre, possivelmente, devido a efeitos ambientais nas interações entre aptidão e atributos, nos quais fenótipos alternativos podem levar a aptidões semelhantes (Yang *et al.* 2014, Pistón *et al.* 2019). A funcionalidade do atributos das espécies pode ser melhor analisada por meio do uso do aprendizado de máquinas, como as *boosted regression trees*, que permitem a análise de grandes conjuntos de dados com diferentes tipos de distribuição entre as variáveis analisadas (De'ath 2007, Elith *et al.* 2008, Pistón *et al.* 2019). Portanto, a utilização de novas técnicas e ferramentas analíticas, e a inclusão dos efeitos ambientais na ecologia funcional se tornou importante para investigar os processos ecológicos que atuam sobre a coexistência de espécies e dinâmica de Florestas Tropicais (Wiegand *et al.* 2017, Martins *et al.* 2018).

A Floresta Atlântica, um *hotspot* de diversidade (Myers *et al.* 2000, Rezende *et al.* 2018), ocorre no leste do Brasil, englobando complexos montanhosos, como a Serra do Mar e a Serra da Mantiqueira, cobrindo uma ampla variação latitudinal, longitudinal e altitudinal (Fiaschi & Pirani 2009) se apresentando como um sistema ecológico ideal para testar diversas hipóteses dentro da ecologia de comunidades. Assim, utilizando diferentes abordagens e métricas de diversidade, análises em diferentes arranjos de espécies e escalas espaciais, e um novo método de análise sobre a ecologia funcional, este projeto teve três objetivos gerais sobre a ecologia de comunidades arbóreas de Florestas Tropicais: (1) elucidar o efeito da variação atitudinal sobre o padrão de diversidade de espécies e diversidade filogenética, em diferentes arranjos de espécies (e.g. toda a comunidade vs. famílias mais abundantes); (2) analisar como o filtro ambiental de elevação e corte seletivo de madeira afetam a diversidade taxonômica e a estrutura filogenética de comunidades arbóreas, e se esses efeitos são mediados pela abordagem metodológica da escala espacial e taxonômica utilizada nas análises; e (3) associar as interações entre atributos funcionais, contextos de habitat e intervalo de tempo entre amostragens para avaliar como esses fatores moldam a demografia das espécies, separadamente e simultaneamente.

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CAPÍTULO I

Splitting and merging: The importance of using different ecological approaches to understand diversity-elevation relationships

ABSTRACT

Aim: Unraveling the ecological processes driving relationships between diversity and the environment remains a central goal in ecological studies. Here, we investigated the variation patterns of both alpha and beta diversity under species and phylogenetic approaches, and across different species arrangements to assess the mechanisms and ecological processes driving the diversity-elevation relationships in mega-diversity tropical forests.

Location: Atlantic Forest, southeast Brazil.

Methods: We compiled a forest plot dataset encompassing 22,236 trees (DBH ≥ 4.8 cm) from 17 plots (1 ha each) distributed along an elevational gradient (0 – 1,200 m a.s.l). We computed alpha diversity by means of Hill numbers, for the whole community and for the most abundant families, and phylogenetic diversity for the whole community under two species arrangements, including or not the tree ferns. Species and phylogenetic beta diversities were evaluated as turnover and local contributions to regional beta diversity (LCBD). We used linear mixed-effects models and Mantel tests to assess diversity-elevation relationships.

Results: Overall, we found unimodal patterns of species diversity for the whole community and four different variation patterns among the 12 most abundant families. Regarding phylogenetic diversity, we found a monotonic decrease in relation to elevation for both species arrangements analyzed. Species and phylogenetic rates of turnover increased with the elevational differences between communities, and the LCBD was different between both approaches, in which plots at higher had higher LCBDs regarding phylogenetic analyzes.

Main conclusions: The community´s diversity-elevation relationship emerges from the combination of diversity variation patterns of its most abundant families, and however species and phylogenetic alpha diversity can differ between them, both approaches for rates of turnover were similar. Our findings highlight that species competition and environmental filtering, and not dispersion limit, was the most important ecological processes associated with assembly mechanisms along elevational gradients. Thus, for evaluating mechanisms and processes driving diversity-environment relationships we recommend considering both ecological and evolutionary approaches, different spatial scales, and species arrangements, depending on the research questions being investigated.

Keywords: Beta diversity; ecological processes; environmental filtering; elevational gradient; niche conservatism; Tropical forest.

1.INTRODUCTION

Changes in the composition of species assemblages are associated with bounded abiotic conditions (Soberón 2007, Scheele *et al.* 2017), in which resource constraints should drive limitations on species distribution (Huston 1994, Wang *et al.* 2020). Elevational gradients are among the most prominent abiotic conditions affecting species diversity and might be considered a mirror of latitudinal plant distribution patterns (Gaston 2000, Rahbek 2005). Alongside elevation, other environmental factors change along these gradients, such as temperature, atmospheric pressure, and UV-B radiation, and other factors may also vary, such as precipitation, wind speed and seasonality (Körner 2007). Among these abiotic factors, temperature and humidity are expected to be the most important factors related to plant distributions (Gentry 1988, McCain & Grytnes 2010, Wang *et al.* 2020).

Elevational gradients are natural ‘laboratories’, suitable for studying mechanisms that cause of variation in species distribution, and thus, changes in plant diversity patterns (Lomolino 2001, Körner 2007). There are broadly four contrasting spatial patterns to describe species diversity variation along elevational gradients: (i) monotonic decrease in diversity with elevation, (ii) unimodal pattern with a peak at intermediate elevations, (ii), plateaus in diversity across low elevations then decreasing with increasing elevation, and (iv) no significant changes in species diversity (Rahbek 2005, McCain & Grytnes 2010). However, variation patterns of species diversity are not consistent when analyzed among different geographic areas (Hsu *et al.* 2014, Khine *et al.* 2019) and species arrangements (Peters *et al.* 2016). For example, variation patterns can differ between single-taxa, families, and the whole community (see Yu *et al.* 2013, Descombes *et al.* 2017, Kamimura *et al.* 2017). Thus, it is also crucial to assess how predictors of elevational diversity gradients drive diversity patterns among different species arrangements (Vetaas & Grytnes 2002, Kessler *et al.* 2005, Kamimura *et al.* 2017), allowing us to elucidate ecological drivers conducting species assemblage and diversity-gradient relationships (Kreft & Jetz 2007, Peters *et al.* 2016).

The assemblages of co-occurring species are expected as results of their interactions and environment constraints, which is generally designated by species niches (Hutchinson 1957, Tokeshi 1990). At the community level, environmental changes among different habitat types should conduct different species assemblages (Levine & HilleRisLambers 2009, Krishnadas *et al.* 2016) and drive the variation patterns of diversity (Valencia *et al.* 2004, Laiolo *et al.* 2018). Although niche conservatism is expected over time, in which related species should present ecological similarities (Losos 2008), studies of mega-diverse plant communities have not found consistent niche segregation for hundreds of species as projected by classical niches theory (Valencia *et al.* 2004, Tiede *et al.* 2016). Consequently, the mechanisms and ecological processes explaining species co-occurrence and distribution remain controversial (Clarke & Gaston 2006, Mittelbach *et al.* 2007, Condamine *et al.* 2019). Overall, at the local scale, the various forms of observed diversity patterns are postulated to be associated with deterministic processes, such as environmental filtering, competitive exclusion, interactions between them (Mayfield & Levine 2010, Graham *et al.* 2014, Kraft *et al.* 2015), or neutral processes, such as dispersal limitation and stochastic recruitments (Hubbell 2001, Ricklefs 2006, Wiegand *et al.*

2017). Regarding elevational gradients, deterministic as well as random processes have been found to explain the spatial variation of species diversity in relation to elevational increases (Webb 2000, Rahbek 2005, Swenson 2013, Peters *et al.* 2016).

To understand multiple ecological processes and mechanisms that shape diversity in elevational gradients (Graham *et al.* 2014, Laiolo *et al.* 2018), it is necessary to assess diversity-environment relationships across spatial, ecological, and evolutionary complementary approaches (Pavoine *et al.* 2011, Graham *et al.* 2014). In this way, mechanisms conducting current spatial patterns of species distribution and ecological processes driving the composition of local communities can be unraveled by using both species and phylogenetic diversities (Pavoine & Bonsall 2011, Pavoine & Ricotta 2019). Along environmental gradients, the assessment of variation patterns of species diversity, allows us to evaluate the species diversity-resource relationships (Gaston 2000) and assess the spatial constraint on species ranges (Colwell *et al.* 2004, 2016). Measures of phylogenetic diversity are appropriate to unravel the mechanisms that build species assemblages (Pavoine & Ricotta 2019). Moreover, disentangling species and phylogenetic diversity into their alpha and beta components improves the test of ecological hypotheses, such as niche-based, environmental filtering or dispersal limitation hypotheses (Fitzpatrick *et al.* 2013, Ibanez *et al.* 2018). Thus, integrated approaches are promising in shedding light on ecological processes and mechanisms driving local diversity and patterns of species distribution (Baselga 2010, Anderson *et al.* 2011, Chao *et al.* 2014, Kubota *et al.* 2018).

The patterns of species distribution are usually studied in large elevational ranges (ca. 2500 m, e.g. Vetaas & Grytnes 2002, Lieberman *et al.* 2013, Yu *et al.* 2013, Manish *et al.* 2017, Monge-González *et al.* 2020). However, smaller gradients of mega-diversity forests also present great variation in species diversity patterns (Zhang *et al.* 2016, Descombes *et al.* 2017), including the Atlantic Forest in Brazil (Joly *et al.* 2012, Sanchez *et al.* 2013, Caglioni *et al.* 2018). The Atlantic Forest is a hotspot of biodiversity (Myers *et al.* 2000), which occurs in eastern Brazil, encompassing important mountain systems, such as the *Serra do Mar* and *Serra da Mantiqueira*, and covers a broad latitudinal, longitudinal and elevational variation (Fiaschi & Pirani 2009). For this vegetation type, studies have been reporting effects of elevation, individually or together with other environmental factors, on the vegetation patterns of tree communities and some of its abundant families (e.g. Sanchez *et al.* 2013, Duarte *et al.* 2014, Eisenlohr & de Oliveira-Filho 2015, Saiter *et al.* 2015, Kamimura *et al.* 2017). Moreover, the Atlantic Forest presents a great phylogenetic differentiation among its forest types (Duarte *et al.* 2014). Hence, these forests are suitable systems for studying diversity-elevational relationships, and mechanisms of ecological processes driving their local diversity.

Here, we used a large plot-dataset of preserved tree communities, distributed along an elevational gradient in the Atlantic Forest, to investigate the mechanisms and ecological processes driving the diversity-elevation relationships of a mega-diverse tropical forest, through an integrated approach of species and phylogenetic diversity metrics at different species arrangements. Specifically, we addressed three questions: (i) are there differences in species diversity variation patterns among rare and abundant species, abundant families, and the whole community? (ii) is the variation of species diversity reflected by the variation in phylogenetic diversity? (iii) species and phylogenetic variation are similar both locally and regionally? We hypothesize that the species diversity of the whole community presents a unimodal pattern of species diversity along the elevational gradient (Rahbek 2005, Eisenlohr *et al.* 2013), emerging from a combination of different variation patterns of rare species and abundant families (see Peters *et al.* 2016, Kamimura *et al.* 2017). We expect a close covariation between species and phylogenetic diversity (Sandel 2018), and the increase of phylogenetic clustering along the gradient due to stronger environmental filters at a higher elevation (Körner 2007, Zhang *et al.* 2016, Qian *et al.* 2020). Finally, we predict similar rates of turnover of species and phylogenetic beta diversity rather explained by the elevational distance between plots (Condit *et al.* 2002, Elliott & Davies 2019).

2. METHODS

2.1 Study area

The study is based on sampling plots of the tree community of a tropical montane system called *Serra do Mar* State Park (PESM, 23° 22’ S and 45° 05’W), southeastern Brazil. The plots are located in three of the Park’s Conservation Nuclei (*Cunha, Picinguaba and Santa Virgínia*). Overall, the climate is humid subtropical (Cfa type in Koppen system), with no dry season, an average annual rainfall over 2,200 mm and an average annual temperature of 22 °C (Sentelhas & Angelocci 2009, Joly *et al.* 2012). Soils are mainly characterized by high levels of aluminum and low availability of nutrients (Martins *et al.* 2015).

The plots were distributed along an elevational gradient (0-1,200 m a.s.l.) in the Brazilian Atlantic Forest (Table S1). Temperature variation is related to elevational gradient, showing a decrease of 0.6 to 1.0° C every 100 m (Vieira *et al.* 2011). In the study area, forest types are defined by their position in relation to the latitudinal and elevational belts, but the soil composition and the influence of flooding are also important to characterize other specific forest types (IBGE 2012). In this manner, our study covers five general forest types as follows: (i) Seasonally flooded coastal forest (herein, “*Restinga*”, one plot); (ii) Lowland forest (four plots); (iii) Submontane forest (four plots); (iv) Montane forest (seven plots); (v) Seasonally flooded montane forest (one plot).

2.2. Sampling design and data compilation

We conducted a compilation and revision of a forest plot dataset, representing 17 plots of 10,000 m² each, here used as local communities, surveyed in the study area. All tree individuals with a diameter at breast height (DBH) ≥ 4.8 cm, including palm trees and arborescent ferns, were sampled. All individuals were measured by their heights and DBH. The forest inventory dataset was obtained from databases of three projects (BIOTA / Functional Gradient - FAPESP n ° 03 / 12595-7, ECOFOR - RCUK & FAPESP n ° 12 / 51872-5 and MCTI / CNPq nº 34/2012

PELD), and published papers (Assis *et al.* 2011, Joly *et al.* 2012, Silva *et al.* 2016, Kamimura *et al.* 2017, De Souza *et al.* 2018). Fertile materials were incorporated in the herbarium UEC, IAC and HRCB (acronyms according to Index Herbariorum 2020). The specimen revisions of the abundant and richest families were done by consulting specialist or are available in Silva et al. (2016) and Kamimura et al. (2017). The species classification among families followed the system of the Angiosperm Group of Phylogeny (APG IV; Chase *et al.* 2016) and Pteridophyte Phylogeny Group (PPG I; Cole *et al.* 2016). In the final dataset, we only included individuals identified to the species level (c.a. 86% of the total abundance), excluding dead individuals and morphotypes (not revised by specialists).

2.3. Data analysis

We computed the species diversity for two different groups: (i) whole community (all species) and (ii) most abundant families in the study area (which comprised at least 75% of the total tree abundance). For each local community, we estimated species diversity in the matter of Hill numbers (Chao et al. 2014), reporting: (i) effective species richness (q=0), in which is given equal weight to frequent and infrequent species; (ii) 'typical' species (the exponential of Shannon's entropy index, q=1), is given emphasize the contributions of frequent species; and (iii) the effective number of dominant species (the inverse of Simpson's concentration index; q=2). For the selected families, we calculated the species diversity in terms of species richness (Hill numbers, q=0). We also computed the total number of rare species (which comprised at most 10% of the total tree abundance of each community).

Phylogenetic diversity and structure were analyzed under two scenarios of species arrangement, including or not the tree ferns (Cyatheaceae), as including basal groups should influence the phylogenetic analyzes (Feng *et al.* 2014, Qian *et al.* 2019). To do so, we built two phylogenetic trees, considering the whole community and excluding Cyatheaceae species, from a consensus tree for seed plants, GBOTB (Smith & Brown 2018), using the function *phylo.maker* (Jin & Qian 2019). Branch lengths were estimated with the BLADJ algorithm (Webb *et al.* 2008), and the unresolved genders were placed as basal polytomies within their families. We then computed the phylogenetic diversity for each community. The phylogenetic diversity was expected to be correlated to species diversity; thus, we used a phylogenetic diversity index (PDI), which standardizes the phylogenetic diversity measure of Faith (1992), according to species richness, to avoid accounting for other sources of variation in phylogenetic structure (Sandel 2018). Finally, we assessed the phylogenetic structure, by means of the net relatedness index (NRI) (Webb 2000, Swenson *et al.* 2012). NRI was calculated using the standardized effect size (SES) of mean phylogenetic distance (MPD), with 999 probability times of the SES for MPD giving the NRI (Webb 2000, Kembel & Hubbell 2006). Negative values of NRI indicate an over-dispersed phylogenetic structure, while positive values of NRI show clustering (Webb 2000, Kraft & Ackerly 2010). We performed phylogenetic analyses using *PhyloMeasures* (Tsirogiannis & Sandel 2016) and *picante* (Kembel *et al.* 2010) packages in R.

To detect the effects of elevation on species and phylogenetic diversity and phylogenetic structure, we performed linear mixed-effects models (LMM) using the 'lme4' package (Bates *et al.* 2015). In all models, we used elevation and its quadratic term as fixed effects, whereas forest types as a random factor to account for the different numbers of plots across forest types. We then tested the significance of each explanatory variable using the *Anova* function in the *car* package (Firth *et al.* 2009). Finally, we used the pairwise Kendall rank (Newson 2020) to assess the correlations between diversity and elevation.

We assessed the influence of elevation on both species and phylogenetic beta diversity by means of species composition and phylogenetic similarity decay, respectively. Species beta diversity was calculated using the Jaccard similarity, by means of *beta.pair* function in the *betapart* pacakage (Baselga *et al.* 2018), and it was partitioned into the turnover and nestedness-resultant components. Phylogenetic beta diversity was calculated by the mean pairwise distance

(MPD), using the *comdist* function in the *picante* library (Kembel *et al.* 2010). We assessed correlations among elevational divergence and both species and phylogenetic beta diversity with Mantel tests, using the *mantel* function in the *vegan* package (Oksanen *et al.* 2019). We then verified the local contributions to regional beta diversity (LCBD), according Legendre & De Cáceres (2013), to identify plots with unusual unique composition under both ecological approaches analyzed. To compute the LCDBs, we used the *beta.div* function implemented in the *adespatial* package (Bauman *et al.* 2018). To compute species LCBD and phylogenetic LCBD, we employed the distances matrix of compositional Jaccard and phylogenetic (MPD) dissimilarities matrices, respectively.

All analyses were performed using R 6.2.2 (R Core Team 2019), adopting $\alpha \leq 0.05$, and permutational tests were based on 999 randomized datasets obtained from Monte Carlo randomizations.

3. RESULTS

We evaluated 22,236 tree individuals belonging to 626 species distributed among 75 families. Myrtaceae presented the highest richness (20.9% of the total number of species), followed by Lauraceae (11.7%), Rubiaceae (7.82%) and Fabaceae (7.18%). A total of 455 species (72.6%) presented one or two individuals. *Euterpe edulis* (Arecaceae) was the most abundant specie /in the study area (12.4% of the total abundance); only two species occurred in all plots analyzed (*Euterpe edulis* and *Guapira opposita*), while 244 species were present in only one plot.

3.1 Changes in species diversity along the elevation gradient

Overall, we found significant effects of the elevation on the variation patterns of species diversity. For the whole community, we found unimodal patterns of species diversity (Hill number, q=0) and ‘typical’ species diversity (Hill number, q=1) variation along the elevational gradient (Figures 1a and 1b), but no significant variation in dominant species diversity (Hill number, q=2; Figure 1c). The variation pattern of the number of rare species (Figure 1d) followed the same pattern found for the species diversity and Shannon diversity (Hill number, q=1), in which the communities at about 300 m presented the highest number of species.

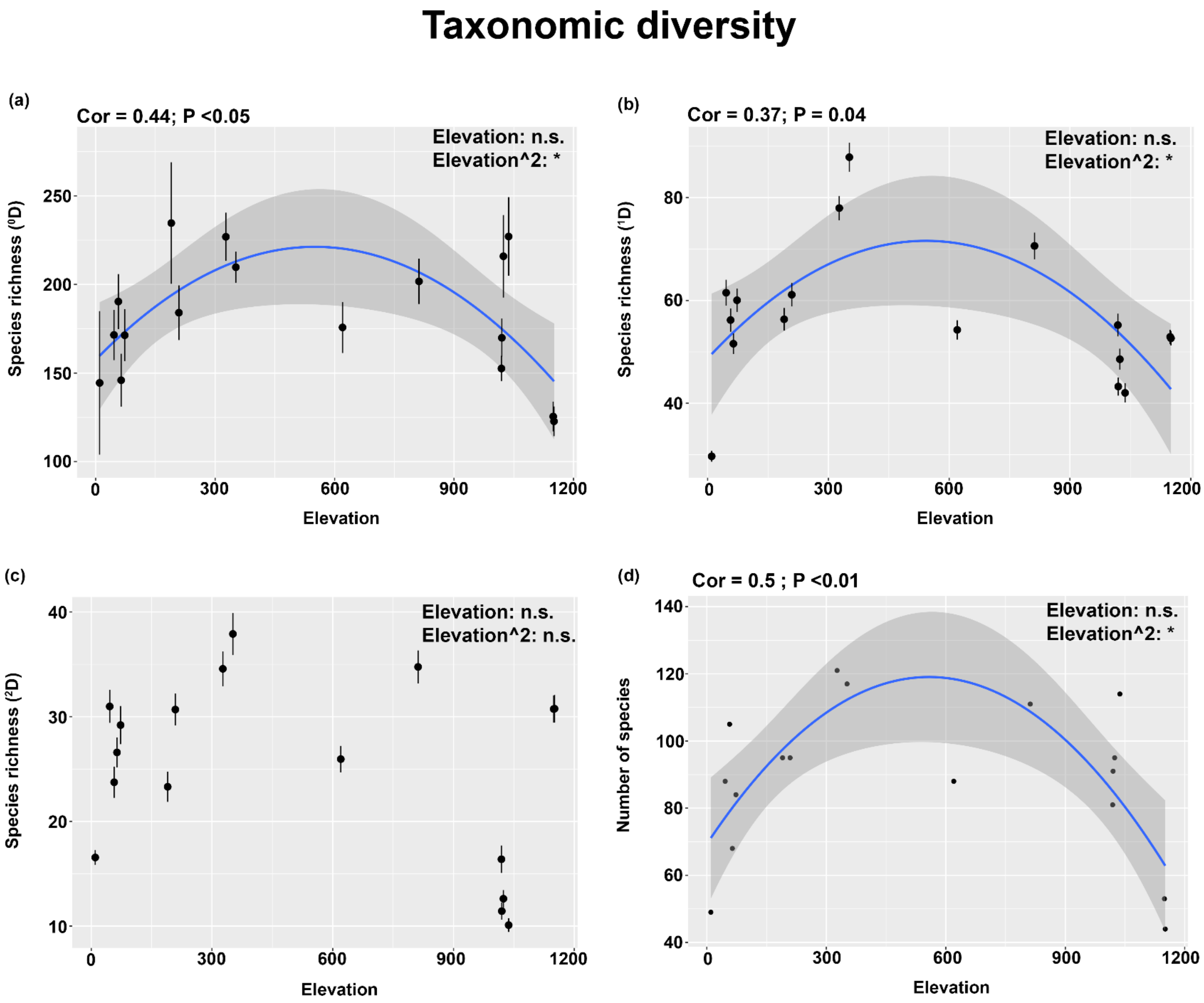


Figure 1. The relationship between species diversity of tree communities and elevational gradient in the Atlantic Forest, southeastern Brazil. Species diversity was computed by means of Hill numbers (a; ^{0}D), Shannon index (b; ^{1}D), Simpson index (c; ^{2}D) and rare species (d). A quadratic term was included in the linear mixed models. Shaded areas are the 95% confidence interval and bars are the standard deviations. Cor = Kendall´s correlation; n.s. – not significant; * P <0.05.

Regarding the most abundant families, four different variation patterns were found (Figure 2): (i) unimodal variation pattern (comprising 6 families); (ii) monotonic decrease in species diversity with elevation (comprising 4 families); (iii) monotonic increase in species diversity with elevation (one family), and (iv) no significant changes in species diversity (one family).

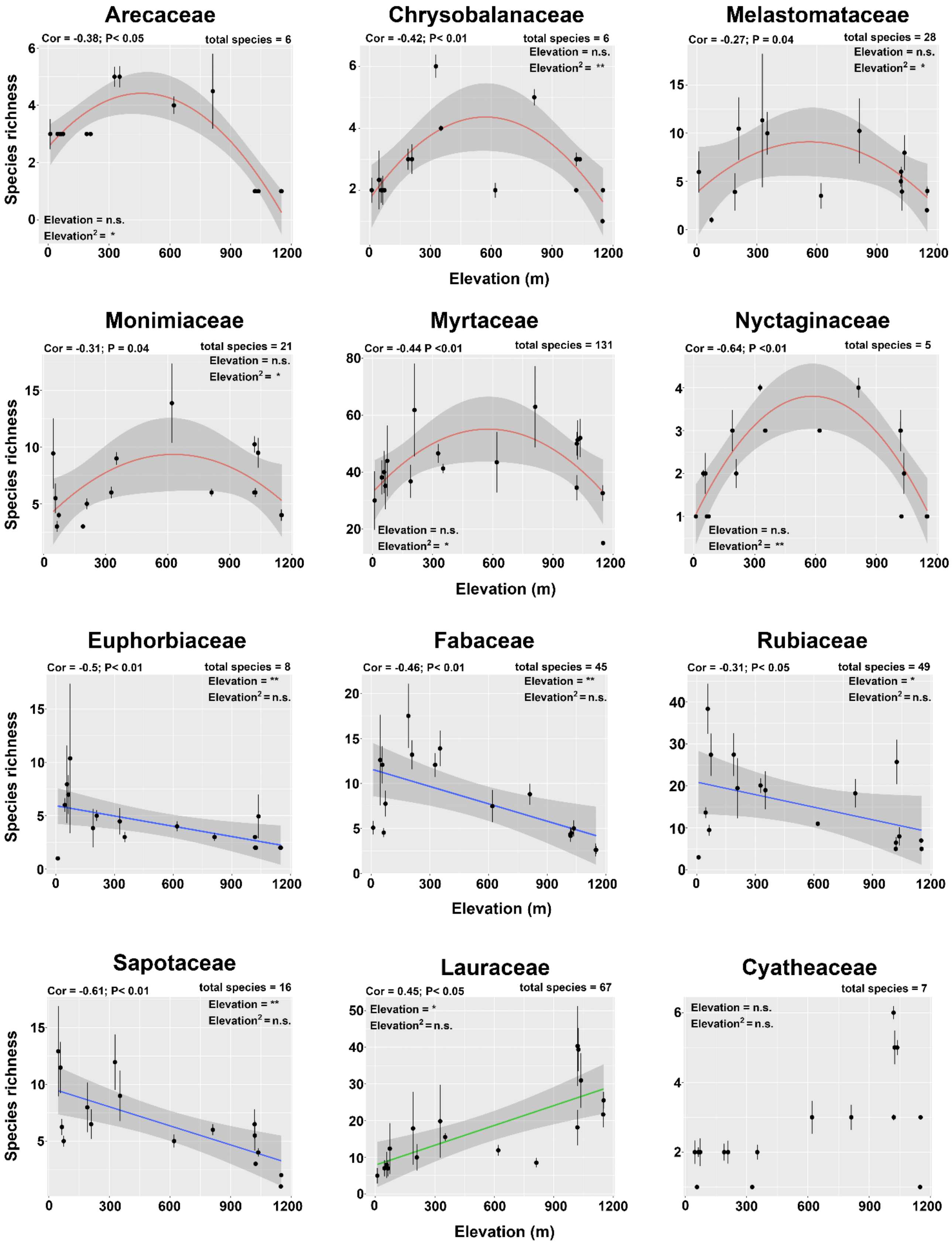
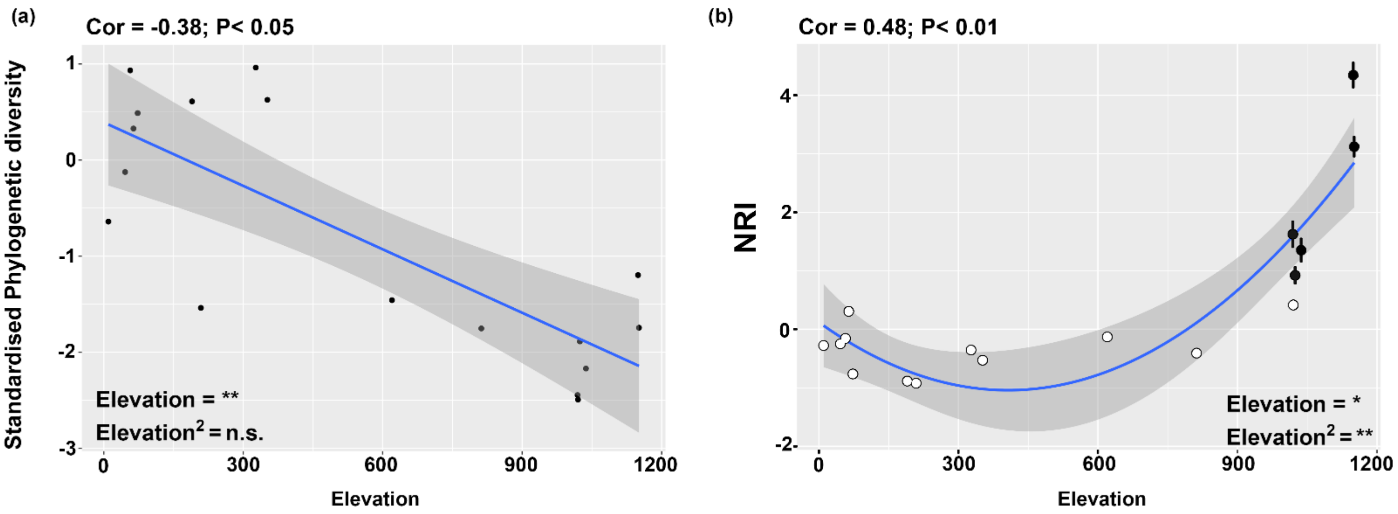


Figure 2. Changes in species richness (Hill numbers, ^{0}D) of the ten most abundant families along an elevational gradient in the Atlantic Forest, southeastern Brazil. A quadratic term was included in the linear mixed models. Shaded areas are the 95% confidence intervals, and bars are the standard deviations. Cor = Kendall´s correlation; n.s. – not significant; * P <0.05.

3.2 Elevational patterns of phylogenetic diversity and structure

For both scenarios (including or not the tree ferns), we found a monotonic decrease in phylogenetic diversity with elevation (Figures 3a and 3c). The inclusion of Cyatheaceaes strongly affected the results of the phylogenetic structure. In the first scenario (all species - Figure 3b), there was a significant effect of elevation in the phylogenetic structure, driving an inverted humped-shape along the gradient. The random phylogenetic structure was predominant among the plots (65% of the total), while four plots above 1.000 m a.s.l presented a clustered phylogenetic structure. On the other hand, in the second scenario (without Cyatheaceae - Figure 3d), we found no effect of elevation on the phylogenetic structure, although the *Restinga* presented phylogenetic overdispersion.

All species



Whitout Cyatheceae

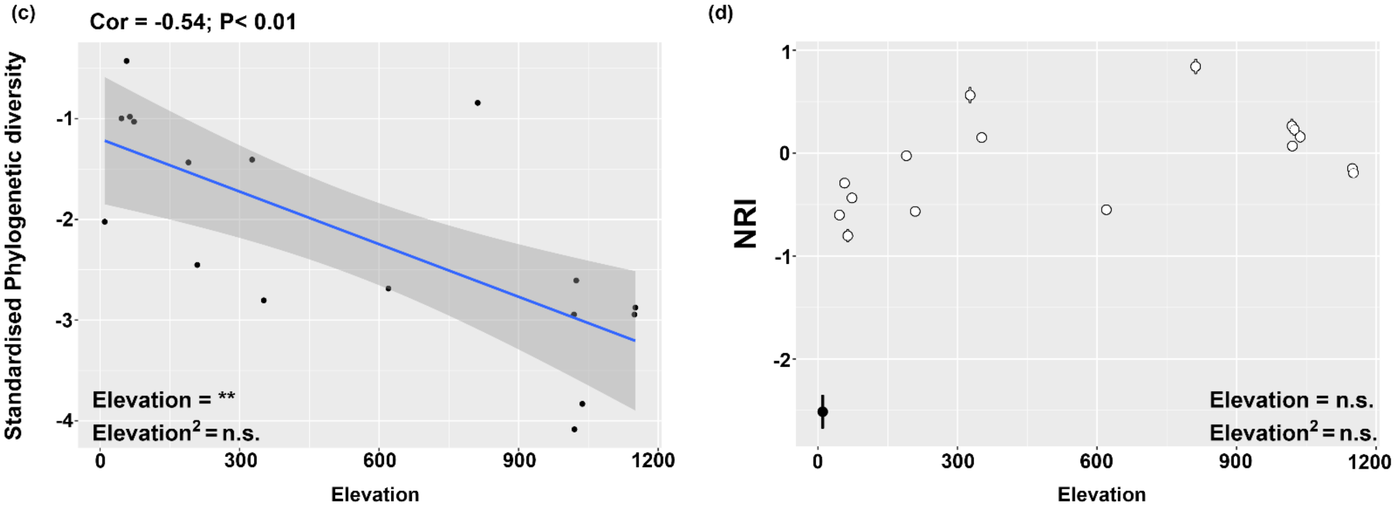


Figure 3. Phylogenetic diversity index (standardized measures of Faith´s diversity; a and c) and standardized effect size of mean pairwise distances (b and d; NRI- Nearest Relative Index) in relation to elevational for tree communities in the Atlantic forest, southeastern Brazil. A quadratic term was included in the linear mixed models. Shaded areas are the 95% confidence intervals and bars are the standard deviations. Cor = Kendall´s correlation; n.s. – not significant; * P <0.05; filled dots – significant values of NRI.

3.3 Elevational patterns of species and phylogenetic beta diversity

In general, the species dissimilarity increased with increased elevational divergence (R^2 =0,47; pseudo-F = 112.91; P <0.01). The species beta diversity was mainly generated by species turnover (βturn mean: 0.71, sd 0.14), while the contribution of nestedness to total dissimilarity was extremely low (βnest mean: 0.04, sd 0.03). For both species and phylogenetic beta diversity, the dissimilarity between communities was higher with greater elevational divergence (Figures 4a and 4b), but this pattern was much pronounced for species composition turnover (Mantel r = 0.67) in comparison to phylogenetic turnover (Mantel r = 0.24).

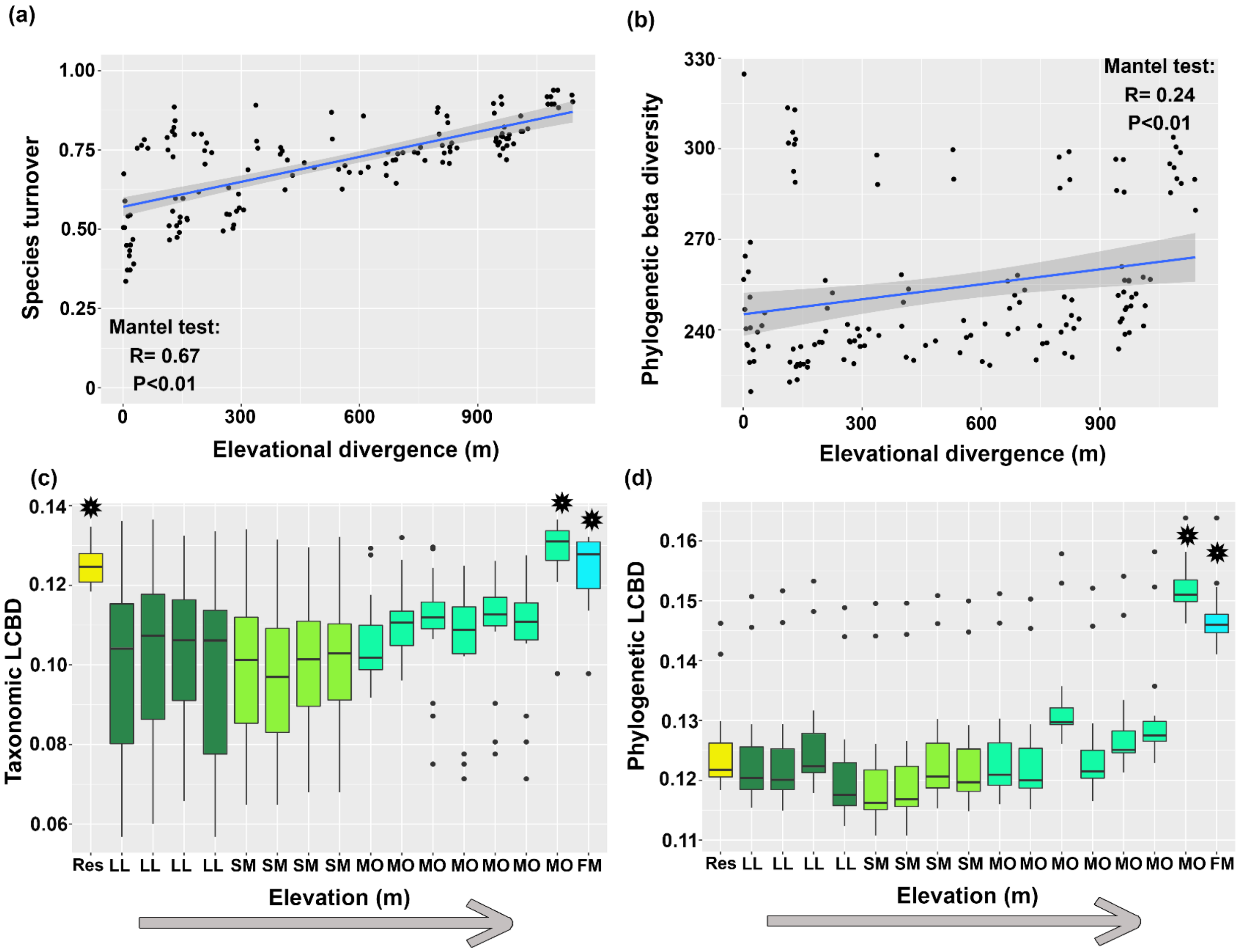


Figure 4. Species (Jaccard's index) and phylogenetic (mean pairwise distance) beta diversities in relation to elevational distance (a, b), and mean local contribution in the beta diversity (LCBD) of each community (c,d), for seventeen tree communities of the Atlantic forest in southeastern Brazil. Shaded areas are the 95% confidence intervals. Res – *Restinga* forest; LL – Lowland forest; SM – Submontane forest; MO – Montane forest; FM – Seasonally flooded montane forest. ✸ – Significant LCBD (P <0.05).

Regarding the communities’ contributions to the total beta diversity, we found great differences between the species diversity and phylogenetic diversity approaches (Figures 4c and 4d). Although higher contributions for both beta diversity approaches were found for communities located at higher elevations, the mean contributions of each plot to the total sepcies beta diversity were close but presented great within-plot variation, while those differences in the community contributions to phylogenetic beta diversity presented the opposite direction.

4. DISCUSSION

We showed the importance of assessing the diversity-environment relationships at different species arrangements to understand how tropical tree community patterns emerge from its different components, and how merging species diversity and phylogenetic diversity approaches shed lights on the process that conducts the spatial patterns of biodiversity. We decoupled the species diversity analyzes at three species arrangements and showed that diversity variation patterns are congruent when comparing the patterns of the whole community and the rare species. Additionally, within the most abundant families, there are four different effects of elevation on their diversity patterns. The tree community showed strong differences between the variation patterns of species and phylogenetic diversity, in which the random pattern of the phylogenetic structure at low and intermediate elevations became clustered at higher elevations. Lastly, the species and phylogenetic rates of turnover increase with the elevational divergence between communities, but the patterns of communities´ contributions to total beta diversity showed great differences between both approaches.

3.1. Diversity-elevation relationships: the species arrangement matters

In line with our first hypothesis, the species diversity of the whole community presented a unimodal pattern with a peak at intermediate elevations. Along elevational gradients, unimodal patterns of species diversity variation have been associated with a one or more mechanisms, such as: (i) spatial constraints on species ranges, leading to an overlap in their distribution at intermediate elevations (Colwell & Lees 2000, Currie *et al.* 2004); (ii) unimodal relationships between spatial distribution and productivity, which have usually been explained by optimal climatic conditions found at middle elevations (Rahbek 2005, McCain & Grytnes 2010) and; (iii) unimodal relationships between species diversity and environmental heterogeneity (Klopfer & MacArthur 1961, Carmelo *et al.* 2012, Stein *et al.* 2014). In our case, the various forms of spatial distributions found among 'typical', dominant species and rare species, and among abundant families indicate an interaction between environmental drivers and constraints on species distribution conducting the community diversity pattern (Colwell *et al.* 2016).

Along the elevational gradient in the Atlantic Forest, local heterogeneity of environmental conditions, mainly topographic and edaphic variations, but not elevation, have been reported as predictors of tree diversity variation (Eisenlohr *et al.* 2013, Sanchez *et al.* 2013). The larger the environmental heterogeneity, the higher co-occurrence of species (Levine & HilleRisLambers 2009, McCain & Grytnes 2010), while harsher conditions at higher elevations are expected to decrease species diversity (Zhang *et al.* 2016, Martínez-Camilo *et al.* 2018). Here, we argue that an interplay of abiotic factors and constraints on species spatial distribution lead to the changes in species diversity along the elevational gradient. The species diversity peak at middle elevations was related to the highest number of 'frequent', dominant, and rare species in the plots at about 300 m a.s.l. (Figures 1b, c, d). This fact can be related to the intermediate fertility and intrinsic topographic factors at middle elevations (Eisenlohr *et al.* 2013, Sanchez *et al.* 2013), together with a species distribution overlap (Colwell & Lees 2000) of rare species at those elevations. Mutually, the smaller number of 'frequent' species at lower and higher elevations led to a decrease in the total species diversity of plots in that gradient direction.

Historically, the southern Atlantic Forest was considered unstable during the Quaternary climatic oscillations (Graham *et al.* 2014), however, recent studies have demonstrated that optimal forest conditions must have occurred (Aguiar-Melo *et al.* 2019). This fact implies that, even in a cold and drier period, rainfall must be enough in this part of the Serra do Mar, allowing the maintenance of a forest refugium in the lowlands at the windward and, in the highlands, scattered montane (cloud) forests occurred in protected valleys surrounded by a matrix of grasslands (Behling & Safford 2010). In this way, this factor helps to explain the high diversity in the lower to intermediated altitudes, which maintained forested during the climatic oscillations, and supported the strong differentiation of the high-altitude flora, mainly exemplified by the presence of typical cold environments taxa (e.g. Cyatheceae, Winteraceae), and also Lauraceae which exhibits a high diversity in the montane forests of the Atlantic Forest and Andes (Gentry 1988, Kamimura *et al.* 2017, Brotto *et al.* 2019). The main patterns of the diversity of the families and the whole communities at lower to the intermediary peak of diversity, also reflect the biogeographic history of these families of tropical wet and hot climate and can help to explain the actual patterns observed (Chanderbali *et al.* 2001, Bardon *et al.* 2013, Berger *et al.* 2016). In this way, we reveal different elevation effects on the species diversity of different families and showed that differences in species distributions drive the general diversity-elevation relationship of the whole community.

3.2 Employing phylogenetic metrics to understand ecological processes driving local tree assemblages

By using a phylogenetic approach to analyze diversity-elevation relationships, we found a clear difference between the variation patterns of phylogenetic and species diversities. Although a trend for tree phylogenetic diversity along elevation gradients has not explicitly been described (Zhang *et al.* 2016, Chun & Lee 2018, Ramírez *et al.* 2019), a monotonic decrease or unimodal pattern of phylogenetic diversity is frequently found for different plant groups along elevational gradients in different mountain systems (e.g., Bryant *et al.* 2009, Chun & Lee 2018, Manish & Pandit 2018, Qian *et al.* 2019). A close covariation of phylogenetic diversity with species diversity is usually reported for tree communities in mega-diverse regions (e.g., Gómez-Hernández *et al.* 2016, Zhang *et al.* 2016). Our results did not corroborate these predictions, since phylogenetic diversity was negatively correlated with elevation, and the higher number of species at middle elevations did not lead to higher phylogenetic diversity, especially when tree ferns were excluded from analyzes. These patterns seem to be associated with local mechanisms, such as elevated temporal turnover of lineages, which may drive high species diversity and low phylogenetic diversity (Oommen & Shanker 2005). As well, our findings suggest that mechanisms associated with local factors (e.g. environmental heterogeneity) promote the unimodal pattern of local diversity, based on the diversity variation of abundant families, but which are not directly connected with the increase in phylogenetic diversity.

Here, we combined phylogenetic diversity and structure analysis to obtain a better understanding of assemblage structure (Mazel *et al.* 2016). In general, we found that random processes were dominant in driving the community assemblages along the elevational gradient. However, comparing taxonomic scenarios with and without tree ferns, the results were quite different for the plots of *Restinga* and Montane forests. The sensitivity of including basal groups in phylogenetic structure analyzes has been reported in other studies (e.g. Feng *et al.* 2014, Qian *et al.* 2019). By analyzing the phylogenetic structure of the whole community, we found that more extreme temperature conditions at higher elevations (Vieira *et al.* 2011) drove a plot-level clustered phylogenetic structure. Also, the exclusion of tree ferns from the analyzes modified this pattern and revealed a prevalence of random phylogenetic structure, except for the outstanding phylogenetic clustering in the *Restinga* forest. By analyzing all species, our findings follow the Tropical Niche Conservatism hypothesis (Hutchinson 1957, Tokeshi 1990), and the changes in local conditions should have conducted the local assemblages whose resident species show similar environmental tolerances (Webb *et al.* 2002, Cardillo 2011). On the other hand, by excluding tree ferns from the analyses, environmental filtering of elevation did not show effects on conducting any pattern of local tree assemblages. This result can be related to differences of phylogenetic dispersion sensitivity to harsh environments among families with different evolutionary history (Qian *et al.* 2019). Hence, we showed the importance of applying adequate taxonomic approaches to phylogenetic analyses to understand the variation diversity patterns using complementary ecological approaches and at different species arrangements, according to the research questions (Peters *et al.* 2016, Qian & Chen 2016). This is especially necessary since the variation patterns of species and phylogenetic diversities can be different along elevational gradients (e.g., Manish & Pandit 2018, Qian *et al.* 2019), and the loss of phylogenetic diversity may have negative effects on ecosystem function and stability (Cadotte *et al.* 2012, Gerhold *et al.* 2015, Knapp *et al.* 2017).

3.3 The importance of using an integrated approach of species and phylogenetic beta diversity

In our case, the larger the elevational divergence between the plots, the lager the species turnover and, therefore, beta diversity. The analyses of different metrics of beta diversity achieve a better understanding of the spatial structure and elucidate the mechanisms conducting local species assemblages (Anderson *et al.* 2011, Socolar *et al.* 2016). It is expected that species dissimilarity between communities increases with the geographical distance between them (Whittaker 1972, Soininen *et al.* 2007, Anderson *et al.* 2011, König *et al.* 2017). Jointly, under the phylogenetic niche conservatism assumption, there is a prospect of indices of phylogenetic beta diversity that should be rather sensitive in detecting frontiers between those communities (Graham & Fine 2008). Nevertheless, the relationship between phylogenetic turnover and community distances was less clear. These differences suggest that dispersal limitation did not present a great effect, since elevation led to high species turnover rates, but weak phylogenetic turnover rates, indicating low evolutionary divergences between local communities (Graham & Fine 2008, González-Caro *et al.* 2014). These differences between species and phylogenetic diversities responses have been related to species competition and environmental filtering, being the main ecological processes associated with assembly mechanisms along environmental gradients (Weiher *et al.* 1998, Webb *et al.* 2002).

A clear pattern of LCBD for both species and phylogenetic approaches shows that local communities presented lower species and phylogenetic diversities and a high contribution to beta diversity. Both plots of seasonally flooded forests, at the lower and higher elevations, presented greater LCBD, while the Submontane plots represented the lowest values of LCBD. This reinforces that temperature, resources and energy limitations along the elevational gradient and the harsh local conditions in stressful habitats, but not the species capacity of dispersed diasporas, are the main mechanisms in conducting tree species dissimilarities along elevational gradients (Qian 2009, Wang *et al.* 2020). Therefore, harsh local conditions may produce greater phylogenetic distance among abundant families in relation to less stressful habitats (Pitman *et al.* 2001), while an inverted pattern may be found for species diversity, where lower abiotic constraints and species competition should allow higher species cooccurrence (Levine & HilleRisLambers 2009, Mayfield & Levine 2010).

5. CONCLUSIONS

By splitting the analyzes of alpha species diversity into different species arrangements, we showed that diversity-elevation relationships can be different among the abundant families, but their combination leads to the general pattern of the whole community. We demonstrated that the possibilities of species and phylogenetic patterns of alpha diversities differ between them but clarifies the understanding of the processes driving community assemblages. We also showed that inclusion of basal plant groups had significant effects on phylogenetic analyzes of diversity. Finally, by analyzing beta diversity under species diversity and phylogenetic diversity approaches, we were able to demonstrate that elevation and local harsh conditions can lead different responses in species turnover and local community beta contribution between those approaches. Thus, we recommend the merging of ecological and evolutionary approaches and splitting the analyzes into different species arrangements to advance the comprehension of processes and mechanisms leading to diversity-environment relationships.

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SUPPORTING INFORMATION

Table S1. Environmental and structural characteristics of seventeen 1-ha plots surveyed at the Atlantic forest along an elevation gradient in southeastern Brazil.

Plot (names)	Forest type	Number of individuals	Number of families	Species richness	Elevation (m .a.s.l)	Annual mean temperature (ºC)	Annual precipitation (mm)
A	*Restinga*	1,634	31	83	10	22.6	2,406
B	Lowland	1,143	37	147	46	22.6	2,406
C	Lowland	1,167	36	122	64	22.6	2,406
D	Lowland	1,324	40	158	57	22.6	2,406
E	Lowland	1,253	40	139	73	22.3	2,324
G	Submontane	1,513	40	149	190	18.3	1,975
H	Submontane	1,519	40	159	209	18.3	1,975
I	Submontane	2,003	48	203	327	17.5	1,865
J	Submontane	1,823	47	208	352	17.5	1,865
P	Submontane	1,490	43	154	600	16.8	1,820
Q	Submontane	1,490	46	185	800	16.5	1,760
K	Montane	1,767	42	177	1,037	16.3	1,724

Plot (names)	Forest type	Number of individuals	Number of families	Species richness	Elevation (m .a.s.l)	Annual mean temperature (°C)	Annual precipitation (mm)
L	Montane	1,664	37	168	1,020	16.3	1,724
M	Montane	1,822	38	171	1,024	16.3	1,724
N	Montane	1,397	40	149	1,015	16.3	1,724
S	Seasonally flooded Montane	2,183	44	141	1,100	14,8	1,737
U	Montane	2,092	38	134	1,100	14,8	1,737

Dataset was compiled from Alves et al., (2010); Eisenlohr et al., (2013); Joly et al., (2012); Kamimura, Morais, Joly, & Assis, (2018); Leitold, et al., (2014); Martins, Seger, Wiegand, & Santos, (2018)the databases of ‘Functional Gradient’ and ‘EcoSpace’ Projects.

CAPÍTULO II

Phylogenetic structure sheds light on the effect of selective logging along an elevation gradient in Atlantic Rainforest tree communities

ABSTRACT

In Tropical Forests, environmental filtering and human management are considered the most important factors affecting the assembly rules of tree communities. We studied four plots, comprising 100 subplots of 10 x 10 m each, in the Atlantic Rainforest of southeastern Brazil, to test the effects of elevation and selective logging in the phylogenetic diversity and structure of tree communities. The plots were distributed in two elevation ranges, lowland and montane, and two management conditions, one submitted to selective logging in 1976 and another undisturbed. Also, we assessed whether the results were mediated by the spatial scale, fine-scale, of 100 m², and broad-scale, of 400 m², and the inclusion or exclusion of Cyatheaceae in the analysis. We sampled 3,101 individuals of 330 species and 58 families. The phylogenetic diversity was higher for montane areas and in the disturbed communities, but the exclusion of Cyatheaceae in analysis changed this pattern. Elevation and selective logging tend to increase phylogenetic diversity and lead to a phylogenetic clustering, but the results were mediated by the clades used in the analysis. Also, the effects of elevation and logging were stronger at a broad scale, highlighting the importance of experimental design selection to understand the role of environmental and disturbances in processes acting on community structuring. The environmental filter of elevation led to a clustered phylogenetic structure of communities and overshadowed the selective logging effects. Moreover, when the elevation-filter was excluded, it revealed open niche-spaces probably created by disturbance of logging, leading to the co-occurrences of distantly related species.

Keywords: Cyatheaceae; disturbance; environmental filtering, Faith’s diversity; phylogenetic analysis, spatial scale; Tropical Forest.

1. INTRODUCTION

Understanding the processes that that control the assembly of ecological communities is necessary to maintain biodiversity, especially under the current scenario of anthropogenic disturbances (Chazdon 2008; Swenson and Enquist 2009). It is essential to understand the relationship between diversity and assembly rules in the way to predict species responses future scenarios of filters and disturbances' frequencies (Petchey et al. 2004; Mason et al. 2005; Gerhold et al. 2015). To do so, we can perform analysis both on species diversity and on the phylogenetic structure of communities along environmental filtering gradients and under different disturbance frequencies, aiming to understand the patterns that determine these assembly rules (Weiher et al. 1998; Webb et al. 2002). In this context, studies on ecological and phylogenetic similarity of co-occurring species provide key information to detect the interconnected processes acting on the communities' structure (Webb et al. 2002; Ackerly 2003; Swenson 2013).

Changes in species diversity might occur due to changes in environmental filters and to disturbances, especially anthropogenic impacts, which may lead to limiting similarity among species (Hooper et al. 2005). In Tropical Forests, environmental filtering is considered an important factor affecting the assembly rules and ecosystem properties in tree communities (Hooper et al. 2005; Baraloto et al. 2012). Specifically on the Brazilian Atlantic coast, one of the most important environmental filters is elevation, which affects temperature, another key element determining vegetation species (Oliveira-Filho and Fontes 2000; Scudeller et al. 2001; Alves et al. 2010; Eisenlohr et al. 2013). Elevation and its derived abiotic gradients alter species diversity in these tropical forest tree communities, but its effect on the phylogenetic structure has not yet being studied (Sanchez et al. 2013; Eisenlohr et al. 2013, but see de Mattos et al. 2019).

The effect of environmental filtering might be coupled to the presence and intensity of disturbances, such as the increase of human impacts in structuring the vegetation communities, modifying the species' distribution and diversity in Tropical Forests (Gibson et al. 2011; Putz et al. 2012). One major disturbance in Tropical Rainforest is selective logging, which might lead to a clustered phylogenetic pattern in Tropical tree communities and change its structure and the recovery capacity in disturbed areas (Hirota et al. 2011; Ding et al. 2012; Whitfeld et al. 2012; Berenguer et al. 2014). Selective logging is a common management strategy performed by local human communities and allowed in many sites of the Tropical Forests (Verissimo et al. 1992; Ribeiro et al. 2009; Matricardi et al. 2010). Therefore, the intricate dynamic of Tropical forests combining environmental filter and disturbance can hamper the understanding of ecological process emerging by the phylogenetic structure of their communities (Kembel and Hubbell 2006; Mayfield and Levine 2010; Baraloto et al. 2012).

Besides the effects of environmental filtering and disturbances, the spatial scale and clades used in the analysis may change the results on the phylogenetic structure of plant communities (Swenson et al. 2007; Cadotte et al. 2009; Vamosi et al. 2009; Srivastava et al. 2012; Ndiribe et al. 2013). Abiotic filters are determinant across habitats, considering broad spatial scales, whilst limiting similarity caused by disturbances shall be dominant within habitats, in small spatial scales (Götzenberger et al. 2012). Filters shall leave a clustered pattern in the phylogenetic structure of plant communities due to the grouping of similar strategies of survival and spread among species. Biotic interactions or disturbances, on the contrary, usually leave an overdispersed pattern in the phylogenetic structure (Webb et al. 2002, but see Mayfield and Levine 2010). The effect of environmental filtering on the assembly rules might, in general, overcome the one caused by limiting similarity, so its effect shall be overshadowed (de Bello et al. 2012).

The inclusion of different clades when constructing a phylogenetic tree may significantly contribute to the phylogenetic diversity and structure. When vegetation sampling is narrowly defined by the researchers (i.e. not including distantly related clades, such as Cyatheaceae), we might find different outcomes and conclusions of the experiments (Cavender-

Bares et al. 2006). For this reason, we incorporated and excluded Cyatheaceae, a distantly related clade often discarded in vegetation census, in our analysis (Srivastava et al. 2012; Ndiribe et al. 2013). We tested how the environmental filter of elevation and selective logging affected the species diversity and the phylogenetic structure in the tree communities of Atlantic Rainforest in southeast Brazil, and whether these effects were mediated by the methodological approach of spatial scale used and the taxa inclusion in the phylogenetic analysis.

2. MATERIAL AND METHODS

Study area

The study site is in a continuous area of 1.3 million km^2 of Atlantic Rainforest in Southeast Brazil (Morellato and Haddad 2000), a hotspot for conservation (Myers et al. 2000). However only 11 to 16% of this biome persist conserved, most of the remaining fragments are located in the same area of the present study (Ribeiro et al. 2009). The climate of the region is tropical, with the highest precipitation mean in the summer (Vieira et al. 2011). In general, soils present low fertility and nutrients, with high levels of aluminum (Sousa Neto et al. 2011).

We analyzed four plots of 1 ha each (Figure 1), divided into 100 sub-plots of 10 x 10 m in the State Park Serra do Mar (23°58' S, 46°38' W). The sub-plots were used to reassemble the data and calculate the effect of changing the spatial scale of the analysis on the results. The plots were placed in two ranges along an elevation gradient: two hectares in the so called lowland, or *Floresta Ombrófila Densa das Terras Baixas* (IBGE 2012), with elevation around 100 m, and two hectares in the Montane, or *Floresta Ombrófila Densa Montana* (IBGE 2012), with elevation around 1,000 m. In each elevation range, we analyzed one undisturbed hectare and one hectare that suffered selective logging in 1976 (Padgurschi et al. 2011; Ramos et al. 2011). We identified all tree individuals in each of the four hectares, those with perimeter at breast height equal or higher than 15 cm, including palms and tree ferns (Cyatheaceae) species

(Joly et al. 2012). All botanical material was placed in the Herbaria of University of Campinas (UEC), Agronomic Institute of Campinas (IAC) and São Paulo State University (HRCB).

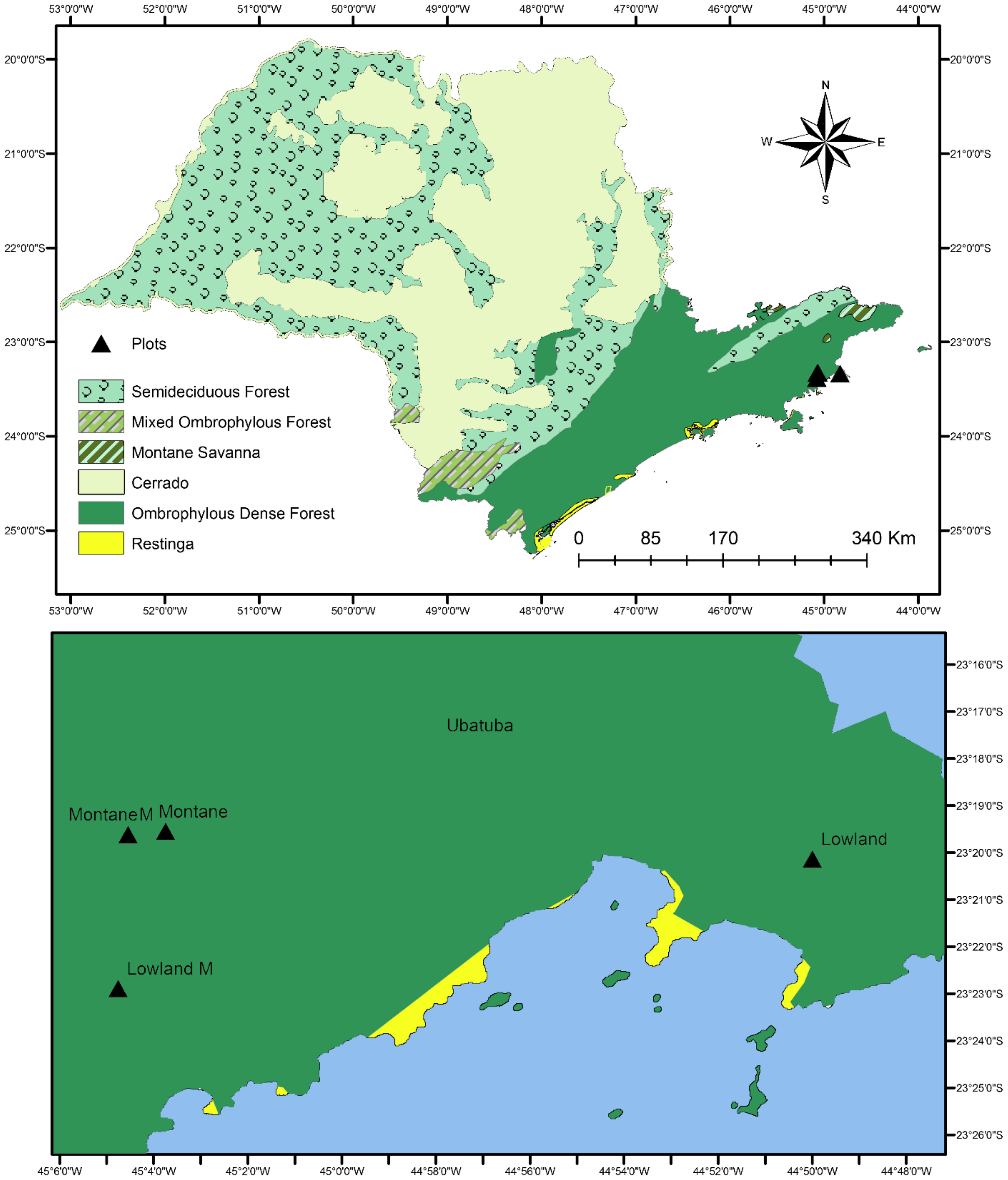

Figure 1. Distribution map of study plots (100 x 100 m each) in the Atlantic Rainforest, São Paulo, Brazil. The tree communities (1-hectare plots) were distributed in relation to the disturbance of

selective logging (referred with “M”) and to elevation ranges (lowland and montane). Adapted from (Olson et al. 2001).

Data analysis

We calculated the species diversity using the Shannon-Weaver index (H', Magurran, 2004), the standardized Phylogenetic Diversity (Faith´s PD, Faith 1992; Webb et al. 2008), the mean phylogenetic distance (MPD, Swenson 2014), and the nearest relative index (NRI, Webb et al. 2008) of each sub-plot. We used the subplots to account for two different spatial scales: (1) fine scale, taken out of 50 subplots of 10 x 10 m sampled randomly of each plot; (2) broad scale, taken out of the random pick of 10 subplots of 20 x 20 m of each plot. For each spatial scale, we conducted the analysis considering all tree species, and again excluding fern species (Cyatheaceae).

We built a phylogenetic trees (Appendix 1) based on the hypothetical supertree for all species sampled, using the software Phylomatic (Webb et al. 2008). The standardized effect size of phylogenetic diversity was calculated with the independent swap algorithm (Gotelli 2000) maintaining species occurrences and richness of each sub-plot. The supertrees were built based on given phylogeny (Webb and Donoghue 2005), adding information on family and genus with good resolution further published (Fabaceae: Doyle et al. 2000; Lauraceae: Chanderbali et al. 2001; Myrtaceae: Lucas et al. 2007). The phylogenetic trees were built using randomly samples from the Bayesian pseudo-posterior distribution of trees provided by Kuhn et al. (2011). After building the trees, the algorithm Bladj was used to date the nodes in each species pools of the supertrees using data from (Wikström et al. 2001).

We calculated the mean phylogenetic distance (MPD, Swenson 2014) and the nearest relative index (NRI) by standardized values of MPD, using the independent swap algorithm (Gotelli, 2000). The NRI was calculated as $\mathrm{NRI} = -1\mathrm{x}\ \frac{MPDobs - MPDrnd}{sdMPDrnd}$, with *MPDobs* being the mean distance observed in each sub-plot; *MPDrnd* is the mean value from 999 randomly generated assemblages; and *sdMPDrnd* is the standard deviations of the mean distance of null communities. The phylogenetic distances between species were square-rooted, to incorporate cases in which evolutionary relatedness is not related to ecological distance linearly (Letten and Cornwell 2015). Finally, we used an analysis of variance followed by t-tests, using Bonferroni correction, to test for differences between the two elevation ranges and under two different selective logging conditions. For all analysis, the significance level was set at 0.05. The species classification followed the Angiosperm Phylogeny Group system (Chase et al. 2016) and Pteridophytes Phylogeny Group (Schuettpelz et al. 2016).

3. RESULTS

Floristic composition

We sampled 3,101 tree individuals, of 330 species distributed among 58 families (Appendix 2). Arecaceae presented the highest abundance (18.2 % of the individuals), and Myrtaceae showed the highest richness (19.7 %, or 65 species). Among the two elevation ranges surveyed, the undisturbed montane area showed the greater tree abundance (995 individuals) and species richness (160 species), whereas the managed lowland area presented the lowest abundance (735) and richness (95 species).

Effects of environmental filter and disturbance on diversity and phylogenetic structure

Species diversity was not different among the treatments; however, we did find an effect of elevation ($P < 0.05$) when we excluded tree ferns at broad scale (Table 1). Elevation however affected phylogenetic diversity in all? analysis, especially in broad scale, both considering all species and excluding ferns (Figure 2; $P < 0.01$). All-community analysis showed higher phylogenetic diversity in montane areas, whereas the exclusion of ferns reverted this pattern (Figure 2). For the phylogenetic structure, although the effects of elevation were found in all analysis, the mean values of NRI were just consistent and positive for undisturbed montane area (Table 1).

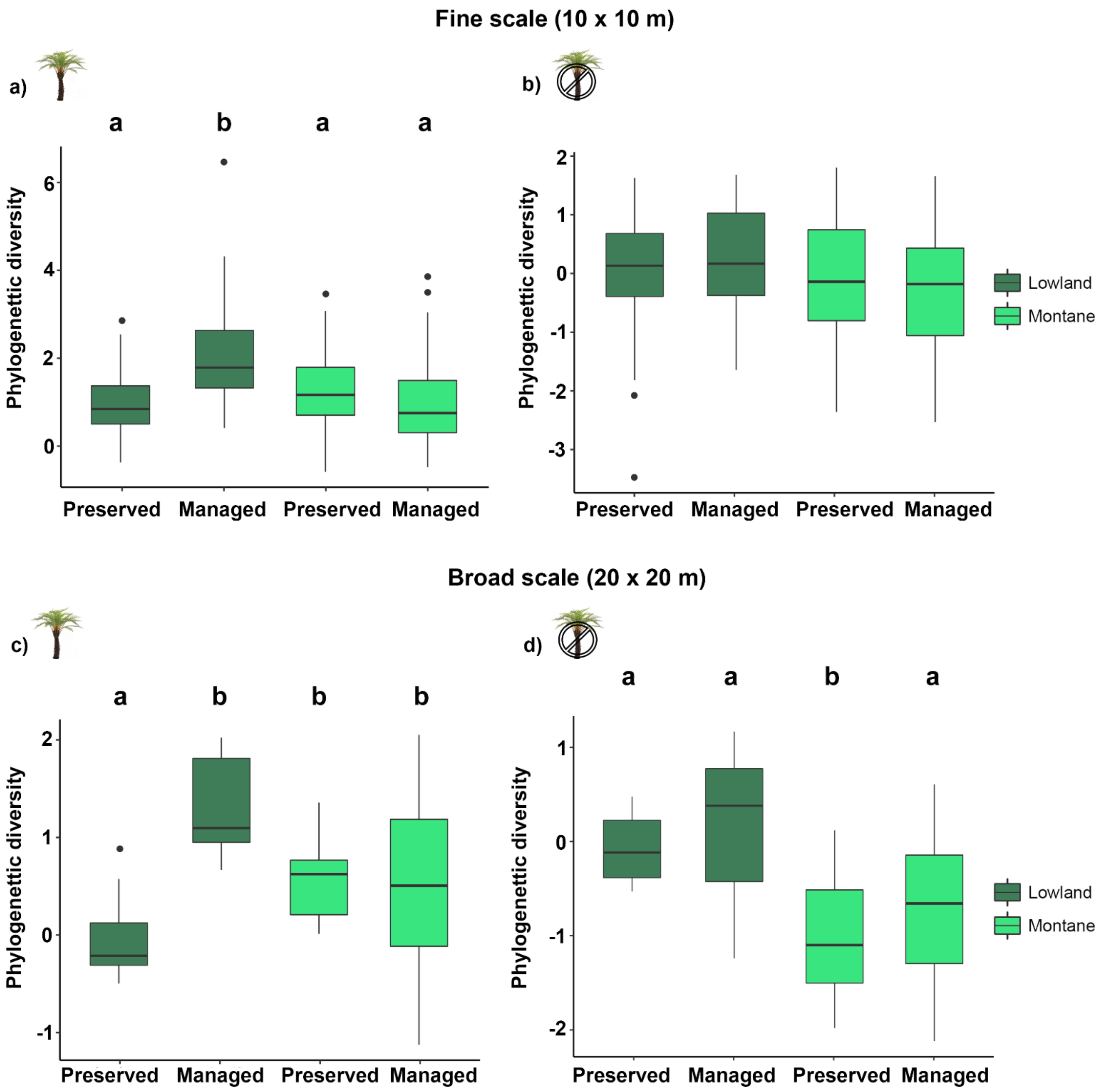

Figure 2. Phylogenetic diversity (Faith´s PD) in relation to disturbance (Preserved vs. Managed) and to elevation ranges (lowland and montane), at two spatial scales (fine scale, or 10 x 10 m, and broad scale, or 20 x 20 m) and including (a and c) or not (b and d) the tree ferns in the analyzes. Different letters indicate significant differences in the mean values of standardised effect size of PD (S.E.S. PD, *P* < 0.05).

Species and phylogenetic diversity of communities are different between undisturbed and disturbed areas, only when elevation was excluded from the analysis (*P* < 0.01). Although the lowland undisturbed area presented the greater average species diversity (Shannon-Weaver index, Magurran 2004), for Faith´s phylogenetic diversity, the higher values were found in managed lowland area, for both spatial scales. In the montane, where elevation and, consequently, temperature, plays important roles as environmental filters, disturbance of logging showed no effect on the phylogenetic diversity of the plots (*P* > 0.05). When we excluded ferns of our analysis, the differences between undisturbed and disturbed communities was less evident, but not reversed (Figure 2). Undisturbed communities showed a lower phylogenetic diversity than the disturbed ones (Table 1).

Table 1. Shannon-Weaver index (H'), average of the phylogenetic diversity (Faith´s PD) and phylogenetic structure (NRI; Nearest relatedness Index) of tree communities in relation to the disturbance of selective logging (referred with "M") and to elevation ranges (lowland and montane), at two spatial scales. Fine scale – 10 x 10 m; broad scale – 20 x 20 m; M – Managed. Different letters indicate significant differences in the mean values of the diversity indices H' and PD, and NRI (*P* < 0.05).

Areas	Lowland	Lowland M	Montane	Montane M
SW – fine scale	2.09 ± 0.44^{a}	1.87 ± 0.43^{b}	2.03 ± 0.47^{ab}	2.08 ± 0.38^{ab}
Without Ferns	2.08 ± 0.43^{a}	1.79 ± 0.46 ^{b}	1.95 ± 0.49 ^{ab}	2.01 ± 0.45 ^{ab}
SW – broad scale	3.06 ± 0.22	2.85 ± 0.22	2.82 ± 0.44	2.98 ± 0.29
Without Ferns	3.06 ± 0.21^{a}	2.78 ± 0.22^{ab}	2.75 ± 0.47^{b}	2.92 ± 0.32^{ab}
PD – fine scale	0.97 ± 0.72^{a}	2.01 ± 1,16^{b}	1.25 ± 0.87^{a}	1.01 ± 1.01^{a}
Without Ferns	0.02 ± 1.0	0.23 ± 0.83	-0.9 ± 1.09	-0.24 ± 0.98
PD – broad scale	-0.04 ± 045^{a}	1.29 ± 0.51^{b}	0.55 ± 0.42^{b}	0.51 ± 1.0^{b}
Without Ferns	-0.01 ± 0.36^{a}	0.14 ± 0.83^{a}	-0.99 ± 0.71^{b}	-0.69 ± 0.96^{a}
NRI – fine scale	0.28 ± 0.55^{a}	-0.23 ± 0.64^{b}	0.18 ± 0.57^{a}	0.23 ± 0.7^{a}
Without Ferns	-0.17± 0.67^{a}	0.03 ± 0.59^{ac}	0.36 ± 0.63^{b}	0.17 ± 0.59^{bc}
NRI – broad scale	0.64 ± 0.68^{a}	-0.33 ± 0.57^{b}	0.25 ± 0.65^{b}	-0.18 ± 0.99^{b}
Without Ferns	-0.23 ± 0.43^{a}	-0.08 ± 0.49^{ab}	0.35 ± 0.54^{b}	-0.09 ± 0.47^{a}

For the two spatial scale analyzed, selective logging in lowland communities drove changes in the phylogenetic structure (NRI), and both undisturbed and disturbed areas showed higher and lowest values for average NRI, respectively (Figure 3). However, the results of phylogenetic structure analysis including the tree ferns was different from the results of same analysis excluding this species. For lowlands areas, the effects of selective logging in NRI were found only we included ferns in analysis, while for montane areas we found the opposite results of selective logging in phylogenetic structure.

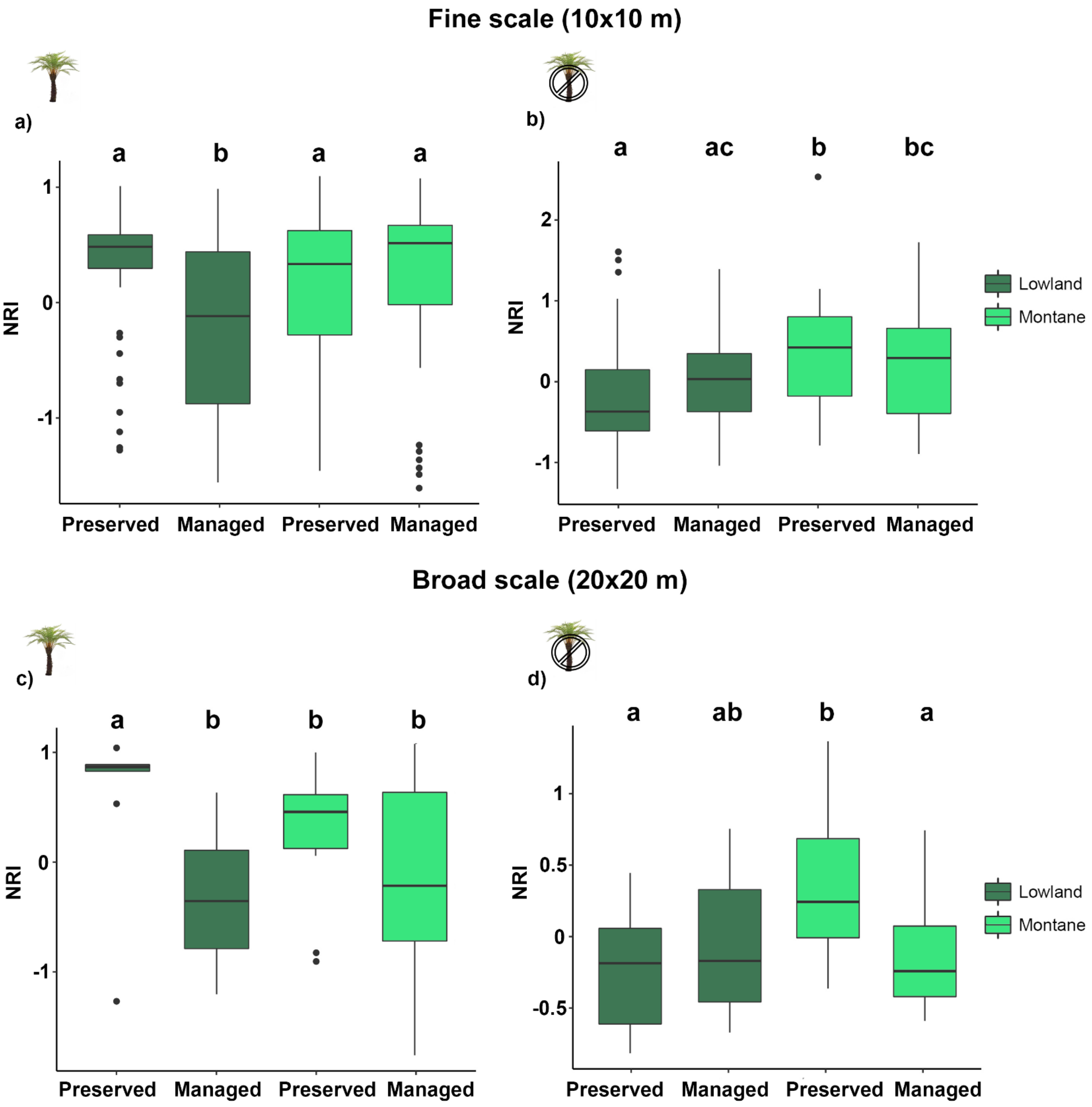

Figure 3. Net Relatedness Index (NRI) representing the phylogenetic community structure in relation to disturbance (Preserved vs. Managed) and to elevation ranges (lowland and montane), at two spatial scales (fine scale, or 10 x 10 m, and broad scale, or 20 x 20 m), and including (a and c) or not (b and d) the tree ferns in the analyzes. Different letters indicate significant differences in the mean values of NRI between disturbance scenarios ($P < 0.05$).

4. DISCUSSION

We identified that selective logging and elevation may interact in their effect on diversity and phylogenetic structure of tropical tree communities. Along elevational gradients, tree assemblages were affected by the environmental filter, presenting more phylogenetic clustering in higher altitudes, as found in other studies (e.g. Culmsee and Leuschner 2013; Qian et al. 2014), but the effect of elevation in species diversity was found only between preserved areas, while the selective logging altered the species diversity only in lowland communities. The environmental filter of elevation and, consequently, temperature (Webb et al. 2002; Cavender-Bares et al. 2009; Norden et al. 2012) might have overshadowed the effect of the disturbance of selective logging, changing the phylogenetic diversity and structure of communities. When we excluded the environmental filter of elevation, we revealed that the phylogenetic diversity increased in areas submitted to selective logging. Additionally, the pattern was stronger when distantly related clades, such as ferns, were included in the analysis at broad scale (20 x 20 m), instead of fine scale (10 x 10 m).

Environmental filters are expected to promote clustered communities, since they select similar species capable of surviving in determined conditions (Webb et al. 2002; Hardy and Senterre 2007; Mayfield and Levine 2010; Srivastava et al. 2012). We found the elevation-temperature filter might be selecting more closely related clades, such as Magnoliids, and ancient’s clades, such as Cyatheaceae, with functional traits that allow their survival in such conditions (Emerson and Gillespie 2008; Culmsee and Leuschner 2013). In this case, selective logging had little or no effect in the phylogenetic structure of plant communities.

However, when we excluded the effect of elevation, we revealed that the phylogenetic diversity increased in areas submitted to selective logging, when compared to undisturbed areas.The niches made available by the selective logging allow the occupation of distantly related species and dominant species with functionally important traits (Letcher 2010; Mayfield and Levine 2010), resulting in higher phylogenetic diversity values. In the lowland, where the filter of elevation is weak, the phylogenetic diversity was associated to the increase in abundance and richness of ferns species, whereas in montane communities, phylogenetic diversity was associated with the increase of Asterids, such as Solanaceae species.

Selective logging increases the phylogenetic diversity as it removes particular species from families with high diversity and abundance in tropical forests (Magnusson et al. 1999; Villela et al. 2006). The extraction of species that are crucial to forest structure, such as *Euterpe edulis* in the Atlantic Rainforest (Genini et al. 2009; Joly et al. 2012), might decrease the competition among the remaining species of the plant community. This indirect effect would be the increase of phylogenetic diversity in the resulting communities, as we observed after 40 years of selective logging (Mayfield and Levine 2010; Feng et al. 2014; Jin et al. 2015).

The inclusion of distantly related groups in the analysis change the results observed of the effect of environmental filter and disturbance on the phylogenetic structure of plant communities. The assessment of phylogenetic structure and ecological role of traits has better interpretation through disentangling the patterns of community assembly considering different species arrangement (Cavender-Bares et al. 2006; Hardy and Senterre 2007; Ndiribe et al. 2013). In tropical and subtropical forest, there were found different effects of filters on the phylogenetic diversity of Angiosperms communities, mostly tree communities, however they have generally excluded an important group in their analysis, as ferns species (Duarte et al. 2014; Feng et al. 2014; Qian et al. 2014). Here, we show that practice might have important impacts in the conclusions of the studies, as they change the outcomes of the analysis. The selection of clades to analysis should be made carefully, and the consequence of this selection should be considered in further studies.

The effects of environmental filters and disturbances on the species diversity and on the phylogenetic structure were affected by the spatial scale considered (Letcher 2010; Feng et al. 2014). Considering two spatial arrangements, the scale used in the analysis of the phylogenetic structure showed that the values of NRI in fine scales (10 x 10 m) were opposite than the one found for a scale four times larger (20 x 20 m). Although the studies in Tropical forests usually shows habitat filtering in phylogenetic community structure from small to intermediate scales (Kraft and Ackerly 2010; Kraft et al. 2015), we have demonstrated that elevation and selective logging was clearer in broad scale. Niche differentiations seem to be the main process structuring communities in managed montane areas at a fine scale, whilst at the broad scale, habitat filtering structures communities.

In conclusion, we show that environmental conditions and methodological decisions have complex effects in identifying changes on the diversity and on the phylogenetic structure of communities. When the environmental filter is strong, it shades the effect of disturbance. The phylogenetic structure of communities is clustered due to elevation, and when the filter becomes weaker, selective logging develops an important role in the communities, leading to open niche-spaces to distantly related species and increasing diversity. These effects could only be observed when we included ferns in the analysis and in broad spatial scale. So, the selection of the methods of analysis used in studies checking for the effect filter and disturbance on the phylogenetic structure should be done carefully, to fully understand the processes and not provide inaccurate conclusions.

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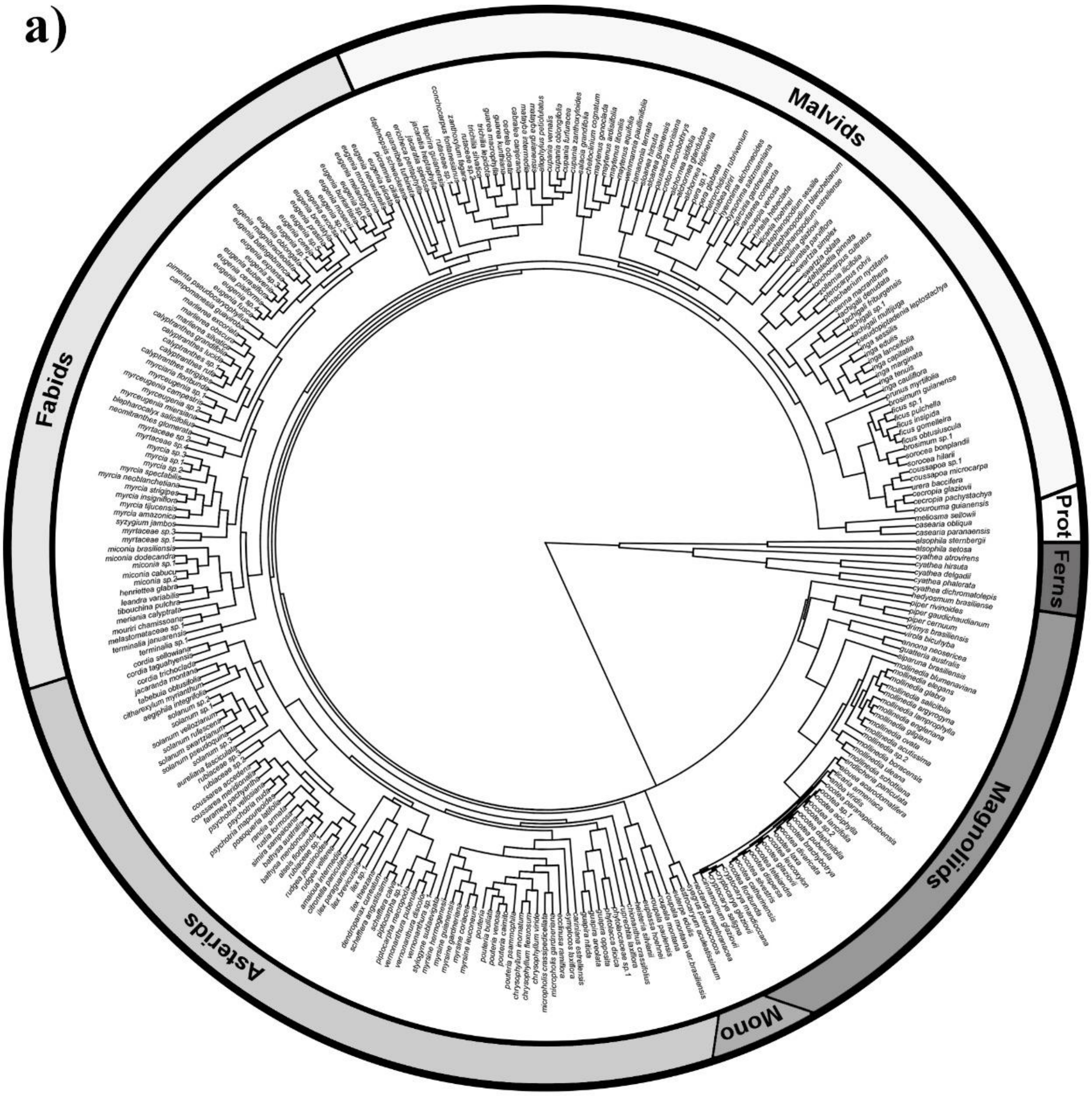
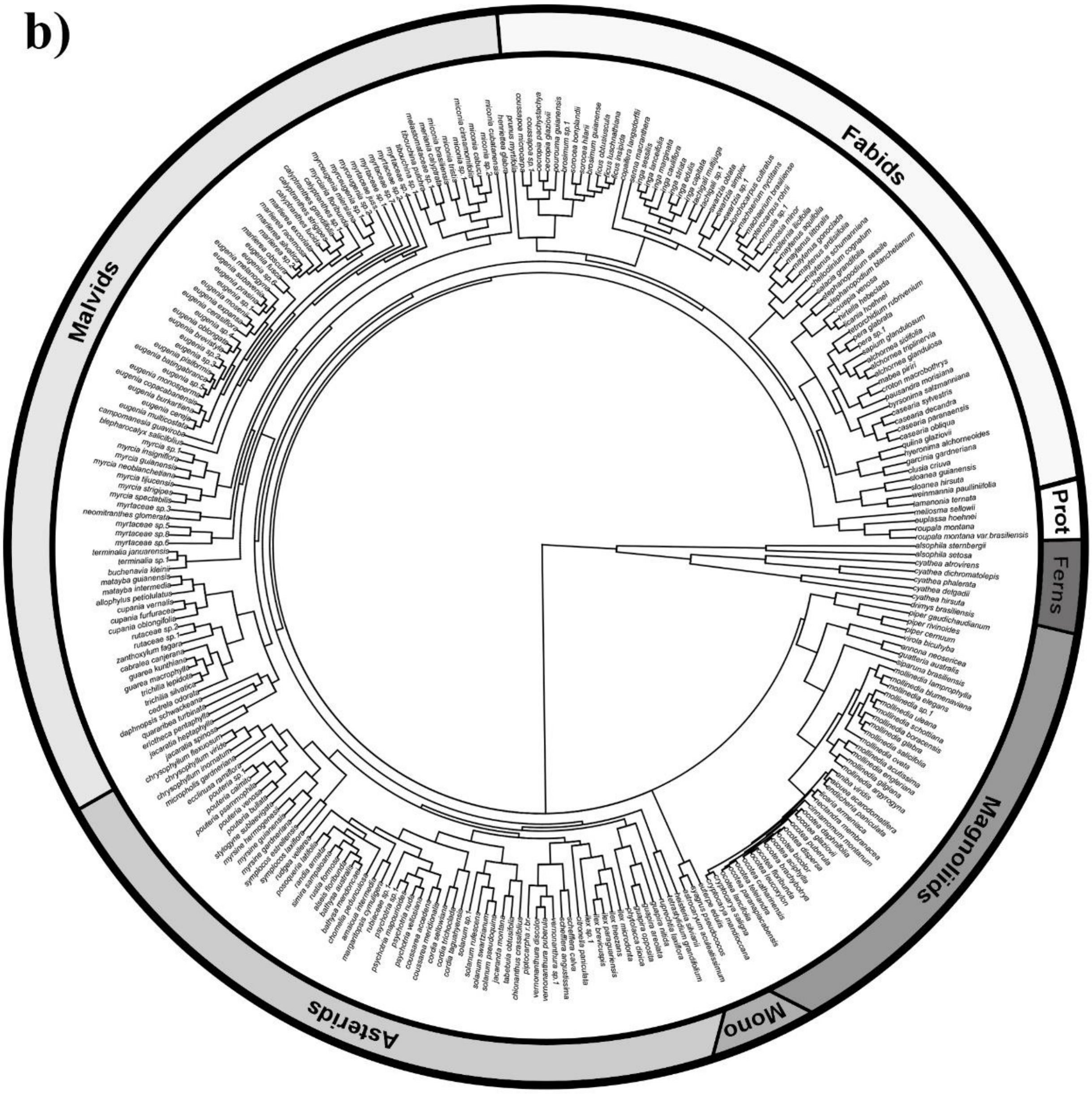
SUPPLEMENTARY MATERIAL

Appendix 1. Phylogenetic trees of four communities surveyed (1-hectare plots) in Southeast of the Brazilian Atlantic Rainforest. a) fine scale, taken out of 50 subplots of 10 x 10 m sampled randomly of each plot; b) broad scale, taken out of the random pick of 10 subplots of 20 x 20 m of each plot; Mono - Moncots; Prot- Proteales.



b)



Appendix 2. Abundance of tree species among four communities (plots of 100 x 100 m) surveyed in Southeast of the Brazilian Atlantic Rainforest. The communities were distributed in relation to the disturbance of selective logging (referred with "M") and elevational ranges (lowland and montane). F –fine scale, taken out of 50 subplots of 100 m² sampled randomly of each plot; B- broad scale, taken out of the random pick of 10 subplots of 400 m² of each plot.

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
Anacardiaceae	*Tapirira guianensis* Aubl.	1 / 0	0 / 0	0 / 0	0 / 0
Annonaceae	*Guatteria australis* A. St.-Hil.	1 / 0	0 / 1	6 / 5	7 / 4
	Annona neosericea H.Rainer	1 / 1	9 / 23	0 / 0	0 / 0
Aquifoliaceae	*Ilex brevicuspis* Reissek	0 / 0	0 / 0	1 / 1	0 / 0
	Ilex microdonta Reissek	0 / 0	0 / 0	0 / 1	0 / 0
	Ilex paraguariensis A. St.-Hil.	0 / 0	0 / 0	1 / 1	0 / 0
	Ilex sp.1	1 / 3	0 / 0	0 / 0	0 / 0
	Ilex theezans Mart. ex Reissek	1 / 1	0 / 0	0 / 0	0 / 0
Araliaceae	*Dendropanax cuneatus* (DC.) Decne. & Planch.	1 / 0	0 / 0	0 / 0	0 / 0
	Schefflera angustissima (Marchal) Frodin	1 / 0	0 / 1	5 / 5	5 / 3
	Schefflera calva (Cham.) Frodin & Fiaschi	2 / 1	1 / 0	3 / 6	5 / 5
Arecaceae	*Astrocaryum aculeatissimum* (Schott) Burret	11 / 9	0 / 0	0 / 0	0 / 0
	Euterpe edulis Mart.	91 / 69	6 / 7	296 / 224	142 / 125
	Syagrus pseudococos (Raddi) Glassman	16 / 10	2 / 1	0 / 0	0 / 0
Asteraceae	*Piptocarpha sp.1*	0 / 0	0 / 0	0 / 0	3 / 2
	Piptocarpha macropoda (DC.) Baker	0 / 0	0 / 0	1 / 0	0 / 0
	Vernonanthura discolor (Spreng.) H.Rob.	0 / 0	2 / 2	1 / 1	1 / 1
	Vernonanthura puberula (Less.) H.Rob.	0 / 0	3 / 4	0 / 0	6 / 2
	Vernonanthura sp.1	0 / 0	2 / 2	0 / 0	0 / 0
Bignoniaceae	*Jacaranda montana* Morawetz	0 / 0	0 / 0	5 / 2	2 / 4
	Tabebuia obtusifolia (Cham.) Bureau	2 / 2	0 / 0	0 / 0	0 / 0
Boraginaceae	*Cordia sellowiana* Cham.	0 / 0	0 / 0	1 / 0	12 / 7
	Cordia taguahyensis Vell.	18 / 13	11 / 11	3 / 0	0 / 0
	Cordia trichoclada DC.	0 / 0	0 / 0	11 / 7	0 / 0
Cardiopteridaceae	*Citronella paniculata* (Mart.) R.A.Howard	4 / 0	1 / 1	0 / 1	1 / 0
Caricaceae	*Jacaratia heptaphylla* (Vell.) A. DC.	1 / 1	0 / 0	0 / 0	0 / 0
	Jacaratia spinosa (Aubl.) A. DC.	0 / 0	0 / 0	1 / 1	0 / 0
Celastraceae	*Cheiloclinium cognatum* (Miers) A.C.Sm.	2 / 1	0 / 0	0 / 0	0 / 0
	Maytenus gonoclada Mart.	0 / 0	0 / 0	0 / 0	3 / 2
	Maytenus aquifolia Mart.	1 / 1	0 / 0	0 / 0	0 / 0
	Maytenus ardisiaefolia Reissek	2 / 3	0 / 0	0 / 0	0 / 0
	Maytenus littoralis R.M. Carvaho-Okano	0 / 0	0 / 0	0 / 0	1 / 1
	Maytenus schumanniana Loes.	0 / 0	0 / 0	0 / 1	0 / 0
	Salacia grandifolia (Mart. ex Schult.) G.Don	2 / 2	0 / 0	0 / 0	0 / 0

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
Chloranthaceae	*Hedyosmum brasiliense* Mart. ex Miq.	0 / 0	0 / 0	0 / 0	1 / 0
Chrysobalanaceae	*Couepia venosa* Prance	1 / 2	2 / 1	8 / 7	0 / 0
	Hirtella hebeclada Moric. ex DC.	1 / 1	0 / 0	9 / 9	3 / 3
	Licania hoehnei Pilg.	0 / 0	0 / 0	19 / 19	27 / 17
Clusiaceae	*Clusia criuva* subsp. parviflora Vesque	0 / 0	0 / 0	0 / 1	0 / 0
	Garcinia gardneriana (Planch. & Triana) Zappi	9 / 7	0 / 0	1 / 1	0 / 0
Combretaceae	*Buchenavia kleinii* Exell	0 / 1	0 / 0	0 / 0	0 / 0
	Terminalia januarensis DC.	2 / 1	2 / 1	0 / 0	0 / 0
	Terminalia sp.1	2 / 3	0 / 0	0 / 0	0 / 0
Cunoniaceae	*Lamanonia ternata* Vell.	0 / 0	0 / 0	1 / 1	0 / 0
	Weinmannia paulliniifolia Pohl ex Ser.	0 / 0	0 / 0	1 / 1	0 / 0
Cyatheaceae	*Alsophila setosa* Kaulf.	0 / 0	0 / 0	3 / 1	3 / 5
	Alsophila sternbergii (Sternb.) D.S.Conant	16 / 9	71 / 26	9 / 3	8 / 7
	Cyathea atrovirens (Langsd. & Fisch.) Domin	0 / 0	0 / 0	0 / 0	3 / 4
	Cyathea delgadii Sternb.	0 / 0	0 / 0	7 / 3	7 / 6
	Cyathea dichromatolepis (Fée) Domin	0 / 0	0 / 0	16 / 14	2 / 0
	Cyathea hirsuta C.Presl	0 / 0	12 / 8	0 / 0	0 / 0
	Cyathea phalerata Mart.	0 / 0	4 / 5	12 / 7	10 / 11
Dichapetalaceae	*Stephanopodium blanchetianum* Baill.	0 / 0	0 / 0	1 / 1	0 / 0
	Stephanopodium estrellense Baill.	0 / 0	0 / 0	0 / 3	3 / 0
	Stephanopodium sessile Rizzini	0 / 0	0 / 0	3 / 0	0 / 0
Elaeocarpaceae	*Sloanea guianensis* (Aubl.) Benth.	10 / 12	4 / 7	0 / 0	0 / 0
	Sloanea hirsuta (Schott) Planch. ex Benth.	0 / 0	0 / 0	4 / 3	2 / 2
Euphorbiaceae	*Alchornea glandulosa* Poepp. & Endl.	0 / 0	9 / 20	6 / 6	12 / 7
	Alchornea sidifolia Müll.Arg.	0 / 0	3 / 2	0 / 0	0 / 0
	Alchornea triplinervia (Spreng.) Müll.Arg.	6 / 6	18 / 12	0 / 0	9 / 9
	Croton macrobothrys Baill.	0 / 0	0 / 0	1 / 1	3 / 3
	Mabea piriri Aubl.	8 / 8	0 / 0	0 / 0	0 / 0
	Pausandra morisiana (Casar.) Radlk.	3 / 4	0 / 0	0 / 0	0 / 0
	Sapium glandulosum (L.) Morong	0 / 1	0 / 1	0 / 0	0 / 0
	Tetrorchidium rubrivenium Poepp.	1 / 1	1 / 1	0 / 0	0 / 0
Fabaceae	*Dahlstedtia pinnata* (Benth.) Malme	0 / 1	0 / 0	3 / 0	0 / 0
	Inga capitata Desv.	1 / 1	0 / 0	1 / 1	0 / 0
	Inga cauliflora Willd.	3 / 2	0 / 0	0 / 0	0 / 0
	Inga edulis Mart.	0 / 0	9 / 5	0 / 0	0 / 0
	Inga lanceifolia Benth.	0 / 0	0 / 0	0 / 1	14 / 10
	Inga marginata Willd.	0 / 0	5 / 2	0 / 0	0 / 0
	Inga sessilis (Vell.) Mart.	0 / 0	0 / 0	0 / 0	1 / 2
	Inga tenuis (Vell.) Mart.	1 / 1	0 / 0	0 / 0	0 / 0
	Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	0 / 0	74 / 39	0 / 0	0 / 0
	Machaerium brasiliense Vogel	0 / 0	0 / 0	0 / 0	0 / 1

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
	Machaerium nyctitans (Vell.) Benth.	0 / 0	0 / 0	0 / 0	1 / 1
	Ormosia minor Vogel	0 / 0	0 / 0	0 / 1	0 / 0
	Ormosia sp.1	0 / 0	0 / 0	0 / 1	0 / 0
	Pseudopiptadenia leptostachya (Benth.) Rauschert	0 / 0	2 / 0	0 / 0	0 / 0
	Pterocarpus rohrii Vahl	0 / 0	0 / 0	0 / 0	2 / 2
	Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	0 / 0	0 / 0	0 / 0	2 / 1
	Swartzia oblata R.S.Cowan	1 / 2	3 / 1	0 / 0	0 / 0
	Swartzia simplex (Sw.) Spreng.	10 / 5	0 / 0	0 / 0	0 / 0
	Swartzia Schreb.	0 / 0	0 / 0	0 / 0	0 / 1
	Tachigali denudata (Vogel) Oliveira-Filho	2 / 0	0 / 0	0 / 0	0 / 0
	Tachigali friburgensis (Harms) L.G.Silva & H.C.Lima	0 / 0	0 / 0	1 / 0	0 / 0
	Tachigali multijuga Benth.	1 / 2	0 / 0	0 / 0	0 / 0
	Tachigali Aubl.	0 / 0	0 / 0	1 / 2	0 / 0
	Zollernia ilicifolia (Brongn.) Vogel	2 / 3	0 / 0	0 / 0	0 / 0
Humiriaceae	*Vantanea compacta* (Schnizl.) Cuatrec.	0 / 0	0 / 0	0 / 0	2 / 0
Lamiaceae	*Aegiphila integrifolia* (Jacq.) Moldenke	0 / 0	1 / 0	0 / 0	0 / 0
Lauraceae	*Aiouea acarodomatifera* Kosterm.	0 / 0	0 / 0	4 / 2	0 / 0
	Aniba viridis Mez	0 / 0	0 / 0	1 / 2	1 / 0
	Cinnamomum montanum (Sw.) J.Presl	0 / 0	0 / 0	4 / 0	1 / 1
	Cryptocarya mandioccana Meisn.	1 / 0	0 / 0	1 / 3	10 / 10
	Cryptocarya saligna Mez	4 / 3	0 / 1	9 / 2	4 / 5
	Endlicheria paniculata (Spreng.) J.F.Macbr.	1 / 1	1 / 2	0 / 0	0 / 0
	Licaria armeniaca (Nees) Kosterm.	0 / 0	1 / 1	0 / 0	10 / 6
	Nectandra membranacea (Sw.) Griseb.	0 / 0	0 / 6	1 / 0	0 / 0
	Ocotea aciphylla (Nees & Mart.) Mez	0 / 0	0 / 0	2 / 2	0 / 0
	Ocotea bicolor Vattimo-Gil	0 / 0	0 / 0	0 / 1	0 / 0
	Ocotea brachybotrya (Meisn.) Mez	1 / 0	3 / 4	0 / 0	0 / 0
	Ocotea catharinensis Mez	0 / 0	0 / 0	19 / 11	21 / 21
	Ocotea daphnifolia (Meisn.) Mez	0 / 0	0 / 0	2 / 3	1 / 2
	Ocotea dispersa (Nees & Mart.) Mez	1 / 4	9 / 9	10 / 8	12 / 11
	Ocotea divaricata (Nees) Mez	0 / 0	0 / 0	1 / 0	0 / 0
	Ocotea floribunda (Sw.) Mez	0 / 0	0 / 0	1 / 1	0 / 0
	Ocotea glaziovii Mez	0 / 0	0 / 0	0 / 0	1 / 2
	Ocotea lancifolia (Schott) Mez	0 / 0	0 / 0	2 / 1	0 / 0
	Ocotea laxa (Nees) Mez	0 / 0	0 / 0	1 / 0	0 / 0
	Ocotea leucoxylon (Sw.) Laness.	0 / 0	0 / 0	1 / 1	0 / 0
	Ocotea paranapiacabensis Coe-Teixeira	0 / 0	5 / 4	0 / 0	0 / 0
	Ocotea puberula (Rich.) Nees	0 / 0	0 / 0	1 / 2	1 / 0
	Ocotea silvestris Vattimo-Gil	0 / 0	0 / 0	1 / 0	1 / 0
	Ocotea sp.1	0 / 0	0 / 0	1 / 0	0 / 0
	Ocotea sp.2	0 / 0	0 / 0	0 / 0	1 / 0

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
	Ocotea teleiandra (Meisn.) Mez	0 / 0	0 / 0	2 / 2	0 / 0
Lecythidaceae	*Cariniana estrellensis* (Raddi) Kuntze	1 / 0	1 / 0	0 / 0	0 / 0
Malpighiaceae	*Byrsonima salzmanniana* A.Juss.	0 / 0	0 / 0	1 / 1	0 / 0
Malvaceae	*Eriotheca pentaphylla* (Vell. & K.Schum.) A.Robyns	4 / 5	0 / 0	0 / 0	0 / 0
	Quararibea turbinata (Sw.) Poir.	4 / 1	0 / 0	0 / 0	0 / 0
Melastomataceae	*Henriettea glabra* (Vell.) Penneys, F.A. Michelangeli, Judd et	0 / 0	0 / 0	3 / 3	0 / 0
	Leandra variabilis Raddi	0 / 0	2 / 0	0 / 0	0 / 0
	Melastomataceae A. Juss.	0 / 0	0 / 0	0 / 0	1 / 1
	Meriania calyptrata (Naudin) Triana	0 / 0	2 / 3	0 / 0	0 / 0
	Miconia brasiliensis (Spreng.) Triana	0 / 0	0 / 0	7 / 2	0 / 0
	Miconia cabucu Hoehne	0 / 0	0 / 0	3 / 3	1 / 1
	Miconia cinnamomifolia (DC.) Naudin	0 / 0	0 / 1	0 / 0	0 / 0
	Miconia cubatanensis Hoehne	0 / 0	0 / 0	0 / 1	0 / 0
	Miconia dodecandra Cogn.	0 / 0	1 / 0	0 / 0	0 / 0
	Miconia sp.1	0 / 0	4 / 3	0 / 0	0 / 0
	Miconia sp.2	0 / 0	0 / 0	0 / 0	14 / 13
	Miconia tristis Spring	0 / 0	0 / 1	0 / 0	0 / 0
	Mouriri chamissoana Cogn.	0 / 0	0 / 0	0 / 0	2 / 0
	Tibouchina pulchra Cogn.	0 / 0	0 / 0	1 / 2	4 / 5
	Tibouchina sp.1	0 / 0	0 / 0	0 / 0	0 / 1
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	0 / 0	6 / 4	2 / 1	6 / 5
	Cedrela odorata L.	0 / 0	0 / 0	0 / 0	1 / 1
	Guarea kunthiana A.Juss.	0 / 0	0 / 0	0 / 0	3 / 3
	Guarea macrophylla Vahl	1 / 2	1 / 3	6 / 4	11 / 4
	Trichilia lepidota Mart.	1 / 1	0 / 0	0 / 0	0 / 0
	Trichilia silvatica C. DC.	2 / 0	0 / 0	0 / 0	1 / 1
Monimiaceae	*Mollinedia acutissima* Perkins	0 / 0	0 / 0	1 / 1	0 / 0
	Mollinedia argyrogyna Perkins	0 / 0	0 / 0	13 / 18	16 / 21
	Mollinedia blumenaviana Perkins	0 / 0	0 / 0	3 / 5	0 / 0
	Mollinedia boracensis Peixoto	0 / 0	0 / 0	1 / 3	0 / 0
	Mollinedia elegans Tul.	2 / 1	0 / 0	0 / 0	6 / 6
	Mollinedia engleriana Perkins	1 / 1	0 / 0	2 / 2	12 / 11
	Mollinedia gilgiana Perkins	0 / 0	0 / 0	4 / 1	0 / 0
	Mollinedia glabra (Spreng.) Perkins	0 / 0	0 / 0	0 / 1	11 / 7
	Mollinedia lamprophylla Perkins	2 / 3	0 / 0	0 / 0	0 / 0
	Mollinedia ovata Ruiz & Pav.	0 / 0	0 / 0	0 / 0	2 / 2
	Mollinedia salicifolia Perkins	0 / 0	0 / 0	17 / 9	0 / 0
	Mollinedia schottiana (Spreng.) Perkins	39 / 26	25 / 24	4 / 9	13 / 10
	Mollinedia sp.1	0 / 0	0 / 0	1 / 1	0 / 1
	Mollinedia uleana Perkins	6 / 3	0 / 0	0 / 0	0 / 0
Moraceae	*Brosimum guianense* (Aubl.) Huber	2 / 2	0 / 0	0 / 0	0 / 0
	Brosimum Sw.	1 / 1	0 / 0	0 / 0	0 / 0

<u>*Family*</u>	<u>Species</u>	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
	Ficus gomelleira Kunth	1 / 0	0 / 0	0 / 0	0 / 0
	Ficus insipida Willd.	1 / 1	2 / 1	0 / 0	0 / 0
	Ficus luschnathiana (Miq.) Miq.	0 / 1	0 / 0	0 / 0	0 / 0
	Ficus obtusiuscula (Miq.) Miq.	0 / 0	1 / 1	0 / 0	0 / 0
	Ficus pulchella Schott	0 / 0	1 / 0	0 / 0	0 / 0
	Ficus sp.1	0 / 0	0 / 0	0 / 0	1 / 0
	Sorocea bonplandii (Baill.) W.C.Burger et al.	2 / 2	0 / 0	0 / 0	0 / 0
	Sorocea hilarii Gaudich.	4 / 4	0 / 0	0 / 0	0 / 0
<u>*Myristicaceae*</u>	*Virola bicuhyba* (Schott ex Spreng.) Warb.	12 / 5	2 / 5	0 / 0	0 / 0
<u>*Myrtaceae*</u>	*Blepharocalyx salicifolius* (Kunth) O.Berg	0 / 0	0 / 0	1 / 1	0 / 0
	Calyptranthes grandifolia O.Berg	0 / 0	0 / 1	15 / 12	0 / 0
	Calyptranthes lucida Mart. ex DC.	1 / 2	2 / 0	19 / 19	20 / 18
	Calyptranthes rufa O.Berg	0 / 0	0 / 0	2 / 0	3 / 0
	Calyptranthes Sw.	0 / 0	0 / 0	4 / 3	4 / 4
	Calyptranthes strigipes O.Berg	6 / 6	0 / 0	3 / 3	11 / 5
	Campomanesia guaviroba (DC.) Kiaersk.	1 / 1	5 / 5	0 / 0	4 / 7
	Eugenia batingabranca Sobral	1 / 0	0 / 0	0 / 0	4 / 2
	Eugenia brevistyla D.Legrand	1 / 1	1 / 3	0 / 0	0 / 0
	Eugenia burkartiana (D.Legrand) D.Legrand	0 / 0	0 / 0	1 / 1	0 / 1
	Eugenia cerasiflora Miq.	2 / 1	0 / 0	0 / 0	1 / 0
	Eugenia cereja D.Legrand	5 / 5	0 / 0	0 / 0	0 / 0
	Eugenia copacabanensis Kiaersk.	0 / 0	0 / 0	0 / 1	0 / 0
	Eugenia excelsa O.Berg	1 / 0	0 / 0	0 / 0	0 / 0
	Eugenia expansa Spring ex Mart.	0 / 0	0 / 0	0 / 0	2 / 1
	Eugenia fusca O.Berg	13 / 14	0 / 0	0 / 0	0 / 0
	Eugenia magnibracteolata Mattos & D.Legrand	1 / 0	0 / 0	0 / 0	0 / 0
	Eugenia melanogyna (D.Legrand) Sobral	3 / 3	0 / 0	0 / 0	0 / 0
	Eugenia monosperma Vell.	11 / 7	0 / 0	0 / 0	0 / 0
	Eugenia mosenii (Kausel) Sobral	2 / 2	0 / 0	0 / 0	0 / 0
	Eugenia multicostata D.Legrand	0 / 0	0 / 0	0 / 1	0 / 0
	Eugenia brevistyla D.Legrand	1 / 0	0 / 0	0 / 0	0 / 0
	Eugenia oblongata O.Berg	7 / 6	1 / 0	4 / 1	3 / 0
	Eugenia plicata Nied.	1 / 0	0 / 0	0 / 0	0 / 0
	Eugenia prasina O.Berg	8 / 2	1 / 2	11 / 11	5 / 3
	Eugenia pisiformis Cambess.	0 / 0	0 / 1	0 / 0	3 / 1
	Eugenia sp.1	0 / 0	19 / 24	0 / 0	0 / 0
	Eugenia sp.2	0 / 0	0 / 0	5 / 3	8 / 13
	Eugenia sp.3	0 / 0	0 / 0	0 / 0	2 / 1
	Eugenia sp.4	0 / 0	0 / 0	2 / 1	0 / 0
	Eugenia sp.5	0 / 0	0 / 0	1 / 2	0 / 0
	Eugenia sp.6	0 / 0	0 / 0	0 / 0	1 / 1
	Eugenia subavenia O.Berg	3 / 2	0 / 0	0 / 0	0 / 0

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
	Marlierea excoriata Mart.	0 / 0	0 / 0	13 / 15	0 / 0
	Marlierea obscura O.Berg	5 / 6	0 / 0	0 / 0	0 / 0
	Marlierea racemosa (Vell.) Kiaersk.	0 / 1	0 / 0	0 / 0	0 / 0
	Marlierea silvatica (O.Berg) Kiaersk.	2 / 1	2 / 1	1 / 1	4 / 3
	Marlierea Cambess.	0 / 1	0 / 0	0 / 0	0 / 0
	Myrceugenia campestris (DC.) D.Legrand & Kausel	0 / 0	0 / 0	2 / 0	0 / 0
	Myrceugenia miersiana (Gardner) D.Legrand & Kausel	0 / 0	0 / 0	4 / 2	0 / 0
	Myrceugenia sp.1	0 / 0	14 / 21	0 / 0	0 / 0
	Myrceugenia sp.2	0 / 0	0 / 0	0 / 0	6 / 4
	Myrcia amazonica DC.	0 / 0	0 / 0	2 / 0	0 / 0
	Myrcia guianensis (Aubl.) DC.	0 / 0	0 / 0	0 / 1	0 / 1
	Myrcia insigniflora M.F.Santos	3 / 3	1 / 0	0 / 0	0 / 0
	Myrcia neoblanchetiana E.Lucas & Sobral	2 / 1	0 / 0	0 / 0	0 / 0
	Myrcia sp.1	0 / 0	1 / 0	0 / 2	0 / 0
	Myrcia sp.2	0 / 0	0 / 0	3 / 0	0 / 0
	Myrcia sp.3	0 / 0	0 / 0	0 / 0	26 / 15
	Myrcia spectabilis DC.	7 / 2	8 / 7	37 / 18	1 / 0
	Myrcia strigipes Mart.	6 / 5	1 / 1	0 / 1	15 / 5
	Myrcia tijucensis Kiaersk.	0 / 1	0 / 0	4 / 4	0 / 0
	Myrciaria floribunda (H.West ex Willd.) O.Berg	4 / 6	3 / 4	8 / 6	7 / 5
	Myrtaceae sp.1	0 / 0	0 / 1	0 / 0	1 / 0
	Myrtaceae sp.2	0 / 0	0 / 0	2 / 0	4 / 1
	Myrtaceae sp.3	0 / 0	0 / 0	1 / 1	0 / 4
	Myrtaceae sp.4	0 / 1	0 / 0	1 / 0	0 / 0
	Myrtaceae sp.5	0 / 0	0 / 0	0 / 1	0 / 0
	Myrtaceae sp.6	0 / 0	0 / 0	0 / 1	0 / 0
	Myrtaceae sp.7	0 / 0	0 / 0	0 / 1	0 / 0
	Myrtaceae sp.8	0 / 0	0 / 0	0 / 2	0 / 0
	Neomitranthes glomerata (D.Legrand) D.Legrand	1 / 1	0 / 0	4 / 4	0 / 0
	Pimenta pseudocaryophyllus (Gomes) Landrum	0 / 0	0 / 0	1 / 0	1 / 0
	Syzygium jambos (L.) Alston	0 / 0	0 / 0	1 / 0	0 / 0
Nyctaginaceae	*Guapira areolata* (Heimerl) Lundell	0 / 0	0 / 0	0 / 0	6 / 9
	Guapira nitida (Mart. ex J.A.Schmidt) Lundell	0 / 0	0 / 0	0 / 0	6 / 5
	Guapira opposita (Vell.) Reitz	28 / 24	37 / 27	35 / 33	1 / 1
Ochnaceae	*Ouratea parviflora* (A.DC.) Baill.	1 / 0	0 / 0	0 / 0	0 / 0
Olacaceae	*Chionanthus crassifolius* (Mart.) P.S.Green	0 / 0	0 / 0	5 / 0	0 / 0
	Heisteria silvianii Schwacke	0 / 0	0 / 0	0 / 0	2 / 1
	Tetrastylidium grandifolium (Baill.) Sleumer	0 / 1	0 / 0	0 / 0	0 / 0
	Chionanthus crassifolius (Mart.) P.S.Green	0 / 0	0 / 0	0 / 2	0 / 0

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
Peraceae	*Pera glabrata* (Schott) Poepp. ex Baill.	1 / 1	0 / 0	0 / 0	0 / 0
	Pera sp.1	0 / 0	0 / 0	1 / 1	0 / 0
Phyllanthaceae	*Hyeronima alchorneoides* Allemão	1 / 1	29 / 31	1 / 0	6 / 3
Phytolaccaceae	*Phytolacca dioica* L.	0 / 0	6 / 5	0 / 0	0 / 0
	Phytolaccaceae sp.1	0 / 0	0 / 0	1 / 0	0 / 0
Picramniaceae	*Picramnia ciliata* Mart.	2 / 0	0 / 0	0 / 0	0 / 0
Piperaceae	*Piper cernuum* Vell.	0 / 0	0 / 0	0 / 0	1 / 2
	Piper gaudichaudianum Kunth	0 / 0	5 / 5	0 / 0	0 / 0
	Piper rivinoides Kunth	0 / 0	1 / 1	0 / 0	0 / 0
Polygonaceae	*Ruprechtia laxiflora* Meisn.	2 / 2	0 / 0	0 / 0	0 / 0
Primulaceae	*Myrsine coriacea* (Sw.) R.Br. ex Roem. & Schult.	0 / 0	1 / 0	0 / 0	0 / 0
	Myrsine gardneriana A. DC.	0 / 0	0 / 0	2 / 1	4 / 2
	Myrsine guianensis (Aubl.) Kuntze	0 / 0	0 / 0	4 / 2	0 / 0
	Myrsine hermogenesii (Jung-Mend. & Bernacci) M.F.Freitas & Kin.-Gouv.	0 / 0	0 / 0	4 / 3	5 / 6
	Myrsine leuconeura Mart.	0 / 0	0 / 0	1 / 0	0 / 0
	Stylogyne lhotzkyana (A.DC.) Mez	1 / 0	4 / 0	0 / 0	0 / 0
Proteaceae	*Euplassa hoehnei* Sleumer	0 / 0	0 / 0	0 / 0	1 / 1
	Roupala montana Aubl.	0 / 3	0 / 0	4 / 0	0 / 0
	Roupala montana var. brasiliensis (Klotzsch) K.S.Edwards	2 / 0	0 / 0	0 / 4	0 / 0
	Roupala paulensis Sleumer	0 / 0	0 / 0	1 / 0	0 / 0
Quiinaceae	*Quiina glaziovii* Engl.	0 / 1	1 / 0	0 / 0	0 / 0
Rosaceae	*Prunus myrtifolia* (L.) Urb.	0 / 0	0 / 0	1 / 1	0 / 0
Rubiaceae	*Alseis floribunda* Schott	2 / 1	4 / 2	0 / 0	0 / 0
	Amaioua intermedia Mart. ex Schult. & Schult.f.	0 / 0	0 / 0	7 / 7	0 / 0
	Bathysa australis (A.St.-Hil.) K. Schum.	2 / 1	108 / 105	33 / 28	9 / 6
	Bathysa mendoncaei K. Schum.	18 / 22	0 / 0	0 / 0	0 / 0
	Chomelia pedunculosa Benth.	0 / 0	0 / 0	0 / 0	0 / 1
	Coussarea accedens Müll.Arg.	20 / 25	3 / 3	0 / 0	0 / 0
	Coussarea meridionalis (Vell.) Müll.Arg.	24 / 20	4 / 3	1 / 1	0 / 0
	Faramea pachyantha Müll.Arg.	1 / 0	0 / 0	0 / 0	0 / 0
	Margaritopsis cymuligera (Müll.Arg.) C.M.Taylor	0 / 0	0 / 1	0 / 0	0 / 0
	Posoqueria latifolia (Rudge) Schult.	0 / 0	0 / 0	3 / 3	1 / 2
	Psychotria mapourioides DC.	1 / 1	0 / 0	0 / 0	0 / 0
	Psychotria nuda (Cham. & Schltdl.) Wawra	0 / 0	15 / 12	0 / 0	0 / 0
	Psychotria sp.1	0 / 0	0 / 0	0 / 1	0 / 0
	Psychotria vellosiana Benth.	0 / 0	0 / 0	3 / 4	2 / 3
	Randia armata (Sw.) DC.	0 / 0	0 / 0	1 / 1	0 / 0
	Rubiaceae sp.1	0 / 0	0 / 0	0 / 0	1 / 1
	Rubiaceae sp.2	1 / 0	0 / 0	0 / 0	0 / 0

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
	Rubiaceae sp.3	1 / 0	0 / 0	0 / 0	0 / 0
	Rudgea jasminoides (Cham.) Müll.Arg.	0 / 0	2 / 0	0 / 0	0 / 0
	Rudgea vellerea Müll.Arg.	2 / 2	0 / 0	2 / 1	0 / 0
	Rustia formosa (Cham. & Schltdl.) Klotzsch	36 / 20	0 / 0	0 / 0	0 / 0
	Simira sampaioana (Standl.) Steyerm.	1 / 1	0 / 0	0 / 0	0 / 0
Rutaceae	*Conchocarpus fontanesianus* (A. St.-Hil.) Kallunki & Pirani	0 / 0	0 / 0	1 / 0	0 / 0
	Rutaceae sp.1	0 / 0	0 / 0	2 / 3	0 / 0
	Rutaceae sp.2	0 / 0	0 / 0	0 / 0	1 / 1
	Zanthoxylum fagara (L.) Sarg.	0 / 0	1 / 1	0 / 0	0 / 0
Sabiaceae	*Meliosma sellowii* Urb.	0 / 0	0 / 0	0 / 0	1 / 1
	Casearia decandra Jacq.	0 / 0	0 / 0	0 / 1	0 / 0
	Casearia obliqua Spreng.	0 / 0	0 / 0	1 / 1	0 / 0
	Casearia paranaensis Sleumer	0 / 0	0 / 0	0 / 0	5 / 3
	Casearia sylvestris Sw.	0 / 0	0 / 1	0 / 1	0 / 0
Sapindaceae	*Allophylus petiolulatus* Radlk.	0 / 0	0 / 1	1 / 3	0 / 0
	Cupania furfuracea Radlk.	0 / 0	0 / 0	1 / 1	1 / 0
	Cupania oblongifolia Mart.	1 / 1	2 / 2	2 / 0	1 / 2
	Cupania vernalis Cambess.	0 / 0	0 / 0	3 / 2	2 / 0
	Cupania zanthoxyloides Radlk.	0 / 0	0 / 0	1 / 0	0 / 0
	Matayba guianensis Aubl.	0 / 0	0 / 0	8 / 11	9 / 10
	Matayba intermedia Radlk.	0 / 0	0 / 0	3 / 1	0 / 0
Sapotaceae	*Chrysophyllum flexuosum* Mart.	20 / 25	0 / 0	1 / 1	0 / 0
	Chrysophyllum inornatum Mart.	0 / 0	0 / 0	1 / 2	0 / 2
	Chrysophyllum viride Mart. & Eichler	1 / 1	0 / 0	24 / 26	8 / 9
	Ecclinusa ramiflora Mart.	7 / 1	0 / 0	0 / 0	1 / 1
	Micropholis crassipedicellata (Mart. & Eichler) Pierre	2 / 0	0 / 0	0 / 0	0 / 0
	Micropholis gardneriana (A.DC.) Pierre	0 / 0	0 / 0	0 / 0	2 / 5
	Pouteria sp.1	1 / 0	0 / 0	0 / 0	14 / 8
	Pouteria bullata (S.Moore) Baehni	1 / 1	0 / 0	0 / 0	0 / 0
	Pouteria caimito (Ruiz & Pav.) Radlk.	0 / 0	0 / 0	23 / 14	0 / 0
	Pouteria psammophila (Mart.) Radlk.	1 / 1	5 / 10	0 / 0	0 / 0
	Pouteria venosa (Mart.) Baehni	9 / 8	0 / 0	0 / 0	0 / 0
Siparunaceae	*Siparuna brasiliensis* (Spreng.) A. DC.	0 / 0	5 / 7	0 / 0	0 / 0
Solanaceae	*Aureliana fasciculata* (Vell.) Sendtn.	0 / 0	0 / 0	0 / 0	1 / 0
	Solanum pseudoquina A.St.-Hil.	0 / 0	0 / 0	0 / 1	1 / 0
	Solanum rufescens Sendtn.	0 / 0	0 / 0	0 / 0	1 / 1
	Solanum sp.1	0 / 0	3 / 0	0 / 0	0 / 1
	Solanum sp.2	0 / 0	1 / 0	0 / 0	0 / 0
	Solanum sp.3	0 / 0	0 / 0	0 / 0	3 / 0
	Solanum swartzianum Roem. & Schult.	0 / 0	1 / 1	0 / 0	3 / 0
	Solanum vellozianum Dunal	0 / 0	0 / 0	0 / 0	1 / 0
Symplocaceae	*Symplocos laxiflora* Benth.	0 / 0	0 / 0	1 / 1	0 / 0

Family	Species	*Lowland (F/ B)*	*Lowland M (F / B)*	*Montane (F / B)*	*Montane M (F / B)*
	Symplocos estrellensis Casar.	0 / 0	0 / 0	0 / 2	0 / 0
Thymelaeaceae	*Daphnopsis schwackeana* Taub.	0 / 0	0 / 0	3 / 1	2 / 1
Urticaceae	*Cecropia glaziovii* Snethl.	8 / 3	22 / 23	2 / 2	0 / 1
	Cecropia pachystachya Trécul	0 / 0	1 / 1	0 / 0	0 / 0
	Coussapoa microcarpa (Schott) Rizzini	0 / 0	1 / 0	3 / 2	2 / 0
	Coussapoa Aubl.	0 / 0	0 / 0	0 / 0	1 / 2
	Pourouma guianensis Aubl.	1 / 2	5 / 1	0 / 0	0 / 0
	Urera baccifera (L.) Gaudich. ex Wedd.	0 / 0	1 / 0	0 / 0	0 / 0
Verbenaceae	*Citharexylum myrianthum* Cham.	0 / 0	1 / 0	0 / 0	0 / 0
Winteraceae	*Drimys brasiliensis* Miers	0 / 0	0 / 0	3 / 4	0 / 0

CAPÍTULO III

Which, where and when traits are functional? Trait interactions control tropical tree demography depending on environmental context

ABSTRACT

1. Although functional traits are defined based on their impact on species fitness and their demographic components, the reported trait-demography relationships are frequently weak. These weak relationships might be due to traits affecting demography in combination with other traits and that environmental conditions also influence the trait-demography relationship.

2. Here, we considered trait-interactions and environmental contexts (habitat and time interval between censuses) to assess how these factors shape species demography, separately and simultaneously. Specifically, we applied boosted regression tree (BRT) models to investigate changes in the trait-demographic rates relationships of tropical tree species along an elevational gradient and among time intervals between censuses (including and excluding one strong drought event). Based on a large-dataset of 18,000 tree individuals from 133 common species, distributed among four forest types (habitats) in the Atlantic forest, we assessed how trait-interactions and the environmental context control the demographic rates (growth, mortality, and recruitment).

3. The BRT models showed excellent trait ability to predict demography after the inclusion of interactions among functional traits and forest types. Such interactions and the relative influence of traits were different among time intervals and for different demographic components. For example, changes in growth rates were best related to specific leaf area, while changes in mortality and recruitment rates were best related to seed mass and wood density, respectively. Moreover, habitat affected growth particularly by interacting with wood density, and mortality and recruitment through interaction with height.

4. Trait-based studies should consider both the environmental context (space and time) and traits interactions to understand the changes in the demography of tropical tree communities. To assess which, where and when traits are functional, it is necessary to fully incorporate the concept of multiple trait-fitness optima, resulting from traits interactions in different habitats and censuses time intervals.

Keywords: Boosted regression trees, demography, functional ecology**,** habitat context, time interval, trait-demography relationships, trait-interactions, tropical forest.

1. INTRODUCTION

Trait-based ecology is largely founded on the primary assumption that functional traits determine the individual fitness and population demography (Adler et al., 2014; Lavorel & Garnier, 2002; Mcgill, Enquist, Weiher, & Westoby, 2006; Salguero-Gómez, Violle, Gimenez, & Childs, 2018). Specifically, to be called ‘functional’, a trait needs to impact ‘fitness indirectly via its effects on growth, reproduction and survival’ (Violle, Navas, Vile, Kazakou, & Fortunel, 2007). Along this line, economic trait spectra (e.g., leaf, seed and wood economic spectra) are expected to represent central trade-off axes that predict life-history strategies (Díaz et al., 2016) and species demography (Salguero-Gómez et al., 2016). The functional economics spectra should help to understand individual fitness (Reich, 2014) and species-demography relationships (Adler et al., 2014). For example, a high specific leaf area is related to faster-growing species (Wright et al., 2004), while high wood density and heavy seeds are negatively correlated with growth and mortality rates (Chave et al., 2009; Wright et al., 2010).

However, evidences of strong trait-demography relationships have been limited in the literature. Among the possible reasons for this, are the overriding environmental effects on demography (Worthy & Swenson, 2019; Yang, Cao, & Swenson, 2018) and the fact that a given trait does not affect fitness independently from other traits. As a matter of fact, trait interactions can cause alternative trait combinations to have similar fitness or demographic effects in a given context (Laughlin & Messier, 2015; Pistón et al., 2019). Despite the expectations of both trait interactions and environmental conditions on species demography (Ackerly et al., 2006; Dwyer & Laughlin, 2017; Laughlin & Messier, 2015), trait-based studies traditionally focus on single trait-demography relationships and do not consider environment constraints on demographic rates (Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010).

Different phenotypes can have similar fitness since multiple functional strategies might result in comparable performances (i.e. alternative designs) (Laughlin & Messier, 2015; Pistón et al., 2019; Worthy & Swenson, 2019). It is thus crucial to consider trait combinations in order to understand trait-demography relationships and species dynamics (Pistón et al., 2019; Yang et al., 2018). Moreover, environmental factors can shape functional traits and their combinations, also affecting species demography (Bruelheide et al., 2018; Ordoñez et al., 2009). Environment may shift the relationship between traits and species' performance along environmental gradients, wherein different habitats lead to different effects of traits on demography in response to stress or competition (Dwyer & Laughlin, 2017; Yang et al., 2018). Hence, the trait-demography relationship can vary across environmental gradients, in terms of the strength of trait influences and the interactions among functional traits (Salguero-Gómez et al., 2018; Worthy & Swenson, 2019).

In addition to changes across the spatial environmental gradient, trait- demography relationships can also change across time. For instance, population dynamics might be affected by stochastic temporal variations (Griffith, Salguero-Gómez, Merow, & Mcmahon, 2016; Körner, 2018) and the variation of species vital rates could be related to the specific habitat conditions at different points in time (Worthy & Swenson, 2019), here also considered as 'environmental context'. Thus, it is unlikely to expect unvarying tree population dynamics and those functional strategies predict species demography similarly across time (Aleixo et al., 2019; Dwyer & Laughlin, 2017; Worthy & Swenson, 2019; Yang et al., 2018). Although trait-demography relationships can be affected by the time interval in which they are taken, unraveling how the temporal changes of habitat conditions modify the plant functional responses and the relationships between traits and vegetation dynamics remains an open question (Ehrlén, Morris, von Euler, & Dahlgren, 2016; Worthy & Swenson, 2019).

To date, there is still a great shortage of studies that have assessed how multiple functional traits affect plant demographic rates, especially under different environmental contexts, including the effects of temporal variations (Salguero-Gómez et al., 2018; Worthy & Swenson, 2019; Yang et al., 2018). Further, most studies have used analytical approaches considering linear and additive responses of demography to single traits, which seems inadequate to deal with interactions and non-linear responses (De'ath, 2007; Elith, Leathwick, & Hastie, 2008). To manage with these tasks, alternative statistical techniques have been indicated, such as regression trees (De'ath, 2007; Elith et al., 2008), which allows us to asses trait interactions and represent a promising tool for functional ecology studies (de Bello et al., 2005; Piston et al. 2018).

Here, we applied Boosted Regression Trees (BRT) models to investigate changes in the trait-demography relationships of tropical tree species along an elevational gradient and at different moments in time. We used demographic data extracted from a forest plot database in combination with a dataset of sampled functional traits from tree communities of the Brazilian Atlantic forest to answer four questions: (i) to which extent did interactions between functional traits modulate tree demography? (ii) Are trait predictions consistent across different forest types (habitats)? (iii) Did trait-demography relationships change across time? (iv) Are these relationships affected by habitat and environmental temporal variations?

2. METHODS

2.1 Site description

Our study is focused on Atlantic forest tree communities distributed along an elevational gradient (0-1,100m a.s.l.) of tropical moist forest in southeastern Brazil. The study area is located in a tropical montane system called Serra do Mar (23° 22' S and 45° 05'W). The elevational gradient covers four broadly defined forest types (IBGE, 2012), here treated as habitats, distributed as follows: (i) Seasonally flooded coastal forest (herein, "*Restinga*", one plot); (ii) Lowland forest (four plots); (iii) Submontane forest (four plots); (iv) Montane forest (three plots). In general, these forest types are defined by their position on altitudinal and latitudinal belts, except for the *Restinga,* which is characterized by its sandy and seasonally flooded soil at the lowest altitude (Assis et al., 2011). Temperature decreases along the elevational gradient, presenting a range elevational lapse rate of 0.6 to 1.0°C every 100m increase in elevation (Vieira et al., 2011).

Soils are generally low in nutrients and have a high level of aluminum (Martins et al., 2015). The climate is humid subtropical (Cfa type in Köppen system), with ca. 2500 mm of rainfall annually, and monthly average temperature range from 19.1 to 25.5°C (Sentelhas et al., 1999). Droughts are rare in southeastern Brazil, but one drought event occurred in this region between 2013 and 2015, resulting in the warmest and driest summers in 50 years (Coelho, Cardoso, & Firpo, 2016). In comparison with long-term data collected by the Brazilian Center for Weather Forecast and Climate Studies of the National Institute for Space Research (CPTEC/INPE) for 1961-2015, the mean precipitation records were 60% and 25% below average in the wet seasons of 2013-2014 and 2014-2015, respectively, and temperatures were 2.5 °C above typical temperatures (Nobre, Marengo, Seluchi, Cuartas, & Alves, 2016). Local climatological records, from the "Centro Integrado de Informações Agrometeorológicas" (CIIAGRO), indicates the lowest total precipitation between 2013 and 2015, with dryer summers and more humid winters than the average for the last 25-year period (Figure S1).

2.2. Sampling design

We used data extracted from a forest inventory dataset representing twelve 1-ha plots (100 x 100 m) at undisturbed areas, distributed along an elevational gradient, ranging from sea level to 1,100 m (Alves et al., 2010; Joly et al., 2012; details in Table S1). All woody stems (trees, palms and tree ferns) with the diameter at breast height (DBH) equal to or larger than 4.8 cm were tagged and measured for diameter and re-censused four times along 10 years. The demographic database represents 22,770 stems from 21,509 tree individuals.

To make a consistent assessment of functional diversity and to increase the accuracy of our models (Májeková et al., 2016), we first selected, from the demographic database, species that presented a minimum of 15 individuals sampled in at least one of 12 plots, and at least five individuals per plot where they had their second-highest abundance (Table S2). The final dataset included 133 species from 37 families, comprising 82% and 84% of the total stem and individual abundances, respectively. These species cover a wide range of ecological strategies, from shade-tolerant species with light seeds (e.g., *Bathysa australis*, Rubiaceae) to light-demanding species with heavy seeds (e.g., *Andira fraxinifolia*, Fabaceae); three of 133 species included are locally abundant palm species. The sampling protocol and further information on species composition, including the species dominance and revisions of the richest families, are available in Alves et al. (2010), Joly et al. (2012), Silva et al. (2016) and Kamimura et al. (2017).

2.3. Demographic rates

We calculated relative growth rate (RGR), mortality (MR) and recruitment (RCT) for each of the 133 selected species (see above) in all forest types where they were sampled. In other words, we computed the different demographic parameters for each species population in each forest type. These parameters then were computed for different time intervals (details in Table S1): (i) between first and fourth census, i.e. whole time interval (ten-years, from 2005 to 2016); (ii) between first and second census, i.e. first time interval (three years); (iii) between second and third census, i.e. second time interval (three years); and (iv) between third and fourth census, i.e. third time interval (four years, which includes the drought event, see above). The demographic rates were taken by means of both growth and vital rates parameters, as described by Kohyama et al. (2018), Sheil, Burslem and Alder (1995).

We computed the relative growth rate (RGR) of each stem, as their performance, employing the formula: RGR = ln(DBHf/DBHi)/Δt, where DBHf and DBHi are the final and initial DBH of each individual, respectively, and Δt is the number of years between two censuses. For each species at each forest type, we considered the potential growth rates as the 95th quantile of the distribution of the RGR of each species at forest type (Wright et al., 2010).The annual vital rates (VR) for each population were estimated as mortality (MR) and recruitment rates (RcR). Both vital rates were calculated using the formula VR= ln(ΔN) /Δt, in which ΔN is the relative difference in the number of individuals of each species at each forest type, between two censuses (Kohyama et al., 2018; Sheil et al., 1995).

2.4. Traits

For each selected species, we collected data on six functional traits representing the leaf, seed and wood economics spectra, which are expected to respond to environmental context and to be related to species demography (Bruelheide et al., 2018, Table S3). We measured leaf area (LA, cm^2), leaf dry matter content (LDMC, mg g^{-1}), and specific leaf area (SLA, cm^2 g^{-1}) from ten leaves of ten individuals per species in each forest type. Leaf traits were measured in the summer of 2016, following standard protocols (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). As a measure of maximum height (H_{max}) under site conditions, we calculated the 95th percentile of the distribution of height values for each species. Individual stem height was calculated using forest type-derived allometric Weibull models based on stem diameter (DBH) (see Alves et al., 2010; Scaranello et al., 2010; Martins, Seger, Wiegand, & Santos, 2018)

Wood density (WD, cm^3 g^{-1}) and seed mass (SM, mg) were obtained from three global repositories, Dryad (Zanne et al., 2009), BIEN (Maitner et al., 2018) and TRY (Kattge et al., 2011), and from the literature (Bello et al., 2017; Bufalo, Galetti, & Culot, 2016; Chave et al., 2009; Gressler, Pizo, & Morellato, 2006; Lorenzi, 1992; Wanderley, Shepherd, Melhem, Giulietti, & Martins, 2016). When the same species was present in two or more dataset, we computed the average for its trait values. Missing trait-values included four traits (LDMC, SLA, WD and SM) and represented 5% of the total trait dataset. The SLA, LA, and SM values were log-transformed before conducting the analysis, as they showed right-skewed distributions.

2.5. Data analysis

We used linear mixed-effects models (LMM) in order to detect the effects of habitat and time and their interaction on performance and vital rates. Species were treated as a random factor to account for different populations of each species across forest types, whereas forest types and time-intervals and their interactions were treated as fixed effects. Linear mixed-effects models were fitted using the '*lme4*' package (Bates, Mächler, Bolker, & Walker, 2015). The significance of each explanatory variable was tested using the '*Anova*' function in the '*car*' package (Firth et al., 2009). We then performed multiple comparisons, based on LMM, to compare the demographic rates across habitats and across time using the '*emmeans*' package (Lenth, Singmann, Love, Buerkner, & Herve, 2019).

We performed a principal component analysis (PCA) on the species' trait matrix, using the *ade4* package (Dray & Dufour, 2007), to visually assess how the functional traits were correlated among them, and to describe the main axes of trait variation among the tree species selected.

We used boosted regression trees (BRT) to investigate the relationships between traits and demographic rates. The association between traits and demography can be ideally explored using the boosted regression tree models (Elith et al., 2008; Pistón et al., 2019), which does not assume linearity and additive effects of predictors. BRTs, based on combining large numbers of regression trees, are a novel and flexible statistical method capable of handling different types of predictors without the need to specify a priori shape to the demography-trait relationship, which makes them particularly powerful for exploring the fitness-trait relationship (Elith et al., 2008; Pistón et al., 2019). Further, BRTs are adequate to evaluate interactions between predictors (De'ath, 2007; Elith et al., 2008). Compared to traditional linear models, BRT's can accommodate missing information of the predictor variables, which is common in trait-based studies, thus having higher predictive performance (Pistón et al., 2019).

The BRT models were built following the methods described by Pistón et al. (2019). We considered as environmental contexts both forest type and different sampling time intervals (including or excluding the drought event). To assess the effects of traits on the components of demography and to check if the trait-demography relationships are consistent across habitats and time, we used z-scores (mean of 0 and a unit standard deviation) for each demographic rate parameter (of each species in each forest type and in each time interval, see above). We did this to focus on the effects of traits on the components of demography beyond the main absolute differences between forest types. We then tested if trait predictions were consistent across forest types by assessing the importance of the interactions between traits and forest type, within each time interval. We thus included forest types (habitats) as a predictor in the BRT models to test if traits were consistent predictors across different forest types, accounting for its relative influence in interaction with functional traits.

We adjusted the BRT parameters for each demographic rate component analysis separately, according to Elith et al. (2008) and Pistón et al. (2019). Based on a minimum of 1,000 trees, we fixed the BRT parameters for each model, which mainly comprised the bag fraction, learning rate, step size, and tree complexity (TC) (Elith et al., 2008; Pistón et al., 2019). We examined the effect of TC in the predictive ability of models by quantifying the R^2 of models with increasing values of TC, ranging from 1 to 20. We then selected the lowest TC value that did not show significant differences compared to the largest TC value, indicating that model performance had reached a plateau (Pistón et al., 2019). Finally, to show the interactions between predictors detected and modeled, and to evaluate the possible changes in predictors interactions among the periods studied, we reported both pairwise interactions ranked with higher relative strengths in each model (Elith et al., 2008). Beyond that, we compared the traits and habitat relative influences in each model, to verify the consistency of the results among different sampling intervals and the response of the trait-demographic rates relationships to the drought time interval. In a nutshell, we used the BRT model for two sets of sampling time intervals, i.e. considering the whole interval and for each of the three sample-interval separately. The statistical analyses were conducted by means of *dismo* package (Hijmans, Phillips, Leathwick, & Maintainer, 2017), and *MuMIn* package (Bartón, 2014).

In addition to the models described above, we inspected the influence of the phylogenetic relatedness influences on our results. We used a dated megaphylogeny for seed plants, GBOTB (Smith & Brown, 2018) to generate the phylogenetic tree, using the function *phylo.maker* (Jin & Qian, 2019). For this, we performed a Principal Coordinates Analysis (PCoA) based on the species pairwise phylogenetic cophenetic distance matrix (Pistón et al., 2019). Then, for each BRT analyzing each demographic parameter rate in each time interval, we included phylogenetic information as the residuals from the regression models between the demographic rate values (response) and the two first axes of the PCoA. Since results were generally consistent when using, or not, species phylogeny into the models, we report in the main paper the results without phylogeny and include part of the results using phylogeny in the supporting information (Figure S2). All statistical analyses were performed in R v 6.3.1 (R Core Development Team, 2019).

3. RESULTS

3.1 Demographic rates

We found significant differences in the demographic rates across forest types and across time intervals (Figure 1). The effect of sampling interval was similar across forest types for relative growth rate and mortality (interaction between time-interval and forest type $p>0.05$) but it changed for recruitment (interaction between time-interval and forest type $p<0.01$). Relative growth rates decreased with the elevation, while mortality rates only differed between *Restinga* and Montane forests. Growth and mortality rates presented differences among the time-intervals, except between the second and the whole time intervals. Recruitment was higher in the *Restinga* and Lowland forests when compared to the Submontane and Montane forests, and among time intervals, recruitment rates at the third interval were different from the other intervals (Figure 1).

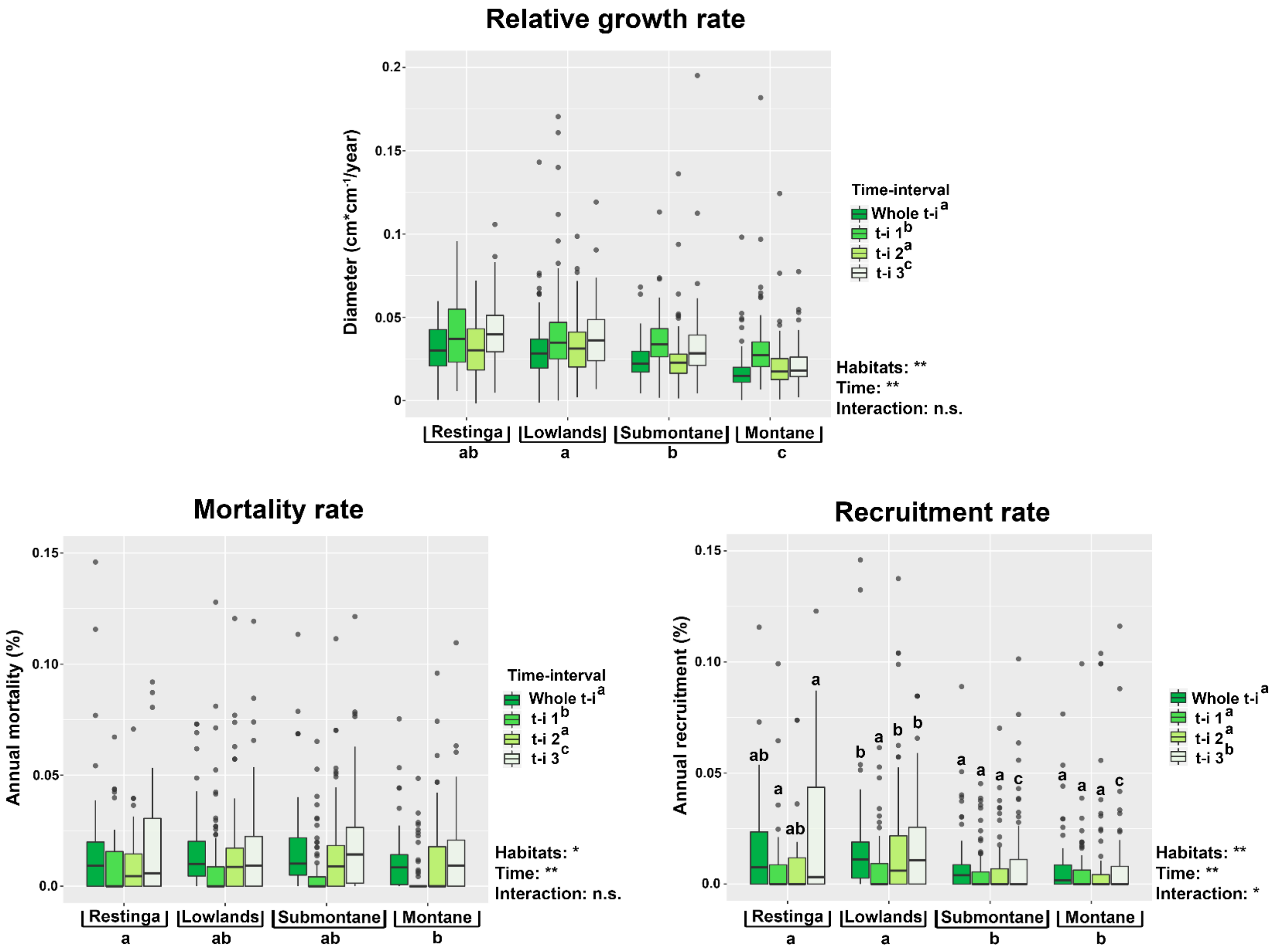


Figure 1. Effects of habitat and time and their interactions in the demography of tree species analyzed along an elevation gradient in the Brazilian Atlantic forest. The results of those effects are indicated on the bottom right of each panel. The results of multiple comparisons of demographic variation across habitats are indicated below the square brackets, and the results of variations across time are presented above the time-intervals legends. For the recruitment rate, multiple comparisons across habitats were performed within each time interval (letter above boxplots), once we found an interaction between habitat and time. Different letters indicate differences at $p < 0.05$. n.s.: not significant; *: $p < 0.05$; **: $p < 0.01$.

3.2 Tree functional patterns

The two first axes of the PCA explained respectively 31% and 20% of the total variation in tree functional traits. The first axis was mostly associated with seed mass and leaf area, whilst leaf dry matter content, specific leaf area, height, and wood density variation greatly determined the second axis (Figure S3). In general, wood density and specific leaf area were positively correlated with each other (Pearson's r = 0.24; p <0.01) and negatively correlated with leaf area (Pearson's r = -0.11 and -0.28, respectively; p <0.01). Leaf dry matter content was positively correlated with seed mass and height (Pearson's r = -0.13 and -0.27, respectively; p <0.01), whereas seed mass was negatively correlated with leaf area (Pearson's r = - 0.52; p<0.01).

3.3. Influence of traits and trait-interactions on tree demographic rates

For the whole time interval, tree demography was strongly related to functional traits and by the interactions among them (Figure 2). The BRT models explained at least 29% of the variance of demographic rates, in which the predictive abilities were significantly improved by the inclusion of interactions among the predictors (Figure S2). The BRT models presented an improvement of at least 15% in R^2 when interactions were included (TC > 1). The inclusion of phylogenetic information on the BRT models presented different effects in the proportion of explained variances, depending on the demographic parameter and time intervals analyzed. Nevertheless, we found that in general, the R^2 values were only slightly different between BRT models including and not including the phylogeny (Figure S2).

The importance of each trait and trait-interactions varied between different demographic parameters (Figure 2). Specific leaf area was the primary trait related to the relative growth rate (24.4% of the total relative influence), while seed mass to mortality (39.6% of the total relative influence) and wood density to recruitment rates (22.3% of the total relative influence). For the whole-time interval studied, trait-interactions strongly impacted all demographic rates ("int" in Figure 2), but these interactions were distinct for each component. For relative growth rates, the interaction between specific leaf area and height was the central trait-interaction, while for mortality the main trait-interaction was found between seed mass and height, and for recruitment, it was the interaction between wood density and leaf dry matter content.

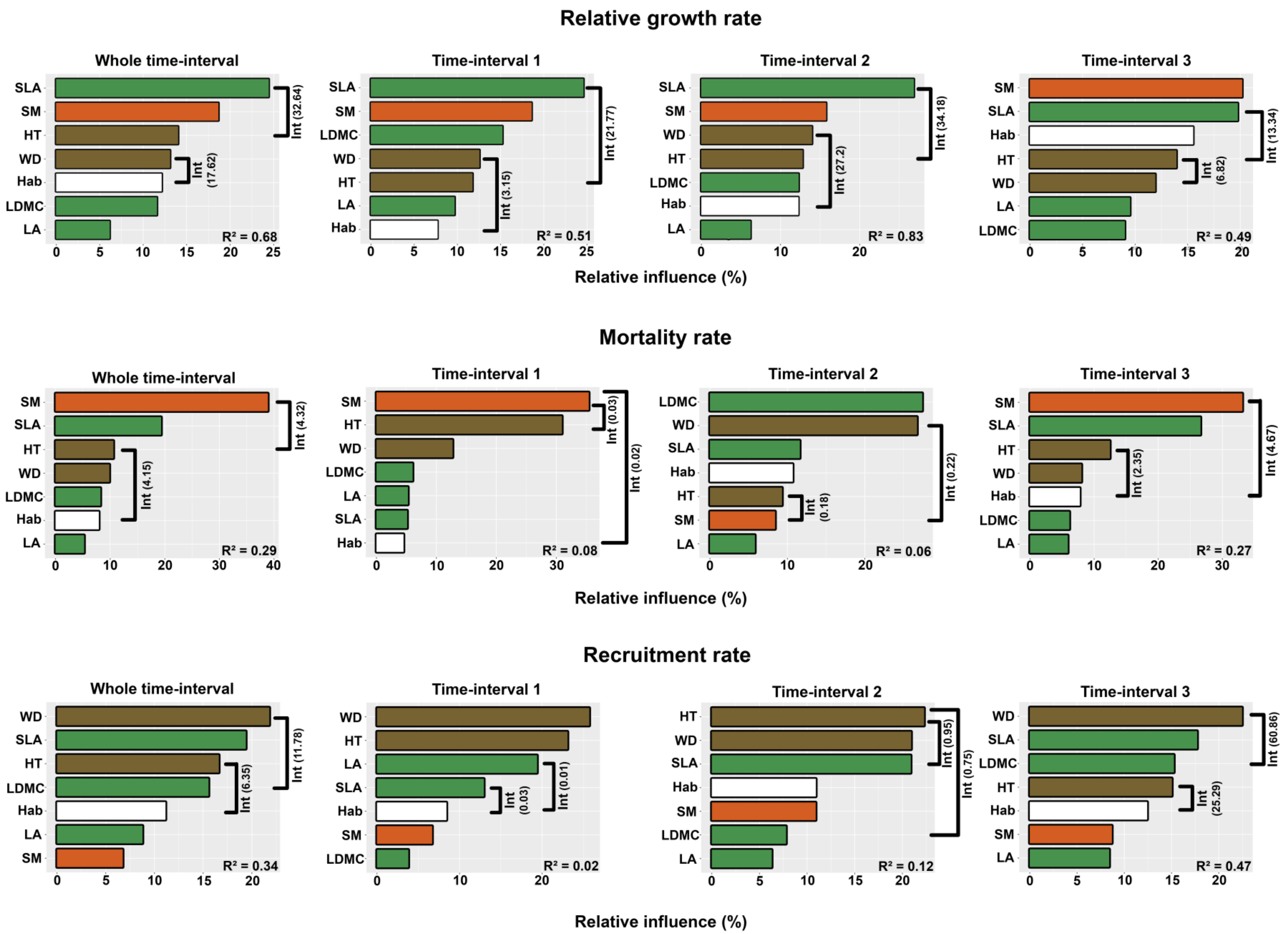

Relative growth rate
Whole time-interval
SLA
SM
HT
WD
Hab
LDMC
LA
Int (32.64)
Int (17.62)
R² = 0.68
0 5 10 15 20 25
Time-interval 1
SLA
SM
LDMC
WD
HT
LA
Hab
Int (21.77)
Int (3.15)
R² = 0.51
0 5 10 15 20 25
Time-interval 2
SLA
SM
WD
HT
LDMC
Hab
LA
Int (34.18)
Int (27.2)
R² = 0.83
0 10 20
Time-interval 3
SM
SLA
Hab
HT
WD
LA
LDMC
Int (13.34)
Int (6.82)
R² = 0.49
0 5 10 15 20
Relative influence (%)
Mortality rate
Whole time-interval
SM
SLA
HT
WD
LDMC
Hab
LA
Int (4.32)
Int (4.15)
R² = 0.29
0 10 20 30 40
Time-interval 1
SM
HT
WD
LDMC
LA
SLA
Hab
Int (0.03)
Int (0.02)
R² = 0.08
0 10 20 30
Time-interval 2
LDMC
WD
SLA
Hab
HT
SM
LA
Int (0.22)
Int (0.18)
R² = 0.06
0 10 20
Time-interval 3
SM
SLA
HT
WD
Hab
LDMC
LA
Int (4.67)
Int (2.35)
R² = 0.27
0 10 20 30
Relative influence (%)
Recruitment rate
Whole time-interval
WD
SLA
HT
LDMC
Hab
LA
SM
Int (11.78)
Int (6.35)
R² = 0.34
0 5 10 15 20
Time-interval 1
WD
HT
LA
SLA
Hab
SM
LDMC
Int (0.03)
Int (0.01)
R² = 0.02
0 10 20
Time-interval 2
HT
WD
SLA
Hab
SM
LDMC
LA
Int (0.95)
Int (0.75)
R² = 0.12
0 5 10 15 20
Time-interval 3
WD
SLA
LDMC
HT
Hab
SM
LA
Int (60.86)
Int (25.29)
R² = 0.47
0 5 10 15 20
Relative influence (%)

Figure 2. Trait-demography relationships in tree species from Brazilian Atlantic forest were explained by multidimensional ecological approach and habitat context. The interactions between predictors and their influence in tree demographics rates were analyzed by boosted regression trees models. The colors represent leaf, seed and wood economics spectra (green, orange and brown, respectively), and habitat context (white; forest types). HT: height; LA: leaf area; LDMC: leaf dry matter content; SM: seed mass; SLA: specific leaf area; Hab: habitat; WD: wood density; Int: interaction. Numbers in parentheses are the interaction values extracted from boosted regression trees models.

3.4. Environment context effects on trait-fitness outcomes

We observed that environmental context, considering both forest type and the sampling time intervals, affected the relationships between functional traits and demographic parameters (Figure 2). The relative influence of habitat varied among demographic parameters and across time, presenting the lowest relative influence in mortality at first time interval (4.4%) and the highest relative influence in growth at third time interval (15.7%). The relative growth rate was further influenced by wood density-habitat interactions, while mortality and recruitment by interactions between height and habitat.

Trait relative influences changed among the time intervals within all demographic parameters. For both vital rates, the models presented a critical variation of R^2 (Figure2). Relative growth rate was best related to specific leaf area and seed mass, and the variations across time were mostly related to leaf dry matter content and habitat. Predictor interactions related to growth changed at the third time interval, but not in other intervals. Regarding the vital rates, functional traits and habitat were good predictors ($R^2 > 0.25$) at the whole and third time intervals.

We represented the variations of relationships between relative growth rates and functional traits across time (Figure 3) once their models presented remarkable R^2 for all time intervals. Overall, taller species with lower wood densities showed higher relative growth rates. However, the relationships between relative growth rates and wood density were different among the forest types: in the *Restinga* and Montane forests, there was the topmost difference between the prediction values of growth rates, in contrast to the lowest differences found in Submontane and Lowland forests populations (Figure 3). Besides that, we found fluctuations in the relationships of traits and growth across time. The growth rates related to height and the interactions between wood density and habitat predicting the species' performance were distinct across the time intervals analyzed.

In relation to the vital rates, the environmental context also had effects on trait-demography relationships (Figures S4 and S5). For mortality rates, the prediction patterns by height were different among forest types, in which higher mortality rates by smaller species were more pronounced in the *Restinga* and Submontane forests in comparison to the species in the Lowland and Montane forests. Also, the effect of habitat on height-mortality relationships changed between the time intervals. At the whole time interval, mortality rates by taller species were similar among all forest types, but this pattern was different at the third time interval, in which mortality of taller species was negatively related to elevation. Regarding the recruitment rates, habitat affected height-recruitment relationships mainly due to higher rates found in the *Restinga* forest in contrast to the other forest types. Finally, the variation patterns of the recruitment predictions by functional traits at the whole time interval were very similar to patterns found at the third time interval analyzed (Figure S5).

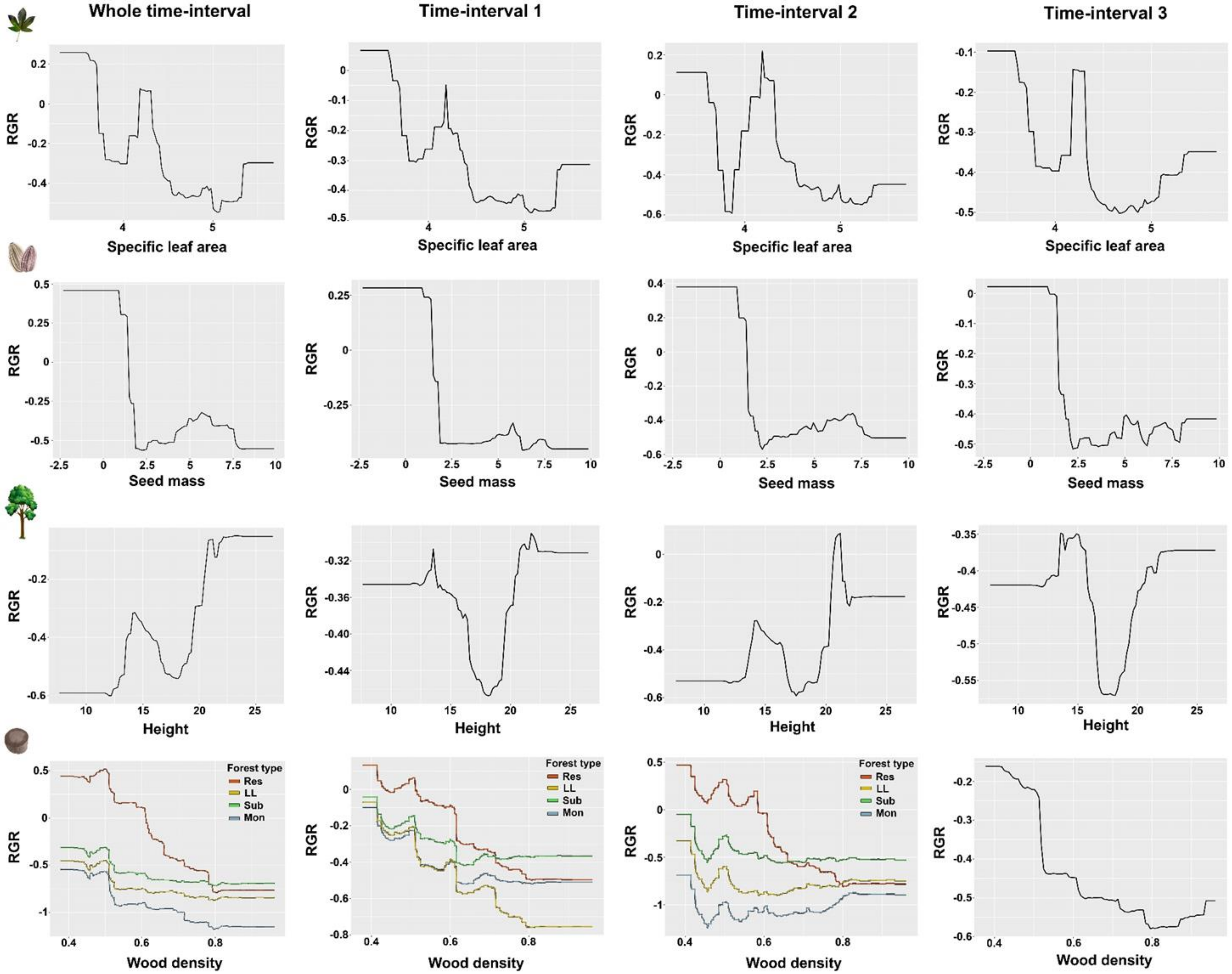

Whole time-interval
Time-interval 1
Time-interval 2
Time-interval 3
RGR
Specific leaf area
4
5
Seed mass
-2.5
0
2.5
5
7.5
10
Height
10
15
20
25
Wood density
0.4
0.6
0.8
Forest type
Res
LL
Sub
Mon

Figure 3. Effects of forest type (habitat) and time interval on outcomes of trait-growth relationships of tree species from Brazilian Atlantic forest. The habitat alters the influence of functional traits on relative growth rate (RGR), and the environmental condition related to time changed the trait-growth relationships. RGR is presented as predicted values from boosted regression trees analysis. Res: *Restinga* forest; LL: Lowland forest; Sub: Submontane forest; Mon: Montane forest.

4. DISCUSSION

By employing multidimensional ecological analyses, we demonstrated that trait-interactions and environmental context are crucial factors to be considered when assessing trait-demography, and therefore, trait-fitness relationships. Our trait-demography approach highlighted the importance of (i) different functional economy spectra (e.g. wood density, seed mass, and specific leaf area) in tropical tree demography; (ii) considering trait interactions to understand functional strategies producing comparable demography, and (iii) trade-offs among trait combinations for the different demographic parameters. Further, our results showed the importance of accounting for (iv) habitat in the context of demography and functional traits relationships (Yang et al., 2018), and (v) the changes on tree demographic rates across time (Worthy & Swenson, 2019) modulating trait-demography relationships. We discuss these subjects in the following sections.

4.1 Traits are functional: which?

Specific leaf area, seed mass, tree height and wood density were the most important predictors of tree performance and vital rates. This pattern is consistent across different tropical plant communities (Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010), However, in contrast to the frequently low percentage of explained variation found in trait-demography relationships (Pistón et al., 2019; Salguero-Gómez et al., 2018), especially for tree communities (Worthy & Swenson, 2019), our models explained a good proportion of the variation in the demographic parameters analyzed, particularly the effect of functional traits (Figure 2). Thus, based on a large dataset of tropical tree species, our results endorse the central point of trait-based studies and confirm the role of key plant traits and their interactions in predicting species demography (Laughlin & Messier, 2015; Violle et al., 2007).

The functionality of traits can be limited for each fitness-component (Salguero-Gómez et al., 2018), and single-trait approaches cannot cover the fundamental idea that species demography is determined by their integrated phenotype (Laughlin & Messier, 2015; Májekova, de Bello, Doležal, & Lepš, 2014). Both these facts are reflected in the considerable variation found due to different effects on the demographic parameters (Adler et al., 2014; Paine et al., 2015; Visser et al., 2016; Wright et al., 2010). In our case, there was a great variation of the relative influence of each trait among the demographic parameters analyzed. For the whole time interval analyzed, wood density was the key-trait related to tree recruitment, and the fourth trait related to growth and mortality, while seed mass presented the highest and lowest relative influence on mortality and recruitment, respectively (Figure 2). The relationships between single traits and demographic rates is widely described and discussed in traits-based studies (Salguero-Gómez et al., 2018; Yang et al., 2018), but the ‘functionality’ of trait interactions, shaping species demography, are rarely considered (Pistón et al., 2019; Worthy & Swenson, 2019).

Traits interactions modulate alternative designs associated with similar demographic rates. Considering the multidimensionality of trait ecology (Laughlin & Messier, 2015) is fundamental to evaluate how alternative designs shape similar demographic rates (Dias, Rosado, de Bello, Pistón, & de Mattos, 2019; Pistón et al., 2019). The inclusion of predictor interactions was fundamental to assess the relationships between traits and demography. Beyond that, different trait-interactions are modulating comparable demographic rates. For example, the interaction between height and specific leaf area was crucial in regulating equivalent relative growth rates. For mortality, the interaction between seed mass and conducted comparable rates, and similar recruitment was modulated by interactions between wood density and height. Thus, incorporating multidimensional ecological analyses (Pistón et al., 2019) and assessing the effects of trait-interactions are fundamental to clarify the relationship between integrated phenotypes and demographic rates (Bruelheide et al., 2018; Paine et al., 2015).

Last, the tree species analyzed present a large number of traits that are conserved (Martins et al., 2018), but the inclusion of phylogenetic information, in our BRT models, did not affect the predictive abilities of demographic rates by multi-traits and habitat. Therefore, we used the results of BRT models without phylogenetic information, once the traits remained related to environmental context and explaining changes on demographic rates, even after accounting for phylogenetic relationships between species, and because we used an approach independent of the result interpretations at different evolutionary scales (de Bello et al., 2015).

4.2 Habitat context matters: where?

Our analyses revealed trait-habitat interactions regulating changes on trait-demography relationships along all the time intervals analyzed. Both species demography and trait-demography relationships are dependent on habitat context (Laughlin & Messier, 2015; Salguero-Gómez et al., 2018). In this sense, by using the z-score of the demographic rates, we were able to focus on the effects of trait-habitat interactions on species demography. For example, wood density was an important trait related to different species' performance by interacting with the habitats, in which taller species with low wood density were related to higher relative growth rates, but those trait-growth relationships were dissimilar among the forest types (Figure 3). Analyzed in general, we see a weak influence of wood density on tree performance, which is probably caused by differences in the wood density response across habitats. Wood density-growth relationships were more pronounced in the *Restinga* and in the Montane forest, whilst the other forest types did not show this relationship. Because the tree species analyzed present variations on their ecological strategies, those differences can be related to the variation in species abundance and distribution within forest types (Joly et al., 2012; Kamimura et al., 2017), and effects of elevation on tree height and wood density variation (Alves et al., 2010; Scaranello et al., 2010).

We found trait-demography relationships depending on the habitat context, in which not all traits are correspondingly functional for all habitats (Violle et al., 2007) and habitat context limits the demographic responses related to each phenotype (Dwyer & Laughlin, 2017; Yang et al., 2018). In this way, we found a negative relationship between growth and wood density, but this pattern was different among forest types. The growth differences between species with low and high wood densities were remarkable in the *Restinga* Forest, while in the Submontane and Montane Forests, tree performances almost did not change in relation to this trait. On the other hand, height was a great predictor of recruitment in most habitats but not in the *Restinga* Forest (Figure S5).

Although trait-demography relationships are often expected to be controlled by correlations between habitat and functional traits (Salguero-Gómez et al., 2018; Shipley et al., 2016), those relationships remain unclear and inconsistent (Adler et al., 2014; Laughlin, Strahan, Adler, & Moore, 2018; Moles, 2018). To cope with this issue, trait-based studies are expected to unravel the effect of environmental context affecting both functional traits and population dynamics (Paine et al., 2015; Worthy & Swenson, 2019). Here, we presented the importance of assessing the differences in relative influence of habitat context on different tree demographic rates, and how the environment affects trait-demography relationships. In this way, understanding how phenotypes depend on habitat context is essential to assess the traits functionality and the variation of relationships between demographic rates and traits along environmental gradients (Worthy & Swenson, 2019; Yang et al., 2018).

4.3 Trait-demography relationships change across time: When?

We found outstanding predictions of tree demography by functional traits and habitat context (Figure 2). However, the variance explained was dependent on the demographic parameter and on the time interval of the censuses. Besides including habitat context in trait-based analyses, we have shed light on how integrated phenotypes respond to environmental changes across time (Salguero-Gómez et al., 2018; Worthy & Swenson, 2019).

Regarding the species' performance and its vital rates, we found significant differences in tree demography in relation to both environmental contexts analyzed (habitat and time-interval). Tree growth and mortality were significantly different across habitats, mainly due to their low values for these demographic parameters in the Montane forest. We found interaction between habitat and time affecting recruitment rates, in which the differences found across forest types were stronger at the third time interval, which includes the drought event. The results of the effect of both habitat and sampling interval, with and without interaction, highlight the importance of the context in assessing absolute demographic differences between species, which need to be accounted for when assessing the specific role of traits.

Assessing the impacts of environmental context on tree performance and vital rates have been widely explored in trait-based studies (e. g. Laughlin et al., 2018; Visser et al., 2016; Wright et al., 2010). Though, proper predictions in changes of species demography also require assessing how the environmental changes across time affect trait-demography relationships (Salguero-Gómez et al., 2018; Worthy & Swenson, 2019). There were changes in relative influences of traits, trait-interactions and trait-habitat interactions among time intervals analyzed. Since changes in habitats conditions of tropical forests are related to their dynamics (Clark, Clark, & Rich, 1993; Schnitzer & Carson, 2001), changes in trait-demography relationships across time can be related to differences of trade-offs in growth and survival within and across the different habitat contexts of tropical forest (Inman-Narahari et al., 2014; Paine et al., 2015).

In order to assess the drivers and mechanisms of the ecological process, it is fundamental to tie the processes under investigation with time and timing resolution of the dataset (Schimel, 2013). Alongside the approach of integrated phenotype and habitat context we assessed the variation on patterns of trait-demography relationships across time by analyzing these relationships for each time interval. Our models were powerful on explaining tree performance for all time intervals, but trait-growth relationships were different for each interval analyzed. Those changes in trait-demography relationships could be related to the variation of environmental context across time (Korner, 2018, Worthy & Swenson, 2019), once the habitat context affects the trait-performance relationships (Salguero-Gómez et al., 2018). Moreover, considering the whole time interval, the relationship between functional traits and growth was expressed as a sum of patterns found in shorter time intervals.

Regarding the vital rates, the main variations in trait-demography relationships across time were found to the explained variation by BRT models. We found greater R^2-values for the models at whole and for the third time intervals. Traits and habitat did not explain mortality or recruitment rates along time intervals which not included the drought event. Although relative contribution of main drivers and mechanisms on vital rates remain unidentified (McDowell et al., 2018; Paine et al., 2015), among-site variations, such as rising temperature, wind events, and lightning are reported as key cause of tree mortality (McDowell et al., 2018). Along non-drought time intervals, tree mortality and recruitment rates appear to be related to a stochastic temporal variation of populations (Doak, Morris, Pfister, Kendall, & Bruna, 2005; Griffith et al., 2016). However, the higher explanation of vital rates by traits and trait-interactions in time intervals which included the drought event, suggests the traits were more important in defining different ecological strategies of species along harsh periods (Salguero-Gómez et al., 2016). Thus, considering the analyzes at different time intervals is crucial to assessing the consequences of environmental changes related to time in trait-demography relationships.

5. CONCLUSIONS

Altogether, our findings indicate that trait interactions and environmental context, i. e. habitat and time interval of the censuses, control tree demographic changes in tropical forests. By using boosted regression trees, we demonstrate the importance of considering trait-trait and environmental-trait interactions to understand the mechanisms modulating tree demographic rates, and the advantages of using appropriate statistical analyses to handle with complex ecology approaches and large datasets. An essential next step is to incorporate spatial patterns and individual-level analyses in trait ecology studies, once the local neighbors characteristics, such as individuals' crowding and neighborhood trait composition, should affect the relationships of functional traits determining individual fitness and demographic rates (Yang et al., 2018; Zambrano, Marchand, & Swenson, 2017).

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SUPPORTING INFORMATION

Table S1. Environmental and structural characteristics and sampling dates of twelve 1-ha plots surveyed at the Atlantic forest along an elevation gradient in southeastern Brazil.

Plot (names)	Forest type	Number of individuals	Number of families	Species richness	Gaps area (m^2)	Elevation (m.a.s.l)	Elevational range (m.a.s.l)	Annual mean temperature (ºC)	Annual precipitation (mm)	1st census	2nd census	3rd census	4th census
A	*Restinga*	1634	31	83	2052.9	10	1	22.6	2406	Dec-2005	Jan-2008	Dec-2011	Apr-2015
B	Lowland	1143	37	147	2598.9	46	23	22.6	2406	Dec-2005	Feb-2008	Jan-2012	May-2015
C	Lowland	1167	36	122	2588.1	64	12	22.6	2406	Mar-2006	Feb-2008	Mar-2012	Jul-2015
D	Lowland	1324	40	158	1870.9	57	26	22.6	2406	Mar-2006	Mar-2008	Apr-2012	Jul-2015
E	Lowland	1253	40	139	1908.1	73	25	22.3	2324	Apr-2006	Apr-2008	Jun-2012	Jul-2015
G	Submontane	1513	40	149	1280.4	190	19	18.3	1975	Jul-2006	Aug-2008	Sep-2012	Sep-2016
H	Submontane	1519	40	159	1196.2	209	16	18.3	1975	Aug-2006	Aug-2008	Oct-2012	Sep-2016
I	Submontane	2003	48	203	939,0	327	48	17.5	1865	Feb-2007	Feb-2009	Oct-2012	Oct-2016
J	Submontane	1823	47	208	1232.2	352	46	17.5	1865	Oct-2006	Nov-2008	Oct-2012	Oct-2016
K	Montane	1767	42	177	1531,0	1037	47	16.3	1724	Sep-2007	Dec-2009	Dec-2012	Feb-2016
L	Montane	1664	37	168	1599,0	1020	50	16.3	1724	Oct-2007	Dec-2009	Dec-2012	Feb-2016
M	Montane	1822	38	171	1317.8	1024	49	16.3	1724	May-2008	Dec-2009	Nov-2012	Nov-2015

Dataset was compiled from Alves et al., (2010); Eisenlohr et al., (2013); Joly et al., (2012); Kamimura, Morais, Joly, & Assis, (2018); Leitold, et al., (2014); Martins, Seger, Wiegand, & Santos, (2018), and updated from the databases of ‘Functional Gradient’ and ‘EcoSpace’ Projects.

Table S2. Summary of forest types distribution, functional trait values, and demographic rate values (z-scores, for further details see the methods), for each time-interval analyzed, of 133 tree species in the Atlantic forest, southeastern, Brazil. Ll – Lowland forest; Sub- Submontante forest; Mon – Montane forest; Res – *Restinga* forest; LA: leaf area; LDMC: leaf dry matter content; SM: seed mass; SLA: specific leaf area; WD: wood density; Max. H.: Maximum height; RGR: relative growth rates; MR – mortality rates; RCT: recruitment rates; NA: not available.

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Alchornea glandulosa	Euphorbiaceae	Ll	21.75	0.68	85.16	330.3	102.5	80	1.21	0.28	0.51	0.24	-0.56	-0.86	0.77	-1.41	-0.65	-0.79	-0.18	-0.98
Alchornea glandulosa	Euphorbiaceae	Mon	21.75	0.68	85.16	330.3	102.5	80	-0.48	0.08	-0.82	-0.37	0.04	-0.87	-0.13	0.46	-0.17	1.39	-0.15	-0.81
Alchornea triplinervia	Euphorbiaceae	Ll	21.55	0.94	60.46	400.81	122.64	100	0.92	0.13	0.37	0.08	0.32	-0.86	-0.48	1.71	-0.74	-0.79	-0.37	-0.98
Alchornea triplinervia	Euphorbiaceae	Mon	21.55	0.95	60.46	400.81	122.64	100	-1.45	-1.17	-1.53	-1.88	-0.45	-0.87	1.37	-1.22	0.42	-0.97	-0.66	1.55
Alchornea triplinervia	Euphorbiaceae	Res	21.55	0.95	60.46	400.81	122.64	100	-0.85	-0.70	0.17	-0.76	-0.41	-0.26	-0.24	-0.55	-0.58	-0.10	-0.61	-0.53
Alchornea triplinervia	Euphorbiaceae	Sub	21.55	0.95	60.46	400.81	122.64	100	-0.99	-0.26	-0.81	-0.92	-0.09	-0.71	0.17	-0.15	-0.83	-0.78	-0.79	-0.70
Amaioua guianensis	Rubiaceae	Mon	17.49	0.59	67.94	421.19	120.1	8	-1.25	-0.13	-1.96	-1.53	-0.59	-0.87	-1.20	-0.07	-1.00	-0.97	-0.66	-0.81
Amaioua intermedia	Rubiaceae	Mon	16.71	0.58	67.94	421.19	120.1	7	-0.89	-0.84	-0.77	-1.04	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Amaioua intermedia	Rubiaceae	Res	16.71	0.58	67.94	421.19	120.1	7	0.19	-0.13	1.60	1.92	-0.58	-0.94	0.07	-0.88	0.19	1.59	0.59	-0.65
Amaioua intermedia	Rubiaceae	Sub	16.71	0.58	67.94	421.19	120.1	7	-1.01	-0.73	-0.76	-1.06	0.06	-0.71	1.61	-1.38	-0.83	-0.78	-0.79	-0.70
Andira fraxinifolia	Fabaceae	Res	15.06	0.79	10.72	403.77	151.61	14285	-0.61	-0.48	-0.89	-0.24	-0.30	-0.20	-0.04	-0.51	-0.99	-0.73	-1.08	-0.65
Annona dolabripetala	Annonaceae	Mon	13.71	0.46	24.25	375	130.25	80	-0.84	-1.16	-1.31	-0.52	-0.76	1.55	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Annona neosericea	Annonaceae	Ll	18.09	0.61	24.94	375.65	128.4	53	-1.54	-1.01	-1.21	-1.18	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Annona neosericea	Annonaceae	Sub	18.09	0.61	24.94	375.65	128.4	53	-0.58	-0.71	-0.58	-0.73	0.71	-0.71	2.62	-1.38	-0.83	-0.78	-0.79	-0.70
Ardisia martiana	Primulaceae	Ll	9.53	0.74	41.45	NA	146.2	98	-1.32	-0.41	-1.00	-1.05	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Ardisia martiana	Primulaceae	Sub	9.53	0.74	41.45	NA	146.2	98	-0.24	-0.19	-0.30	-0.46	-0.06	0.08	-0.17	0.04	-0.15	-0.44	0.02	-0.12
Astrocaryum aculeatissimum	Arecaceae	Ll	12.78	0.96	27.92	364	122.7	11430	-1.10	-0.58	-0.77	-0.76	-0.55	-0.27	0.00	-1.00	-0.64	-0.79	-0.67	-0.37
Astrocaryum aculeatissimum	Arecaceae	Res	12.78	0.96	27.92	364	122.7	11430	-1.66	-1.53	-2.64	3.06	-0.95	-0.94	-0.89	-0.88	1.21	-0.73	5.40	-0.65
Astrocaryum aculeatissimum	Arecaceae	Sub	12.78	0.96	27.92	364	122.7	11430	-1.35	-0.58	-0.87	-0.94	-0.34	-0.34	-0.21	-0.37	-0.76	-0.78	-0.60	-0.70
Bathysa australis	Rubiaceae	Ll	17.15	NA	843.14	200.07	34.57	0.1	0.86	0.51	-0.29	0.05	-0.01	0.68	-0.14	-0.31	-0.05	0.22	0.22	-0.52
Bathysa australis	Rubiaceae	Mon	17.15	NA	843.14	200.07	34.57	0.1	-0.42	-0.74	-0.23	-0.33	-0.53	-0.87	-0.92	-0.16	-0.53	-0.54	-0.24	-0.51
Bathysa australis	Rubiaceae	Sub	17.15	NA	843.14	200.07	34.57	0.1	1.07	0.17	0.62	0.54	-0.37	-0.13	-0.42	-0.25	-0.32	-0.78	0.12	-0.35
Bathysa mendoncaei	Rubiaceae	Ll	13.85	0.67	31.96	277.36	108.71	0.1	-0.17	-0.28	-0.25	-0.47	-0.90	-0.72	-0.64	-0.84	-0.45	-0.59	-0.64	-0.02

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Bathysa mendoncaei	Rubiaceae	Sub	13.85	0.67	31.96	277.36	108.71	0.1	-0.52	-0.55	-0.42	-0.55	-0.79	-0.53	-0.48	-0.91	-0.59	-0.70	-0.56	-0.45
Brosimum guianense	Moraceae	Ll	16.58	0.47	19.89	539.2	52.2	291	-0.15	-0.64	-0.51	-0.25	-0.71	-0.86	-1.21	0.21	-1.06	-0.79	-1.02	-0.98
Brosimum guianense	Moraceae	Sub	16.58	0.47	19.89	539.2	52.2	291	-1.28	-0.86	-0.87	-0.89	-1.00	-0.71	-0.42	-1.38	-0.61	-0.78	-0.16	-0.70
Cabralea canjerana	Meliaceae	Ll	22.44	0.62	42.11	335	163.4	700	-0.42	-0.79	-0.45	-0.38	1.26	-0.86	4.77	-1.41	-1.06	-0.79	-1.02	-0.98
Cabralea canjerana	Meliaceae	Mon	22.44	0.62	42.11	335	163.4	700	-1.06	-0.93	-1.16	-0.93	-0.56	-0.87	-1.20	-0.02	0.24	1.42	-0.66	0.20
Cabralea canjerana	Meliaceae	Sub	22.44	0.62	42.11	335	163.4	700	-0.08	-0.47	-0.15	-0.24	-1.20	-0.71	-0.78	-1.38	-0.83	-0.78	-0.79	-0.70
Calyptranthes grandifolia	Myrtaceae	Mon	17.65	0.62	56.15	299.51	92.35	95	-1.07	-1.12	-0.85	-1.11	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Calyptranthes grandifolia	Myrtaceae	Sub	17.65	0.62	56.15	299.51	92.35	95	-0.58	-0.88	-0.74	-0.55	-1.20	-0.71	-0.78	-1.38	-0.44	-0.78	0.33	-0.70
Calyptranthes lucida	Myrtaceae	Ll	20.54	0.58	39.35	280.72	114.06	380	-0.54	-0.59	-0.58	-0.75	-0.39	-0.86	0.33	-0.61	-0.43	0.71	-1.02	-0.23
Calyptranthes lucida	Myrtaceae	Mon	20.54	0.58	39.35	280.72	114.06	380	-0.57	-1.13	-0.55	-0.95	-0.64	-0.87	-0.91	-0.33	-0.81	-0.97	-0.22	-0.81
Calyptranthes lucida	Myrtaceae	Res	20.54	0.58	39.35	280.72	114.06	380	2.16	0.41	2.77	0.04	-0.95	-0.94	-0.89	-0.88	1.21	-0.73	-1.08	2.64
Calyptranthes lucida	Myrtaceae	Sub	20.54	0.58	39.35	280.72	114.06	380	-0.47	-0.55	-0.34	-0.38	-0.57	-0.71	-0.78	-0.01	-0.09	-0.78	-0.41	0.39
Calyptranthes maritima	Myrtaceae	Ll	17.7	0.83	42.45	312	109.02	285	-1.37	-0.85	-1.20	-0.64	-1.47	-0.86	-1.21	-1.41	-0.20	-0.79	0.75	-0.98
Calyptranthes maritima	Myrtaceae	Mon	17.7	0.83	42.45	312	109.02	285	-0.97	-1.21	-0.66	-1.24	-0.11	-0.87	2.03	-1.22	-1.00	-0.97	-0.66	-0.81
Calyptranthes maritima	Myrtaceae	Sub	17.7	0.83	42.45	312	109.02	285	-0.29	0.19	-0.29	-0.61	-1.06	-0.71	-0.78	-1.08	-0.67	-0.78	-0.79	-0.44
Calyptranthes strigipes	Myrtaceae	Ll	22.21	0.94	31.85	355.8	120.64	380	-0.19	-0.56	-0.63	-0.20	-0.62	-0.86	0.01	-0.78	-0.20	-0.79	-0.22	0.19
Calyptranthes strigipes	Myrtaceae	Mon	22.21	0.95	31.85	355.8	120.64	380	-0.56	-0.39	-0.11	-1.05	-0.96	-0.87	-1.20	-0.72	-0.45	-0.97	-0.66	0.08
Calyptranthes strigipes	Myrtaceae	Sub	22.21	0.95	31.85	355.8	120.64	380	0.09	-0.36	-0.38	-0.41	-0.92	-0.71	-0.53	-1.07	-0.68	-0.05	-0.79	-0.70
Cecropia glaziovii	Urticaceae	Ll	16.42	0.38	898	165.96	26.81	0.5	5.02	5.23	5.06	6.21	4.75	4.18	3.89	3.67	4.84	2.20	4.17	5.85
Cecropia glaziovii	Urticaceae	Mon	16.42	0.38	898	165.96	26.81	0.5	5.05	7.61	6.15	0.11	0.14	-0.87	-1.20	1.18	-1.00	-0.97	-0.66	-0.81
Cecropia glaziovii	Urticaceae	Res	16.42	0.38	898	165.96	26.81	0.5	2.74	1.39	2.98	-1.20	3.69	-0.94	-0.89	8.99	-0.99	-0.73	-1.08	-0.65
Cecropia glaziovii	Urticaceae	Sub	16.42	0.38	898	165.96	26.81	0.5	2.51	0.15	3.90	4.80	6.41	5.07	8.06	2.18	5.60	2.25	2.48	7.56
Chionanthus filiformis	Oleaceae	Mon	13.77	0.65	36.49	421.21	90.87	NA	-0.29	-0.30	0.02	-0.17	-0.72	-0.87	-1.20	-0.31	-1.00	-0.97	-0.66	-0.81
Chrysophyllum flexuosum	Sapotaceae	Ll	15.62	0.55	61.24	304.63	119.38	1999	-0.76	-0.54	-0.85	-0.49	-0.88	-0.54	-0.79	-0.77	-0.90	-0.79	-0.87	-0.75
Chrysophyllum flexuosum	Sapotaceae	Sub	15.62	0.55	61.24	304.63	119.38	1999	-0.42	-0.41	-0.43	-0.46	-0.68	-0.33	-0.43	-0.81	-0.56	-0.45	-0.40	-0.59
Chrysophyllum viride	Sapotaceae	Ll	24.76	0.45	21.77	366.23	154.4	2000	-1.18	-0.93	-0.93	-0.83	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Chrysophyllum viride	Sapotaceae	Mon	24.76	0.45	21.77	366.23	154.4	2000	-0.56	-0.47	-0.81	-0.46	-0.95	-0.87	-0.86	-0.91	-0.77	-0.97	-0.66	-0.44
Citronella paniculata	Cardiopteridaceae	Ll	16.76	0.57	88.13	278.68	113.72	310	-0.46	-0.59	-0.90	-0.70	0.53	-0.86	0.33	1.37	-0.63	-0.79	-0.79	-0.19

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Citronella paniculata	Cardiopteridaceae	Mon	16.76	0.57	88.13	278.68	113.72	310	-0.38	-0.70	-0.12	-1.25	-1.25	-0.87	-1.20	-1.22	2.32	-0.97	7.77	-0.81
Citronella paniculata	Cardiopteridaceae	Sub	16.76	0.57	88.13	278.68	113.72	310	-0.44	-0.03	-0.53	-0.87	0.54	-0.71	-0.16	1.59	-0.83	-0.78	-0.79	-0.70
Cordia sellowiana	Boraginaceae	Mon	15.54	0.46	31.29	405.43	136.6	313	1.56	3.02	-1.22	3.19	-1.25	-0.87	-1.20	-1.22	2.32	-0.97	7.77	-0.81
Cordia taguahyensis	Boraginaceae	Ll	14.64	0.89	30.92	207.63	210.34	136	0.14	-0.58	-0.17	0.05	0.89	0.78	1.99	-0.55	-0.25	-0.79	-0.23	0.07
Cordia taguahyensis	Boraginaceae	Mon	14.64	0.9	30.92	207.63	210.34	136	-1.60	-0.95	-0.87	-2.12	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Cordia taguahyensis	Boraginaceae	Sub	14.64	0.9	30.92	207.63	210.34	136	-0.14	-0.23	-0.44	-0.14	-0.14	-0.26	-0.36	0.22	-0.51	-0.78	-0.08	-0.57
Cordia trichoclada	Boraginaceae	Mon	15.26	0.8	31.1	306.52	173.47	136	-1.51	-1.80	-0.78	-1.38	-0.59	-0.87	-0.29	-0.64	-0.40	-0.97	-0.66	0.17
Couepia venosa	Chrysobalanaceae	Ll	18.08	0.41	68.45	445.1	75.39	210	-0.91	-0.51	-1.05	-0.73	-0.98	-0.86	-0.14	-1.41	-0.83	0.27	-1.02	-0.98
Couepia venosa	Chrysobalanaceae	Mon	18.08	0.41	68.45	445.1	75.39	210	-1.36	-0.59	-1.29	-1.18	-0.56	-0.50	0.03	-0.81	-0.86	-0.97	-0.30	-0.81
Couepia venosa	Chrysobalanaceae	Sub	18.08	0.41	68.45	445.1	75.39	210	-0.27	-0.61	-0.19	-0.76	-0.93	-0.71	-0.78	-0.80	-0.83	-0.78	-0.79	-0.70
Coussapoa microcarpa	Urticaceae	Ll	20.98	0.61	25	272.58	261.51	140	1.35	0.22	0.46	0.50	0.26	-0.86	-1.21	2.28	0.29	-0.79	-1.02	2.39
Coussapoa microcarpa	Urticaceae	Mon	20.98	0.61	25	272.58	261.51	140	1.50	1.29	3.01	1.58	-0.41	1.16	-1.20	-0.47	7.65	-0.97	8.17	7.81
Coussapoa microcarpa	Urticaceae	Res	20.98	0.61	25	272.58	261.51	140	2.75	1.59	0.66	1.58	-0.95	-0.94	-0.89	-0.88	0.19	-0.73	-1.08	1.11
Coussapoa microcarpa	Urticaceae	Sub	20.98	0.61	25	272.58	261.51	140	0.22	0.06	0.71	-0.38	3.41	-0.71	1.68	5.49	1.12	-0.78	1.70	1.24
Coussarea accedens	Rubiaceae	Ll	12.58	0.46	54.58	189.05	143.63	293	-0.14	-0.20	-0.19	0.12	-0.14	-0.36	-0.19	0.12	-0.23	-0.34	-0.03	-0.35
Coussarea accedens	Rubiaceae	Sub	12.58	0.46	54.58	189.05	143.63	293	-0.16	-0.43	-0.15	0.06	0.92	0.22	0.84	0.87	0.26	0.29	0.15	0.26
Coussarea meridionalis	Rubiaceae	Ll	12.34	0.44	144.09	209.79	116.3	293	-0.20	-0.28	-0.08	-0.20	-0.10	-0.47	0.11	-0.03	0.10	-0.26	0.28	0.07
Coussarea meridionalis	Rubiaceae	Sub	12.34	0.45	144.09	209.79	116.3	293	0.18	-0.04	0.11	0.16	0.23	-0.39	0.23	0.36	0.32	0.06	0.66	0.15
Cryptocarya mandioccana	Lauraceae	Ll	23.54	0.68	42.48	323.78	101.62	1826	0.25	-0.58	0.13	0.14	-0.77	-0.86	-1.21	0.09	-0.73	-0.79	-1.02	-0.17
Cryptocarya mandioccana	Lauraceae	Mon	23.54	0.68	42.48	323.78	101.62	1826	-0.66	-0.42	-1.08	-1.13	-1.01	-0.87	-1.20	-0.82	-0.55	1.07	-0.66	-0.81
Cryptocarya mandioccana	Lauraceae	Sub	23.54	0.68	42.48	323.78	101.62	1826	-0.32	-0.30	-0.19	-0.41	-0.64	-0.71	-0.22	-0.85	-0.83	-0.78	-0.79	-0.70
Cryptocarya saligna	Lauraceae	Ll	19.45	0.77	17.97	396.83	119.8	1340	-0.02	-0.58	-0.09	-0.52	-0.11	1.31	-0.45	-0.64	-0.90	-0.79	-1.02	-0.60
Cryptocarya saligna	Lauraceae	Mon	19.45	0.77	17.97	396.83	119.8	1340	-0.90	-0.65	-1.01	-0.92	-0.89	-0.87	-1.20	-0.61	-0.34	0.57	-0.66	-0.28
Cryptocarya saligna	Lauraceae	Sub	19.45	0.77	17.97	396.83	119.8	1340	0.03	-0.31	-0.45	0.01	-0.64	-0.71	-0.78	-0.15	-0.54	-0.78	-0.79	-0.19
Cupania furfuracea	Sapindaceae	Mon	19.25	0.65	27.61	380.46	129.6	263	-0.67	-0.66	-0.97	-0.98	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Cupania furfuracea	Sapindaceae	Sub	19.25	0.65	27.61	380.46	129.6	263	-0.49	-1.11	-0.73	-0.39	-0.65	-0.71	-0.30	-0.78	-0.83	-0.78	-0.79	-0.70
Cupania oblongifolia	Sapindaceae	Ll	22.12	0.51	27.61	380.46	129.6	1110	0.02	0.02	-0.19	-0.24	-0.74	-0.86	-1.21	0.15	-1.06	-0.79	-1.02	-0.98
Cupania oblongifolia	Sapindaceae	Mon	22.12	0.51	27.61	380.46	129.6	1110	-0.48	0.07	-0.40	-0.41	-0.73	-0.87	-0.45	-0.77	0.39	1.23	1.44	-0.81

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Cupania oblongifolia	Sapindaceae	Res	22.12	0.51	27.61	380.46	129.6	1110	1.44	0.94	0.97	-0.58	-0.95	-0.94	-0.89	-0.88	-0.99	-0.73	-1.08	-0.65
Cupania oblongifolia	Sapindaceae	Sub	22.12	0.51	27.61	380.46	129.6	1110	-0.65	-1.15	0.15	-0.65	-0.07	-0.71	1.28	-1.38	0.22	1.90	-0.79	0.20
Dahlstedtia pinnata	Fabaceae	Ll	10.4	0.4	44.49	NA	NA	NA	-1.55	-0.92	-1.36	-1.07	2.37	4.87	3.43	-1.41	-0.33	-0.79	-1.02	0.82
Dahlstedtia pinnata	Fabaceae	Mon	10.4	0.4	44.49	NA	NA	NA	-0.89	-0.51	-0.50	-1.40	-1.25	-0.87	-1.20	-1.22	0.45	-0.97	2.57	-0.81
Dahlstedtia pinnata	Fabaceae	Sub	10.4	0.4	44.49	NA	NA	NA	-1.57	-1.20	-1.01	-1.18	-0.42	-0.71	-0.10	-0.52	-0.83	-0.78	-0.79	-0.70
Daphnopsis schwackeana	Thymelaeaceae	Mon	11.82	0.49	13.73	325.16	82.12	100	0.16	0.57	-0.03	-0.37	-1.25	-0.87	-1.20	-1.22	1.89	-0.97	1.95	2.28
Daphnopsis schwackeana	Thymelaeaceae	Sub	11.82	0.49	13.73	325.16	82.12	100	0.83	0.18	0.04	0.17	1.38	-0.71	0.10	3.06	1.36	-0.78	-0.79	3.14
Ecclinusa ramiflora	Sapotaceae	Ll	22	0.78	152.84	466.53	67.48	575	-0.84	-0.90	-1.03	-0.43	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Ecclinusa ramiflora	Sapotaceae	Sub	22	0.78	152.84	466.53	67.48	575	-0.33	-0.73	-0.42	-0.45	-1.06	-0.71	-0.65	-1.23	-0.46	-0.05	-0.58	-0.45
Endlicheria paniculata	Lauraceae	Ll	16.83	0.8	103.18	284.55	147.4	1298	-0.40	-0.48	-0.34	0.02	0.57	1.24	-0.48	0.89	-0.35	0.57	-0.18	-0.98
Endlicheria paniculata	Lauraceae	Res	16.83	0.8	103.18	284.55	147.4	1298	-2.83	-1.05	-2.60	-2.04	4.91	-0.94	6.76	5.35	-0.99	-0.73	-1.08	-0.65
Endlicheria paniculata	Lauraceae	Sub	16.83	0.8	103.18	284.55	147.4	1298	-0.77	-0.01	-1.02	-0.90	0.28	-0.71	1.80	-1.38	0.48	-0.78	2.98	-0.70
Eriotheca pentaphylla	Malvaceae	Ll	23.45	0.49	46.41	276.7	81.42	176	0.94	0.07	0.02	0.34	-1.14	-0.86	-1.21	-0.71	-0.46	-0.79	-0.54	-0.07
Eriotheca pentaphylla	Malvaceae	Sub	23.45	0.49	46.41	276.7	81.42	176	0.20	-0.25	-0.21	-0.28	-0.84	-0.71	-0.59	-0.83	-0.46	-0.40	-0.23	-0.51
Eugenia cereja	Myrtaceae	Ll	18.84	0.51	32.46	244.42	156.06	1415	-0.89	-0.57	-0.82	-0.15	-0.35	0.33	-0.39	-0.58	-0.41	-0.79	0.00	-0.60
Eugenia copacabanensis	Myrtaceae	Mon	19.64	0.42	17.42	476.66	44.9	1415	-1.05	-1.01	-1.37	-1.23	-0.77	-0.87	-0.53	-0.80	-1.00	-0.97	-0.66	-0.81
Eugenia copacabanensis	Myrtaceae	Sub	19.64	0.42	17.42	476.66	44.9	1415	-1.60	-1.53	-1.03	-1.28	-1.20	-0.71	-0.78	-1.38	-0.83	-0.78	-0.79	-0.70
Eugenia fusca	Myrtaceae	Ll	15.94	0.84	56.22	273.65	65.22	1415	-0.98	-0.74	-0.88	-0.68	-0.47	-0.22	0.10	-0.96	-0.87	-0.79	-0.83	-0.75
Eugenia fusca	Myrtaceae	Res	15.94	0.84	56.22	273.65	65.22	1415	1.11	1.87	0.87	0.12	-0.95	-0.94	-0.89	-0.88	0.72	5.72	-1.08	-0.65
Eugenia fusca	Myrtaceae	Sub	15.94	0.84	56.22	273.65	65.22	1415	-0.59	-0.22	-0.53	-0.96	-0.74	-0.71	0.04	-1.38	-0.83	-0.78	-0.79	-0.70
Eugenia monosperma	Myrtaceae	Ll	14.27	0.61	19.94	296.02	127.82	1415	-0.49	-0.58	-0.38	-0.26	-0.40	-0.18	-0.29	-0.47	-0.23	0.12	-0.63	0.11
Eugenia monosperma	Myrtaeaceae	Sub	14.27	0.61	19.94	296.02	127.82	1415	-0.06	-0.30	-0.34	-0.55	1.21	1.04	0.96	1.05	-0.23	-0.78	-0.79	0.35
Eugenia mosenii	Myrtaceae	Ll	17.68	0.68	24.29	334.44	99.23	4000	-0.64	-0.70	-0.69	-0.47	-1.01	-0.86	-0.71	-0.91	-0.63	-0.28	-0.80	-0.46
Eugenia mosenii	Myrtaceae	Sub	17.68	0.68	24.29	334.44	99.23	4000	-0.89	-0.56	-0.81	-0.77	0.81	1.04	-0.23	1.61	-0.52	-0.78	-0.79	-0.17
Eugenia oblongata	Myrtaceae	Ll	17.42	0.59	43.05	385.45	81.23	1000	-0.78	-0.75	-0.70	-0.75	0.09	-0.38	-0.23	0.65	-0.65	-0.79	-0.59	-0.48
Eugenia oblongata	Myrtaceae	Mon	17.42	0.59	43.05	385.45	81.23	1000	-0.72	0.54	-1.10	-1.29	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Eugenia oblongata	Myrtaceae	Sub	17.42	0.59	43.05	385.45	81.23	1000	0.15	-0.02	-0.25	-0.20	-0.44	0.17	-0.78	-0.03	-0.52	-0.01	-0.34	-0.70
Eugenia pisiformis	Myrtaceae	Ll	14.39	0.68	24.29	334.44	99.23	1415	0.27	-0.54	-0.15	0.04	-0.33	-0.26	0.45	-0.98	-0.40	-0.79	-0.48	0.02
Eugenia pisiformis	Myrtaceae	Mon	14.39	0.68	24.29	334.44	99.23	1415	-0.70	-1.20	0.06	-0.74	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Eugenia prasina	Myrtaceae	Ll	11.6	0.67	22.42	387.1	93.42	1415	-1.10	-0.63	-0.78	-0.36	-0.85	-0.35	-1.21	-0.40	0.62	0.87	1.14	-0.31
Eugenia prasina	Myrtaceae	Mon	11.6	0.67	22.42	387.1	93.42	1415	-1.09	-0.96	-1.01	-0.84	-0.39	-0.87	-0.16	-0.38	0.01	-0.17	-0.66	0.55
Eugenia prasina	Myrtaceae	Sub	11.6	0.67	22.42	387.1	93.42	1415	-0.08	-0.13	-0.36	0.04	0.07	-0.48	-0.12	0.44	0.10	-0.16	-0.06	0.26
Eugenia subavenia	Myrtaceae	Ll	13.58	0.61	6.3	277.78	126	1415	-1.07	1.66	-0.84	-0.59	0.43	2.14	-1.21	0.72	-1.06	-0.79	-1.02	-0.98
Eugenia subavenia	Myrtaceae	Mon	13.58	0.61	6.3	277.78	126	1415	-1.14	-1.03	-1.39	-0.43	-1.07	-0.87	-1.20	-0.91	-0.65	0.61	-0.66	-0.81
Eugenia subavenia	Myrtaceae	Sub	13.58	0.61	6.3	277.78	126	1415	-0.23	-0.21	-0.29	0.13	0.43	2.87	0.40	-0.62	-0.83	-0.78	-0.79	-0.70
Eugenia verticillata	Myrtaceae	Res	11.95	0.68	30.53	334.44	99.23	1415	-1.68	-1.06	-1.49	-1.32	-0.39	-0.94	-0.32	-0.14	1.30	-0.01	0.51	1.69
Eugenia verticillata	Myrtaceae	Sub	11.95	0.68	30.53	334.44	99.23	1415	-1.27	-0.34	-1.02	-1.02	0.14	-0.71	1.72	-1.38	-0.83	-0.78	-0.79	-0.70
Euplassa cantareirae	Proteaceae	Res	17.84	0.56	19.44	NA	NA	4000	-1.39	-1.33	-1.03	-1.43	0.11	-0.18	0.47	-0.06	-0.99	-0.73	-1.08	-0.65
Euplassa cantareirae	Proteaceae	Sub	17.84	0.56	19.44	NA	NA	4000	-1.22	-1.58	-1.21	-0.60	-1.20	-0.71	-0.78	-1.38	-0.83	-0.78	-0.79	-0.70
Euterpe edulis	Arecaceae	Ll	13.66	0.51	40.89	332.42	65.6	1300	1.18	1.29	1.35	0.92	0.57	0.95	0.18	0.42	1.23	1.54	1.34	0.62
Euterpe edulis	Arecaceae	Mon	13.66	0.51	40.89	332.42	65.6	1300	1.17	1.18	1.11	1.15	1.28	1.04	1.12	1.29	0.53	0.29	0.40	0.49
Euterpe edulis	Arecaceae	Res	13.66	0.51	40.89	332.42	65.6	1300	1.50	2.14	1.84	2.09	2.14	2.13	2.16	1.85	1.73	0.65	2.09	1.26
Euterpe edulis	Arecaceae	Sub	13.66	0.51	40.89	332.42	65.6	1300	2.24	2.48	2.30	2.17	1.10	1.72	0.73	0.83	1.87	2.16	2.18	1.21
Faramea pachyantha	Rubiaceae	Ll	18.47	0.5	56.52	351.45	165.7	527	-1.13	-0.98	-1.07	-0.77	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Faramea pachyantha	Rubiaceae	Res	18.47	0.5	56.52	351.45	165.7	527	1.70	-0.27	0.89	1.44	-0.95	-0.94	-0.89	-0.88	-0.46	-0.73	-1.08	0.14
Faramea pachyantha	Rubiaceae	Sub	18.47	0.5	56.52	351.45	165.7	527	-0.49	-0.49	-0.23	-0.61	-0.64	-0.07	-0.58	-0.65	-0.71	-0.50	-0.62	-0.70
Garcinia gardneriana	Clusiaceae	Ll	14.71	0.48	22.96	449.65	81.3	2900	-0.43	-0.70	-0.48	-0.35	-1.13	-0.86	-0.72	-1.16	-0.40	-0.54	-0.80	0.27
Garcinia gardneriana	Clusiaceae	Mon	14.71	0.48	22.96	449.65	81.3	2900	-1.32	-1.33	-1.43	-1.23	0.32	-0.87	0.89	0.21	-1.00	-0.97	-0.66	-0.81
Garcinia gardneriana	Clusiaceae	Res	14.71	0.48	22.96	449.65	81.3	2900	1.22	0.46	0.85	0.51	-0.82	-0.94	-0.89	-0.60	-0.12	0.14	-0.43	-0.01
Garcinia gardneriana	Clusiaceae	Sub	14.71	0.48	22.96	449.65	81.3	2900	-0.35	-0.46	-0.48	-0.23	-0.44	-0.38	-0.37	-0.36	-0.14	-0.49	-0.27	0.08
Guapira hirsuta	Nyctaginaceae	Mon	17.24	0.46	36.35	154.98	134.88	123	-0.90	-1.51	-1.24	-0.95	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Guapira hirsuta	Nyctaginaceae	Sub	17.24	0.46	36.35	154.98	134.88	123	-0.43	-0.42	-0.14	-0.62	-0.97	-0.71	-0.78	-0.89	-0.58	-0.78	-0.79	-0.28
Guapira nitida	Nyctaginaceae	Ll	18.24	0.46	36.72	154.98	130.54	123	-0.71	-0.53	-0.80	-0.69	-0.01	-0.86	1.99	-1.41	-1.06	-0.79	-1.02	-0.98
Guapira nitida	Nyctaginaceae	Sub	18.24	0.46	36.72	154.98	130.54	123	-0.84	-0.26	-0.47	-0.43	-0.12	-0.71	-0.17	0.19	-0.48	-0.78	-0.79	-0.09
Guapira opposita	Nyctaginaceae	Ll	19.03	0.67	35.98	154.98	171.33	300	-0.46	-0.44	-0.54	-0.31	0.63	-0.53	0.63	1.08	-0.46	-0.34	-0.44	-0.43
Guapira opposita	Nyctaginaceae	Mon	19.03	0.67	35.98	154.98	171.33	300	-0.57	-0.75	-0.57	-0.33	0.05	0.07	0.73	-0.32	-0.07	0.67	-0.48	-0.11
Guapira opposita	Nyctaginaceae	Res	19.03	0.67	35.98	154.98	171.33	300	-0.44	-0.61	-0.46	0.11	-0.15	-0.23	0.81	-0.88	0.00	-0.73	0.42	0.07
Guapira opposita	Nyctaginaceae	Sub	19.03	0.67	35.98	154.98	171.33	300	-0.41	-0.54	-0.40	-0.55	-0.12	-0.71	0.00	0.00	-0.55	-0.23	-0.63	-0.51
Guarea macrophylla	Meliaceae	Ll	14.57	0.65	119.12	399.22	77.91	203	-0.05	0.00	-0.27	-0.69	-1.47	-0.86	-1.21	-1.41	-0.56	-0.79	0.00	-0.98

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Guarea macrophylla	Meliaceae	Mon	14.57	0.65	119.12	399.22	77.91	203	-0.65	-0.93	-1.04	-1.23	-0.96	-0.87	-0.65	-1.06	-0.12	-0.97	0.98	-0.53
Guarea macrophylla	Meliaceae	Res	14.57	0.65	119.12	399.22	77.91	203	0.52	1.22	0.18	-0.09	-0.15	-0.30	-0.34	0.08	1.44	3.47	-0.19	0.88
Guarea macrophylla	Meliaceae	Sub	14.57	0.65	119.12	399.22	77.91	203	-0.54	-0.82	-0.19	-0.11	0.01	-0.71	1.38	-1.38	-0.25	2.01	-0.79	-0.70
Guatteria australis	Annonaceae	Ll	16.24	0.71	32.61	402.44	148.2	100	1.21	-0.52	0.81	0.49	-1.47	-0.86	-1.21	-1.41	-0.65	-0.79	-0.24	-0.98
Guatteria australis	Annonaceae	Mon	16.24	0.71	32.61	402.44	148.2	100	-0.39	0.11	0.21	0.30	-0.63	0.13	-1.20	-0.49	0.49	-0.97	-0.66	1.66
Guatteria australis	Annonaceae	Res	16.24	0.71	32.61	402.44	148.2	100	-1.69	-1.19	-1.46	-1.68	-0.95	-0.94	-0.89	-0.88	4.31	-0.73	-1.08	7.27
Guatteria australis	Annonaceae	Sub	16.24	0.71	32.61	402.44	148.2	100	0.34	0.10	-0.28	-0.38	-0.74	-0.71	-0.78	-0.41	-0.36	1.47	-0.79	-0.70
Guatteria sp. 4	Annonaceae	Ll	14.29	0.71	32.61	402.44	148.2	86	-0.56	-0.76	-0.41	0.19	-1.47	-0.86	-1.21	-1.41	0.84	-0.79	2.91	-0.98
Guatteria sp. 4	Annonaceae	Res	14.29	0.71	32.61	402.44	148.2	86	0.65	-0.31	0.54	-0.24	1.23	0.99	0.81	1.51	-0.79	-0.35	-0.80	-0.65
Hieronyma alchorneoides	Phyllanthaceae	Ll	26.53	0.94	90.53	215.66	122.67	20	-0.11	-0.40	-0.37	-0.34	-1.47	-0.86	-1.21	-1.41	-0.91	-0.79	-0.71	-0.98
Hieronyma alchorneoides	Phyllanthaceae	Mon	26.53	0.95	90.53	215.66	122.67	20	-0.10	-0.76	-0.05	-0.33	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Hieronyma alchorneoides	Phyllanthaceae	Res	26.53	0.95	90.53	215.66	122.67	20	0.92	-0.54	0.03	0.61	-0.95	-0.94	-0.89	-0.88	0.72	-0.73	-1.08	1.90
Hieronyma alchorneoides	Phyllanthaceae	Sub	26.53	0.95	90.53	215.66	122.67	20	0.81	1.04	0.02	-0.52	-0.50	-0.71	-0.30	-0.47	-0.68	-0.09	-0.79	-0.70
Hirtella hebeclada	Chrysobalanaceae	Ll	17.69	0.72	50.57	419.06	90.5	512	-0.50	-0.95	-0.53	-0.40	-0.81	-0.86	-1.21	-0.01	-0.47	-0.79	-0.39	-0.27
Hirtella hebeclada	Chrysobalanaceae	Mon	17.69	0.72	50.57	419.06	90.5	512	-1.22	-1.28	-1.27	-1.38	-0.19	0.80	-1.20	0.04	-1.00	-0.97	-0.66	-0.81
Hirtella hebeclada	Chrysobalanaceae	Sub	17.69	0.72	50.57	419.06	90.5	512	-1.06	-0.76	-0.63	-0.98	-0.73	-0.71	-0.23	-1.04	-0.66	-0.78	-0.79	-0.42
Inga edulis	Fabaceae	Ll	19.67	0.8	70.83	423	146.66	493	1.73	0.80	0.74	0.13	4.10	2.84	8.56	-1.41	-0.12	-0.79	-1.02	1.37
Inga edulis	Fabaceae	Res	19.67	0.8	70.83	423	146.66	493	-2.41	-1.61	-1.84	-2.02	-0.95	-0.94	-0.89	-0.88	2.11	-0.73	-1.08	3.98
Inga edulis	Fabaceae	Sub	19.67	0.8	70.83	423	146.66	493	1.11	1.01	0.67	-0.45	-1.20	-0.71	-0.78	-1.38	2.83	-0.78	5.31	2.11
Inga lanceifolia	Fabaceae	Mon	13.58	0.78	58.87	290.9	73.59	493	0.32	-0.18	0.19	0.44	-0.75	-0.38	-0.47	-0.93	-0.69	-0.26	-0.31	-0.81
Inga subnuda	Fabaceae	Res	16.92	0.63	65.85	382.62	37	493	0.42	-0.16	0.57	-0.73	-0.75	-0.94	-0.37	-0.88	-0.99	-0.73	-1.08	-0.65
Jacaranda montana	Bignoniaceae	Mon	18.49	0.61	4.9	357.25	251.85	6	-0.94	0.28	-1.09	-0.48	-0.48	-0.87	-0.51	-0.33	-0.54	1.15	-0.66	-0.81
Jacaranda puberula	Bignoniaceae	Res	15.92	0.59	5.9	444.08	171.3	7	-0.65	-0.68	-0.50	-0.59	-0.23	-0.52	-0.28	-0.03	-0.60	-0.43	-0.40	-0.53
Jacaranda puberula	Bignoniaceae	Sub	15.92	0.59	5.9	444.08	171.3	7	-0.92	-1.45	-0.64	-0.82	-1.20	-0.71	-0.78	-1.38	-0.83	-0.78	-0.79	-0.70
Kielmeyera petiolaris	Calophyllaceae	Res	14.84	0.67	34.16	141	293.78	131	-0.72	-0.08	-0.45	-0.80	-0.79	-0.18	-0.89	-0.88	-0.99	-0.73	-1.08	-0.65
Licania hoehnei	Chrysobalanaceae	Mon	21.77	0.62	43.5	479.85	87	4700	-0.79	-0.76	-0.90	-0.79	-1.14	-0.87	-1.20	-1.04	-0.59	0.28	-0.36	-0.81
Licania hoehnei	Chrysobalanaceae	Sub	21.77	0.62	43.5	479.85	87	4700	-0.65	0.61	-0.32	-0.89	-0.89	-0.71	-0.78	-0.72	-0.66	-0.78	-0.32	-0.70
Licaria armeniaca	Lauraceae	Ll	14.06	0.58	18.5	233.12	115.6	1805	-0.07	-0.69	0.11	-0.18	-1.47	-0.86	-1.21	-1.41	1.34	1.78	0.62	1.63
Licaria armeniaca	Lauraceae	Mon	14.06	0.58	18.5	233.12	115.6	1805	-0.80	-0.84	-0.02	-1.03	-0.36	1.27	-1.20	-0.42	-0.20	2.06	-0.66	-0.81
Licaria armeniaca	Lauraceae	Sub	14.06	0.58	18.5	233.12	115.6	1805	0.17	0.30	-0.28	0.27	1.49	-0.71	2.62	0.29	-0.83	-0.78	-0.79	-0.70

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Lonchocarpus cultratus	Fabaceae	Ll	20.38	0.47	12.84	428.95	27.65	1639	-0.88	-0.69	-0.90	-0.80	5.09	-0.86	-1.21	12.61	0.84	7.99	-1.02	-0.98
Lonchocarpus cultratus	Fabaceae	Sub	20.38	0.47	12.84	428.95	27.65	1639	-0.13	-0.67	-0.36	-0.47	-1.20	-0.71	-0.78	-1.38	-0.83	-0.78	-0.79	-0.70
Mabea piriri	Euphorbiaceae	Ll	22.05	0.5	30.87	363.81	165.08	500	1.79	1.83	0.60	0.42	-0.69	-0.86	-0.09	-0.84	-0.70	-0.79	-0.28	-0.98
Mabea piriri	Euphorbiaceae	Sub	22.05	0.5	30.87	363.81	165.08	500	0.41	0.06	-0.38	0.12	-1.20	-0.71	-0.78	-1.38	-0.20	-0.78	-0.79	0.39
Malouetia cestroides	Apocynaceae	Ll	20.08	0.77	62.03	382.33	170.69	NA	-1.31	-0.37	-1.12	1.65	5.09	8.18	-1.21	6.79	0.84	-0.79	2.91	-0.98
Malouetia cestroides	Apocynaceae	Sub	20.08	0.77	62.03	382.33	170.69	NA	-0.03	0.45	0.02	-0.13	-0.31	-0.71	-0.16	-0.19	-0.31	0.10	-0.27	-0.40
Marlierea excoriata	Myrtaceae	Mon	16.89	0.59	15.77	432.94	85.71	525	-1.03	-0.98	-1.13	-0.97	-0.42	-0.87	0.54	-0.85	0.10	-0.97	-0.66	0.99
Marlierea obscura	Myrtaceae	Ll	16.47	0.42	55.94	306.44	141.62	200	-0.67	-0.58	-0.54	-0.61	-0.19	-0.49	0.04	-0.12	-0.79	-0.79	-0.80	-0.59
Marlierea obscura	Myrtaceae	Mon	16.47	0.42	55.94	306.44	141.62	200	-1.21	-0.55	-1.38	-1.24	-1.02	-0.87	-0.45	-1.22	-0.13	-0.97	-0.66	0.64
Marlierea obscura	Myrtaceae	Res	16.47	0.42	55.94	306.44	141.62	200	-0.04	-1.15	0.36	1.10	-0.95	-0.94	-0.89	-0.88	2.92	-0.73	5.40	1.90
Marlierea racemosa	Myrtaceae	Ll	21.92	0.65	16.01	351	109.9	525	-0.59	-0.86	-0.72	-0.45	-0.81	-0.86	-1.21	-0.01	-1.06	-0.79	-1.02	-0.98
Marlierea racemosa	Myrtaceae	Mon	21.92	0.65	16.01	351	109.9	525	-0.85	-0.63	-1.10	-0.93	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Marlierea racemosa	Myrtaceae	Sub	21.92	0.65	16.01	351	109.9	525	-0.01	-0.56	-0.39	-0.16	-0.54	-0.71	-0.78	0.03	-0.83	-0.78	-0.79	-0.70
Marlierea suaveolens	Myrtaceae	Mon	18.25	0.54	45.09	351	109.9	600	-1.65	-1.84	-1.21	-1.90	-0.11	-0.87	-1.20	0.74	-1.00	-0.97	-0.66	-0.81
Marlierea suaveolens	Myrtaceae	Sub	18.25	0.54	45.09	351	109.9	600	-0.79	-0.09	-0.73	-0.88	-0.14	2.54	-0.31	-0.78	-0.83	-0.78	-0.79	-0.70
Marlierea tomentosa	Myrtaceae	Ll	17.44	0.54	89.17	351	109.9	300	-0.72	-0.68	-0.73	-0.62	-1.03	-0.86	-0.57	-1.09	-0.78	-0.46	-1.02	-0.47
Marlierea tomentosa	Myrtaceae	Mon	17.44	0.54	89.17	351	109.9	300	-1.05	0.20	-1.76	-1.69	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Marlierea tomentosa	Myrtaceae	Res	17.44	0.54	89.17	351	109.9	300	0.27	0.62	-0.92	0.41	-0.75	-0.46	-0.62	-0.88	-0.31	-0.73	0.44	-0.40
Marlierea tomentosa	Myrtaceae	Sub	17.44	0.54	89.17	351	109.9	300	-0.73	-0.61	-0.27	-0.54	-0.56	-0.71	-0.14	-0.78	-0.19	-0.32	0.02	-0.24
Matayba guianensis	Sapindaceae	Ll	12.33	NA	379.34	198.82	94.13	253	-1.96	-1.18	-1.05	-1.14	-1.47	-0.86	-1.21	-1.41	5.44	16.08	2.72	2.39
Matayba guianensis	Sapindaceae	Mon	12.33	NA	379.34	198.82	94.13	253	-0.83	-0.66	-1.11	-0.65	-0.56	-0.87	0.77	-1.22	-1.00	-0.97	-0.66	-0.81
Matayba guianensis	Sapindaceae	Sub	12.33	NA	379.34	198.82	94.13	253	-0.50	-0.86	-0.26	-0.85	1.19	3.96	-0.78	2.18	-0.83	-0.78	-0.79	-0.70
Maytenus gonoclada	Celastraceae	Mon	13.59	0.68	11.02	NA	105.6	210	-0.77	1.14	-1.10	-1.09	1.29	1.91	2.88	0.04	-1.00	-0.97	-0.66	-0.81
Maytenus littoralis	Celastraceae	Res	13.13	0.44	13.31	NA	105.6	210	0.83	-0.15	0.12	0.37	-0.73	-0.59	-0.69	-0.72	-0.73	-0.23	-0.71	-0.65
Meriania calyptrata	Melastomataceae	Sub	10.96	0.45	16.25	NA	NA	NA	0.02	-0.38	-0.48	-0.68	4.08	0.58	4.63	2.94	0.04	-0.78	-0.79	0.82
Miconia atlantica	Melastomataceae	Mon	11.53	0.74	108.55	298.8	144.7	2.3	-1.28	-0.81	-1.05	-1.85	3.07	-0.87	4.07	3.14	-1.00	-0.97	-0.66	-0.81
Miconia atlantica	Melastomataceae	Sub	11.53	0.74	108.55	298.8	144.7	2.3	0.83	0.51	1.17	0.08	0.86	-0.71	-0.78	3.01	-0.83	-0.78	-0.79	-0.70
Miconia cabussu	Melastomataceae	Mon	20.36	0.71	268.14	201.17	97.86	3	1.78	1.47	0.96	1.47	-0.81	-0.87	-1.20	-0.44	-0.58	-0.97	-0.66	-0.12
Miconia cabussu	Melastomataceae	Sub	20.36	0.71	268.14	201.17	97.86	3	-0.48	-0.09	0.20	-0.53	3.41	-0.71	-0.78	8.43	-0.83	-0.78	-0.79	-0.70
Miconia petropolitana	Melastomataceae	Sub	10.49	0.95	188.34	249.98	121.28	2.3	1.02	0.10	-0.29	0.82	1.14	1.98	0.88	0.80	-0.02	-0.78	-0.79	0.70

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Micropholis crassipedicellata	Sapotaceae	Ll	24.05	0.67	8.7	437.99	52.39	465	-1.28	-0.74	-1.07	-0.91	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Micropholis crassipedicellata	Sapotaceae	Mon	24.05	0.67	8.7	437.99	52.39	465	-0.95	-0.81	-0.86	-1.16	-0.97	-0.87	-0.75	-0.98	-1.00	-0.97	-0.66	-0.81
Micropholis crassipedicellata	Sapotaceae	Sub	24.05	0.67	8.7	437.99	52.39	465	0.03	-0.21	-0.17	-0.19	-0.78	-0.71	-0.78	-0.47	-0.83	-0.78	-0.79	-0.70
Mollinedia argyrogyna	Monimiaceae	Mon	19	0.71	32.17	348.33	153.9	470	-0.90	-0.64	-1.09	-1.16	-1.17	-0.87	-1.20	-1.08	-1.00	-0.97	-0.66	-0.81
Mollinedia argyrogyna	Monimiaceae	Sub	19	0.71	32.17	348.33	153.9	470	-0.94	-0.80	-0.80	-1.07	-1.20	-0.71	-0.78	-1.38	-0.21	0.36	0.44	-0.70
Mollinedia elegans	Monimiaceae	Mon	12.8	0.8	26.27	317.49	83.9	470	-1.35	-1.56	-0.81	-1.51	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Mollinedia engleriana	Monimiaceae	Ll	13.43	0.78	40.09	161.66	190.9	470	-1.20	-1.09	-0.57	-0.88	0.65	-0.86	3.43	-1.41	-1.06	-0.79	-1.02	-0.98
Mollinedia engleriana	Monimiaceae	Mon	13.43	0.78	40.09	161.66	190.9	470	-1.45	-1.30	-1.06	-1.51	-0.71	-0.87	0.34	-1.22	-1.00	-0.97	-0.66	-0.81
Mollinedia engleriana	Monimiaceae	Sub	13.43	0.78	40.09	161.66	190.9	470	-1.03	-0.28	-0.59	-0.93	-0.71	-0.71	-0.78	-0.33	-0.83	-0.78	-0.79	-0.70
Mollinedia gilgiana	Monimiaceae	Ll	14.08	0.82	63.65	316.12	124.63	470	-0.47	-0.52	-0.43	-0.88	-1.47	-0.86	-1.21	-1.41	0.29	-0.79	-1.02	2.39
Mollinedia gilgiana	Monimiaceae	Mon	14.08	0.82	63.65	316.12	124.63	470	-0.61	-0.66	-0.50	-1.18	0.76	3.22	0.27	0.21	0.21	2.77	0.24	-0.81
Mollinedia gilgiana	Monimiaceae	Sub	14.08	0.82	63.65	316.12	124.63	470	-0.57	-0.64	-0.66	-0.54	1.06	2.01	1.38	-0.11	-0.83	-0.78	-0.79	-0.70
Mollinedia puberula	Monimiaceae	Ll	15.88	0.74	7.49	316.12	124.63	470	-1.15	-0.73	-0.70	-0.81	-0.56	0.79	-0.25	-1.41	-1.06	-0.79	-1.02	-0.98
Mollinedia puberula	Monimiaceae	Sub	15.88	0.74	7.49	316.12	124.63	470	-0.90	-1.09	-0.58	-0.98	-1.20	-0.71	-0.78	-1.38	0.13	-0.78	1.97	-0.70
Mollinedia salicifolia	Monimiaceae	Mon	13.37	0.61	37.53	247.88	106.92	470	-0.49	-0.23	-0.50	-1.32	-0.90	-0.87	-0.71	-0.92	-1.00	-0.97	-0.66	-0.81
Mollinedia schottiana	Monimiaceae	Ll	11.64	0.5	34.43	448.28	162.48	381	-0.45	-0.41	-0.39	-0.41	0.23	-0.06	0.25	0.29	-0.24	-0.25	-0.25	-0.17
Mollinedia schottiana	Monimiaceae	Mon	11.64	0.5	34.43	448.28	162.48	381	-1.07	-0.59	-0.74	-1.23	-0.92	-0.87	-0.90	-0.85	-0.79	-0.03	-0.66	-0.81
Mollinedia schottiana	Monimiaceae	Sub	11.64	0.5	34.43	448.28	162.48	381	-0.36	-0.24	-0.47	-0.08	0.29	0.08	-0.03	0.69	0.19	0.75	-0.10	0.14
Mollinedia sp. 3	Monimiaceae	Mon	13.68	0.74	44.11	316.12	124.63	470	-1.14	-0.80	-1.76	-1.28	-0.19	-0.87	1.02	-0.58	-1.00	-0.97	-0.66	-0.81
Mollinedia triflora	Monimiaceae	Mon	12.69	0.53	24.07	295.65	205.3	381	-1.40	-1.74	-1.42	-1.01	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Mollinedia triflora	Monimiaceae	Sub	12.69	0.53	24.07	295.65	205.3	381	-0.87	-0.44	-0.53	-0.53	-0.23	-0.71	0.25	-0.50	-0.54	0.18	-0.79	-0.53
Myrceugenia glaucescens	Myrtaceae	Mon	14.67	0.58	13.32	462.96	106.56	180	-1.14	-0.66	-1.19	-0.99	-0.27	-0.87	0.33	-0.34	-1.00	-0.97	-0.66	-0.81
Myrceugenia myrcioides	Myrtaceae	Mon	12.11	0.7	18.79	320.49	102.68	180	-1.42	-0.04	-1.25	-0.90	0.19	-0.87	0.49	0.26	0.04	-0.97	0.16	0.30
Myrceugenia myrcioides	Myrtaceae	Sub	12.11	0.7	18.79	320.49	102.68	180	-1.06	-0.75	-0.89	-0.47	-0.82	-0.71	-0.78	-0.57	-0.07	-0.78	-0.79	0.62
Myrcia brasiliensis	Myrtaceae	Mon	17.38	NA	85.32	327.04	93.47	1090	-0.99	-1.12	-1.07	-1.13	-0.45	-0.87	1.37	-1.22	-1.00	-0.97	-0.66	-0.81
Myrcia brasiliensis	Myrtaceae	Res	17.38	NA	85.32	327.04	93.47	1090	-0.16	-0.68	-0.08	-0.80	-0.18	0.22	-0.33	-0.21	-0.99	-0.73	-1.08	-0.65
Myrcia congestiflora	Myrtaceae	Ll	8.67	0.96	163.49	327.04	95.01	647	-1.16	-0.31	-0.75	-0.84	-1.47	-0.86	-1.21	-1.41	0.56	0.45	0.00	1.15
Myrcia congestiflora	Myrtaceae	Sub	8.67	0.96	163.49	327.04	95.01	647	-0.50	-1.13	-0.40	-0.51	0.28	-0.71	1.28	-0.69	-0.01	-0.78	0.04	0.23
Myrcia insigniflora	Myrtaceae	Sub	12.48	0.7	33.81	379.09	81.08	647	-0.78	-1.01	-0.73	-0.38	-0.57	-0.71	0.32	-1.38	-0.83	-0.78	-0.79	-0.70

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm³ g-1)*	*LA (cm²)*	*LDMC (mg g-1)*	*SLA (cm² g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Myrcia multiflora	Myrtaceae	Res	13.42	0.63	85.32	327.04	95.01	116	-1.55	-0.94	-1.54	-1.22	0.60	1.05	0.68	0.26	-0.59	-0.73	0.09	-0.65
Myrcia racemosa	Myrtaceae	Res	11.92	0.43	85.32	327.04	95.01	720	0.20	-0.07	-0.21	0.24	-0.57	-0.71	-0.50	-0.49	0.07	0.41	0.01	-0.06
Myrcia spectabilis	Myrtaceae	Ll	14.99	0.78	162.68	311.87	74.62	647	-0.59	-0.29	-0.30	0.08	1.22	2.08	-0.29	1.56	0.47	0.26	0.42	0.53
Myrcia spectabilis	Myrtaceae	Mon	14.99	0.78	162.68	311.87	74.62	647	0.59	-0.31	0.74	0.73	-0.68	-0.32	-0.53	-0.80	0.28	0.25	-0.08	0.41
Myrcia spectabilis	Myrtaceae	Res	14.99	0.78	162.68	311.87	74.62	647	1.69	0.57	0.92	0.16	-0.95	-0.94	-0.89	-0.88	-0.99	-0.73	-1.08	2.64
Myrcia spectabilis	Myrtaceae	Sub	14.99	0.78	162.68	311.87	74.62	647	0.99	-0.40	0.43	0.42	-0.67	-0.71	-0.78	-0.25	-0.83	-0.78	-0.79	-0.70
Myrciaria floribunda	Myrtaceae	Ll	18.31	0.92	4.51	275	205	425	-0.84	-0.74	-0.74	-0.63	-0.16	0.17	-0.51	0.04	-0.76	-0.10	-0.72	-0.98
Myrciaria floribunda	Myrtaceae	Mon	18.31	0.92	4.51	275	205	425	-1.18	-1.50	-0.75	-0.90	-1.08	-0.87	-1.20	-0.93	0.82	1.42	0.12	0.66
Myrciaria floribunda	Myrtaceae	Sub	18.31	0.92	4.51	275	205	425	-0.25	0.02	-0.30	-0.33	-0.70	-0.71	-0.78	-0.29	0.58	1.10	-0.43	0.92
Myrsine venosa	Primulaceae	Res	13.27	NA	52.5	333	35.1	63	-1.39	-1.04	-0.97	-1.08	0.45	1.06	0.32	0.22	-0.53	0.16	-0.41	-0.65
Nectandra oppositifolia	Lauraceae	Res	17.17	0.92	58.8	509.73	43.4	2500	-1.08	-0.91	-0.82	-0.65	-0.32	-0.23	-0.49	-0.19	-0.48	-0.73	-0.32	-0.27
Ocotea aciphylla	Lauraceae	Mon	18.63	0.46	14.45	305.5	131.36	380	0.22	-0.11	-0.30	-0.05	-0.01	1.47	0.43	-0.76	1.48	3.91	1.38	-0.17
Ocotea catharinensis	Lauraceae	Mon	21.6	0.49	15.14	487.71	124.7	833	-0.88	-1.24	-0.48	-0.88	-0.83	-0.25	-0.91	-0.86	-0.61	-0.07	-0.44	-0.65
Ocotea dispersa	Lauraceae	Ll	18.02	NA	34.1	435.41	93.68	300	0.17	-0.46	0.07	0.01	-0.16	-0.86	0.18	0.04	-0.10	-0.79	0.70	-0.67
Ocotea dispersa	Lauraceae	Mon	18.02	NA	34.1	435.41	93.68	300	-0.62	-0.70	-0.42	-0.21	-0.49	-0.87	-0.67	-0.23	0.17	-0.17	-0.27	0.53
Ocotea dispersa	Lauraceae	Sub	18.02	NA	34.1	435.41	93.68	300	0.67	0.14	0.13	0.04	0.47	1.21	-0.17	0.76	-0.38	0.31	-0.47	-0.51
Ocotea elegans	Lauraceae	Mon	15.66	0.8	19.8	404.32	148.02	1078	-0.45	-1.22	-0.28	0.43	-1.01	-0.87	-0.51	-1.22	-1.00	-0.97	-0.66	-0.81
Ocotea sp.	Lauraceae	Mon	15.37	0.38	19.61	359.02	115.45	1078	-0.66	-0.10	-0.33	0.45	-1.25	-0.87	-1.20	-1.22	5.05	-0.97	4.07	5.72
Ocotea teleiandra	Lauraceae	Mon	16.44	0.68	15.74	385.2	104.24	1900	-0.94	-0.89	-0.73	-1.17	-0.97	-0.87	-1.20	-0.75	-1.00	-0.97	-0.66	-0.81
Ocotea teleiandra	Lauraceae	Sub	16.44	0.68	15.74	385.2	104.24	1900	-0.68	-0.33	-0.55	-0.75	-0.67	-0.71	-0.78	-0.25	-0.83	-0.78	-0.79	-0.70
Ouratea parviflora	Ochnaceae	Ll	7.62	0.84	7.91	450.52	78.04	108	-0.94	-0.76	-0.79	-0.82	-0.20	-0.86	1.57	-1.41	0.84	-0.79	1.14	1.15
Ouratea parviflora	Ochnaceae	Sub	7.62	0.84	7.91	450.52	78.04	108	-1.03	-0.73	-0.96	-0.59	0.11	-0.71	-0.35	0.89	1.36	2.76	-0.12	1.46
Pausandra morisiana	Euphorbiaceae	Ll	13.9	0.49	159.86	361.86	108.01	380	-0.41	-0.46	-0.51	-0.50	-0.64	-0.86	-0.62	-0.22	-0.33	-0.79	-0.24	-0.11
Pausandra morisiana	Euphorbiaceae	Sub	13.9	0.49	159.86	361.86	108.01	380	-0.41	-0.32	-0.47	-0.59	-0.42	-0.71	-0.34	-0.25	-0.83	-0.78	-0.79	-0.70
Pera glabrata	Peraceae	Ll	15.4	0.46	10.29	321.5	142.7	12	-1.30	-0.93	-0.86	-1.08	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Pera glabrata	Peraceae	Res	15.4	0.46	10.29	321.5	142.7	12	-0.57	-0.46	-0.60	-0.26	-0.76	-0.72	-0.72	-0.71	-0.44	-0.62	-0.11	-0.37
Pera glabrata	Peraceae	Sub	15.4	0.46	10.29	321.5	142.7	12	-0.62	-0.53	-0.54	-0.53	-0.65	-0.71	0.27	-1.38	-0.83	-0.78	-0.79	-0.70
Pouteria caimito	Sapotaceae	Ll	18.35	0.62	89.24	386.97	88.36	3128	-1.43	-0.99	-1.07	-1.19	1.26	-0.86	-1.21	4.41	-1.06	-0.79	-1.02	-0.98
Pouteria caimito	Sapotaceae	Mon	18.35	0.62	89.24	386.97	88.36	3128	-0.38	-0.73	-0.17	-0.46	-0.97	-0.87	-1.20	-0.73	-0.60	0.05	-0.66	-0.59
Pouteria caimito	Sapotaceae	Sub	18.35	0.62	89.24	386.97	88.36	3128	-0.66	-0.41	-0.40	-0.79	-0.94	0.83	-0.78	-1.38	-0.29	-0.78	-0.79	0.23

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Pouteria psammophila	Sapotaceae	Ll	20.35	0.68	64.23	328.25	101.02	3128	-0.92	-0.75	-0.83	-0.91	0.65	-0.86	-1.21	3.11	-1.06	-0.79	-1.02	-0.98
Pouteria psammophila	Sapotaceae	Sub	20.35	0.68	64.23	328.25	101.02	3128	-0.38	-0.47	-0.09	-0.17	-0.71	-0.10	-0.78	-0.54	-0.83	-0.78	-0.79	-0.70
Pouteria venosa	Sapotaceae	Ll	20.28	0.59	39.22	269.53	113.68	3128	-0.75	-0.63	-0.97	-0.47	0.18	-0.22	0.10	0.43	-0.96	-0.79	-0.83	-0.98
Pouteria venosa	Sapotaceae	Sub	20.28	0.59	39.22	269.53	113.68	3128	-1.15	-1.11	-0.73	-0.28	-1.20	-0.71	-0.78	-1.38	-0.20	-0.78	1.05	-0.70
Psychotria nuda	Rubiaceae	Ll	7.81	0.57	36.07	201.08	228.2	380	-1.44	-0.96	-1.28	-0.97	-1.47	-0.86	-1.21	-1.41	6.49	-0.79	5.37	9.74
Psychotria nuda	Rubiaceae	Sub	7.81	0.57	36.07	201.08	228.2	380	0.36	0.17	-0.18	0.29	0.91	0.50	-0.02	1.78	2.00	-0.78	2.20	2.50
Roupala montana	Proteaceae	Ll	21.66	0.8	129.8	496.3	148.63	25.5	-1.54	-1.04	-1.24	-1.01	-1.47	-0.86	-1.21	-1.41	-1.06	-0.79	-1.02	-0.98
Roupala montana	Proteaceae	Mon	21.66	0.8	129.8	496.3	148.63	25.5	-1.64	-0.35	-1.18	-1.90	-0.59	-0.87	0.67	-1.22	-1.00	-0.97	-0.66	-0.81
Roupala montana	Proteaceae	Res	21.66	0.8	129.8	496.3	148.63	25.5	-0.97	-0.19	-1.07	-0.29	-0.95	-0.94	-0.89	-0.88	-0.99	-0.73	-1.08	-0.65
Roupala montana	Proteaceae	Sub	21.66	0.8	129.8	496.3	148.63	25.5	-1.51	-1.35	-0.84	-1.17	-0.90	-0.71	-0.20	-1.38	-0.51	-0.78	0.21	-0.70
Rudgea jasminoides	Rubiaceae	Mon	10.65	0.75	49.35	310.93	159.3	200	-1.67	-1.77	-1.59	-1.48	-1.25	-0.87	-1.20	-1.22	3.98	11.56	2.04	0.93
Rudgea jasminoides	Rubiaceae	Sub	10.65	0.75	49.35	310.93	159.3	200	-0.68	-0.34	-0.68	-0.28	0.18	-0.53	-0.11	0.69	-0.33	-0.30	-0.46	-0.21
Rudgea vellerea	Rubiaceae	Ll	12.82	0.52	154.01	180.58	94.66	200	-0.27	-0.44	-0.52	-0.17	-1.01	-0.86	-0.20	-1.41	-0.43	-0.79	-1.02	0.58
Rudgea vellerea	Rubiaceae	Mon	12.82	0.52	154.01	180.58	94.66	200	-1.24	-0.95	-1.34	-1.62	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Rudgea vellerea	Rubiaceae	Sub	12.82	0.52	154.01	180.58	94.66	200	0.24	-0.14	-0.39	-0.02	-0.90	0.17	-0.78	-1.06	-0.51	-0.78	0.13	-0.70
Rustia formosa	Rubiaceae	Ll	17.92	0.65	452.12	176.55	117.31	NA	-0.63	-0.46	-0.50	-0.57	-0.59	-0.41	-0.81	-0.20	-0.58	-0.09	-0.55	-0.73
Rustia formosa	Rubiaceae	Sub	17.92	0.65	452.12	176.55	117.31	NA	-0.78	-0.51	-0.61	-0.70	-0.91	-0.71	-0.40	-1.23	-0.60	-0.38	-0.79	-0.44
Schefflera angustissima	Araliaceae	Ll	20.85	0.64	60.76	307.47	62.35	15	-0.25	-0.53	-0.72	0.09	0.43	-0.86	0.67	0.72	-1.06	-0.79	-1.02	-0.98
Schefflera angustissima	Araliaceae	Mon	20.85	0.64	60.76	307.47	62.35	15	0.38	-0.61	0.03	0.54	-0.76	-0.87	-0.43	-0.79	-1.00	-0.97	-0.66	-0.81
Schefflera angustissima	Araliaceae	Res	20.85	0.64	60.76	307.47	62.35	15	1.56	0.69	1.74	-0.29	0.31	0.88	-0.54	0.70	-0.16	0.88	0.10	-0.65
Schefflera angustissima	Araliaceae	Sub	20.85	0.64	60.76	307.47	62.35	15	0.22	-0.51	0.05	-0.50	0.54	-0.71	1.15	-0.03	-0.29	-0.78	0.74	-0.70
Sloanea guianensis	Elaeocarpaceae	Ll	23.97	0.72	48.83	424.26	112	200	-0.14	-0.34	-0.35	-0.22	-0.79	0.25	-0.71	-1.16	-0.55	-0.29	-0.70	-0.36
Sloanea guianensis	Elaeocarpaceae	Mon	23.97	0.72	48.83	424.26	112	200	-1.78	-1.08	-1.84	-2.01	1.81	14.32	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Sloanea guianensis	Elaeocarpaceae	Res	23.97	0.72	48.83	424.26	112	200	1.16	-0.09	1.44	0.24	-0.39	-0.94	-0.89	0.32	-0.09	-0.73	-1.08	0.70
Sloanea guianensis	Elaeocarpaceae	Sub	23.97	0.72	48.83	424.26	112	200	-0.08	-0.50	-0.37	0.04	-0.86	0.08	-0.66	-1.09	-0.34	-0.43	-0.38	-0.22
Sorocea bonplandii	Moraceae	Ll	20.38	NA	41.38	353.18	94.26	321	-0.27	-0.12	-0.31	-0.11	2.91	-0.86	5.03	1.88	-0.89	-0.79	-1.02	-0.56
Sorocea hilarii	Moraceae	Ll	14.02	0.69	41.38	353.18	94.26	325	-0.99	-0.48	-0.90	-0.95	1.07	1.05	1.57	0.09	-0.79	-0.79	-1.02	-0.31
Sorocea hilarii	Moraceae	Sub	14.02	0.69	41.38	353.18	94.26	325	-0.57	-0.06	-0.36	-0.60	-1.01	-0.71	-0.78	-0.95	0.06	0.25	0.40	-0.20
Swartzia simplex	Fabaceae	Ll	16.8	0.69	45.18	333.06	109.93	1732	-0.55	-0.28	-0.52	-0.75	-1.08	-0.86	-0.79	-0.99	-0.28	-0.79	-0.27	0.06

Specie	*Family*	*Forest Type*	*Max. height (m)*	*WD (cm^3 g-1)*	*LA (cm^2)*	*LDMC (mg g-1)*	*SLA (cm^2 g-1)*	*SM (mg)*	*RGR whole interval*	*RGR interval 1*	*RGR interval 2*	*RGR interval 3*	*MR whole interval*	*MR interval 1*	*MR interval 2*	*MR interval 3*	*RCT whole interval*	*RCT interval 1*	*RCT interval 2*	*RCT interval 3*
Swartzia simplex	Fabaceae	Res	16.8	0.69	45.18	333.06	109.93	1732	-0.59	-0.71	-1.24	-0.53	0.27	-0.94	-0.89	1.71	-0.99	-0.73	-1.08	-0.65
Syagrus pseudococos	Arecaceae	Ll	22.61	0.59	34.53	477.07	79.28	19090	0.23	0.04	-0.16	-0.35	0.82	-0.56	1.29	0.87	-0.56	-0.58	-0.84	-0.06
Syagrus pseudococos	Arecaceae	Sub	22.61	0.59	34.53	477.07	79.28	19090	-0.82	-0.76	-0.66	-0.61	0.38	0.85	-0.18	0.78	-0.74	-0.78	-0.70	-0.60
Tetrastylidium grandifolium	Olacaceae	Ll	19.33	0.81	43.52	151.97	291.84	380	-0.46	-0.67	-0.44	-0.25	-1.03	-0.86	-1.21	-0.47	0.55	-0.79	0.97	0.64
Tetrastylidium grandifolium	Olacaceae	Sub	19.33	0.81	43.52	151.97	291.84	380	-0.69	-0.81	-0.43	-0.80	-0.46	-0.71	0.54	-1.38	-0.83	-0.78	-0.79	-0.70
Trichilia silvatica	Meliaceae	Ll	21.69	0.51	6.2	317.93	52.95	93	-0.90	-0.66	-0.61	-0.76	0.37	1.05	1.57	-1.41	-1.06	-0.79	-1.02	-0.98
Trichilia silvatica	Meliaceae	Sub	21.69	0.51	6.2	317.93	52.95	93	-0.51	-0.53	-0.34	-0.64	-0.86	-0.71	-0.78	-0.66	-0.83	-0.78	-0.79	-0.70
Vantanea sp.	Humiriaceae	Mon	18.85	0.64	14.34	403.92	64.58	2683	-1.93	-1.48	-1.10	-2.07	-1.25	-0.87	-1.20	-1.22	-1.00	-0.97	-0.66	-0.81
Vantanea sp.	Humiriaceae	Sub	18.85	0.64	14.34	403.92	64.58	2683	-0.92	-0.47	-0.64	-0.89	-0.91	-0.71	-0.22	-1.38	-0.52	0.82	-0.79	-0.70
Vernonanthura puberula	Asteraceae	Sub	19.66	0.59	13.56	395.11	37.7	6	0.56	0.06	-0.35	-0.07	3.41	-0.71	-0.78	8.43	2.08	-0.78	-0.79	4.40
Virola bicuhyba	Myristicaceae	Ll	24.73	0.53	41.94	249.69	65.39	2300	-0.01	-0.49	0.33	-0.40	-0.79	-0.86	0.29	-1.41	-0.45	-0.19	-0.89	0.06
Virola bicuhyba	Myristicaceae	Res	24.73	0.53	41.94	249.69	65.39	2300	-0.84	-0.87	-0.37	-1.52	-0.95	-0.94	-0.89	-0.88	7.41	-0.73	-1.08	11.90
Virola bicuhyba	Myristicaceae	Sub	24.73	0.53	41.94	249.69	65.39	2300	0.66	0.20	0.68	-0.12	-0.52	-0.71	0.12	-1.01	-0.65	-0.78	-0.28	-0.70
Virola gardneri	Myristicaceae	Sub	24.46	0.68	41.94	259.5	97.42	5600	-0.51	-1.14	-0.64	-0.60	-0.87	-0.71	-0.78	-0.67	-0.65	0.06	-0.79	-0.70

Table S3. Overview of the functional traits used in this study and their relation to demography components and function in the community, followed by key references.

Functional Trait	Description	Expected relation to tree demographic components	Function	References
Leaf area (LA)	One-side projected surface area of a single or an average leaf or leaf lamina	LA has important consequences for the leaf energy and water balance and can be linked to allometric factor	Productivity and competitive ability	Bruelheide et al., (2018); Cornelissen et al., (2003)
Leaf dry matter content (LDMC)	Oven-dry mass of a leaf divided by its water-saturated fresh mass	LDMC has been shown to correlate negatively with potential relative growth and positively with survival	Productivity and competitive ability	Bruelheide et al., (2018); Cornelissen et al., (2003)
Specific leaf area (SLA)	One-side area of a fresh leaf divided by its oven-dry mass	SLA of a specie is in many cases a positive correlate of its potential relative growth rate	Productivity and competitive ability	Bruelheide et al., (2018); Cornelissen et al., (2003)
Seed mass (SM)	Oven-dry mass of an average seed of a specie	Seeds with high storage facilitate establishment and increase survival	Nutrient supply	Bruelheide et al., (2018); Cornelissen et al., (2003)
Maximum height	95th quantile of individual height of adult plant	Tree size is expected to be positively correlated with relative growth rates	Competitive ability	Bruelheide et al., (2018); Cornelissen et al., (2003); Iida et al., (2014)
Wood density (WD)	Oven-dry mass of a section of a plant´s main stem divided by the volume of the same section when still fresh	Fast growth species are expected to present low values of WD	Productivity and drought tolerance	Bruelheide et al., (2018); Cornelissen et al., (2003). Pérez-Harguindeguy et al., (2013)

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FIGURES

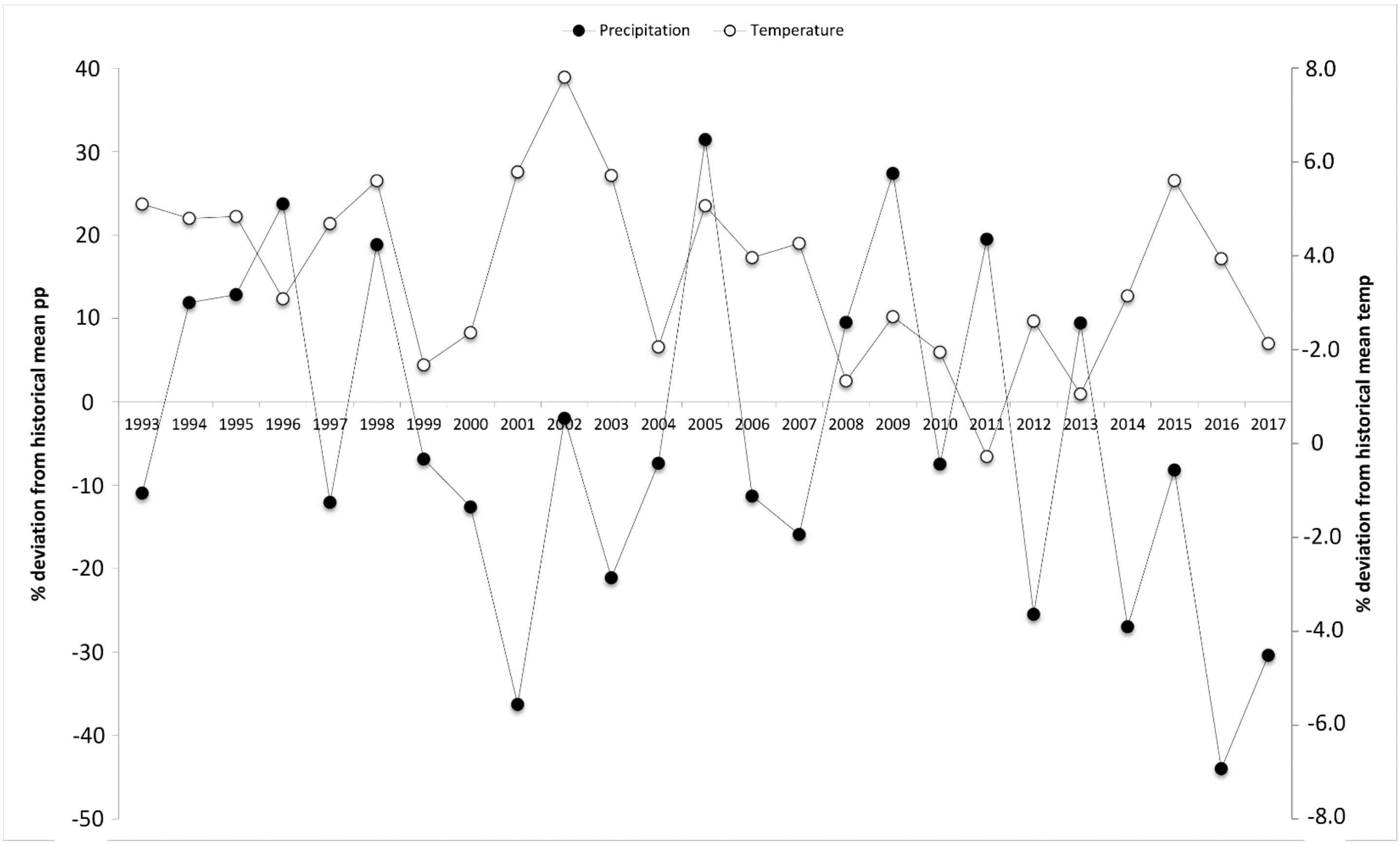


Figure S1. Climate anomalies displayed as percentage deviations in mean annual precipitation (black points) and temperature (white points) from the historical mean of 25 years (1993 - 2017). The climate data was extracted from a database of the municipality of Ubatuba city, São Paulo state, southeastern Brazil. The climate data are collected and made available by the "Centro Integrado de Informações Agrometeorológicas" (CIIAGRO in www.ciiagro.sp.gov.br). pp: precipitation; temp: temperature.

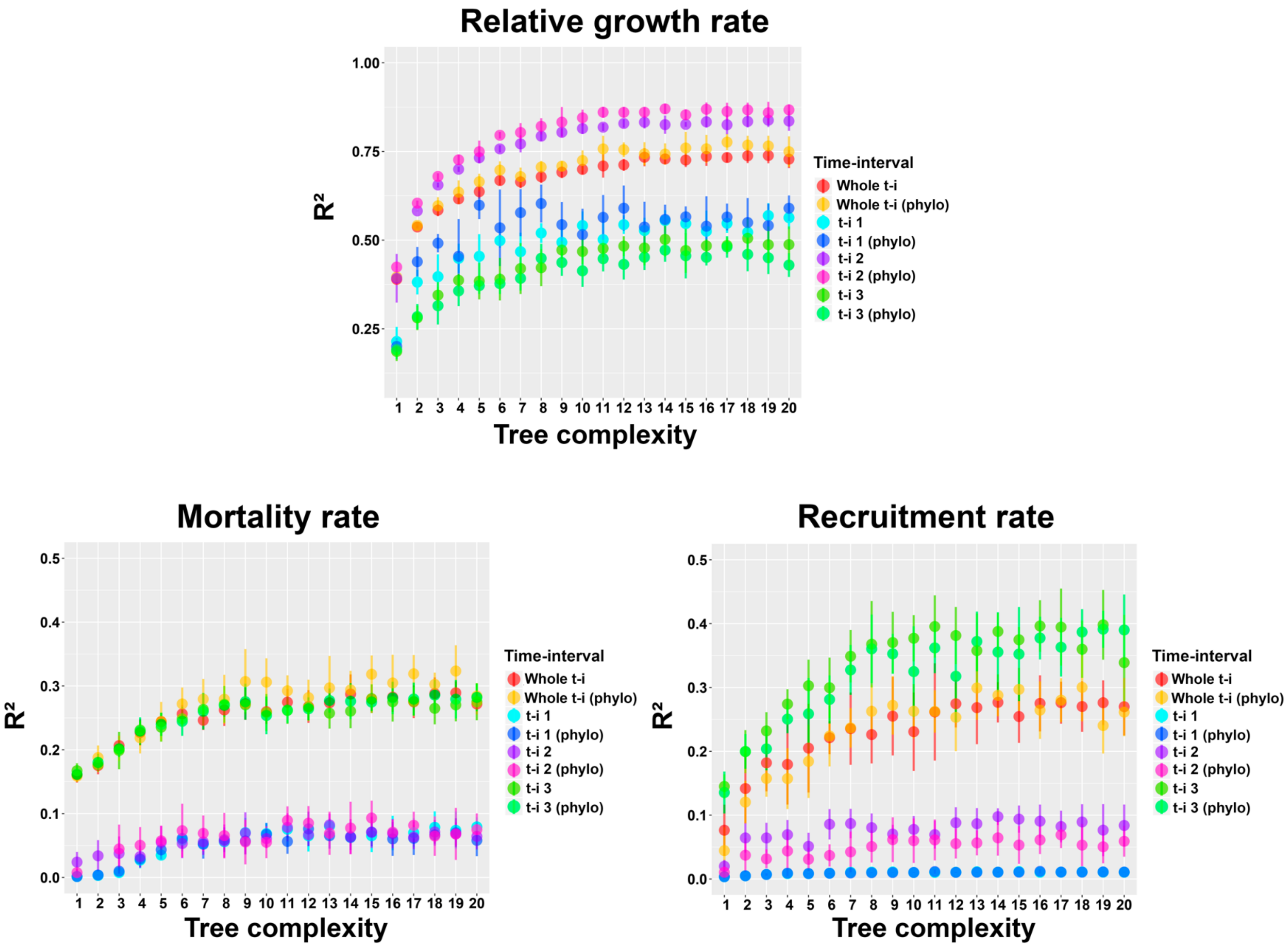


Figure S2. Results of explained variation (R^2) in relation to systematic increasing of tree complexity in the boosted regression tree models (for further information, see the methods). phylo: boosted regression tree models including phylogenetic information; t-i: time-interval.

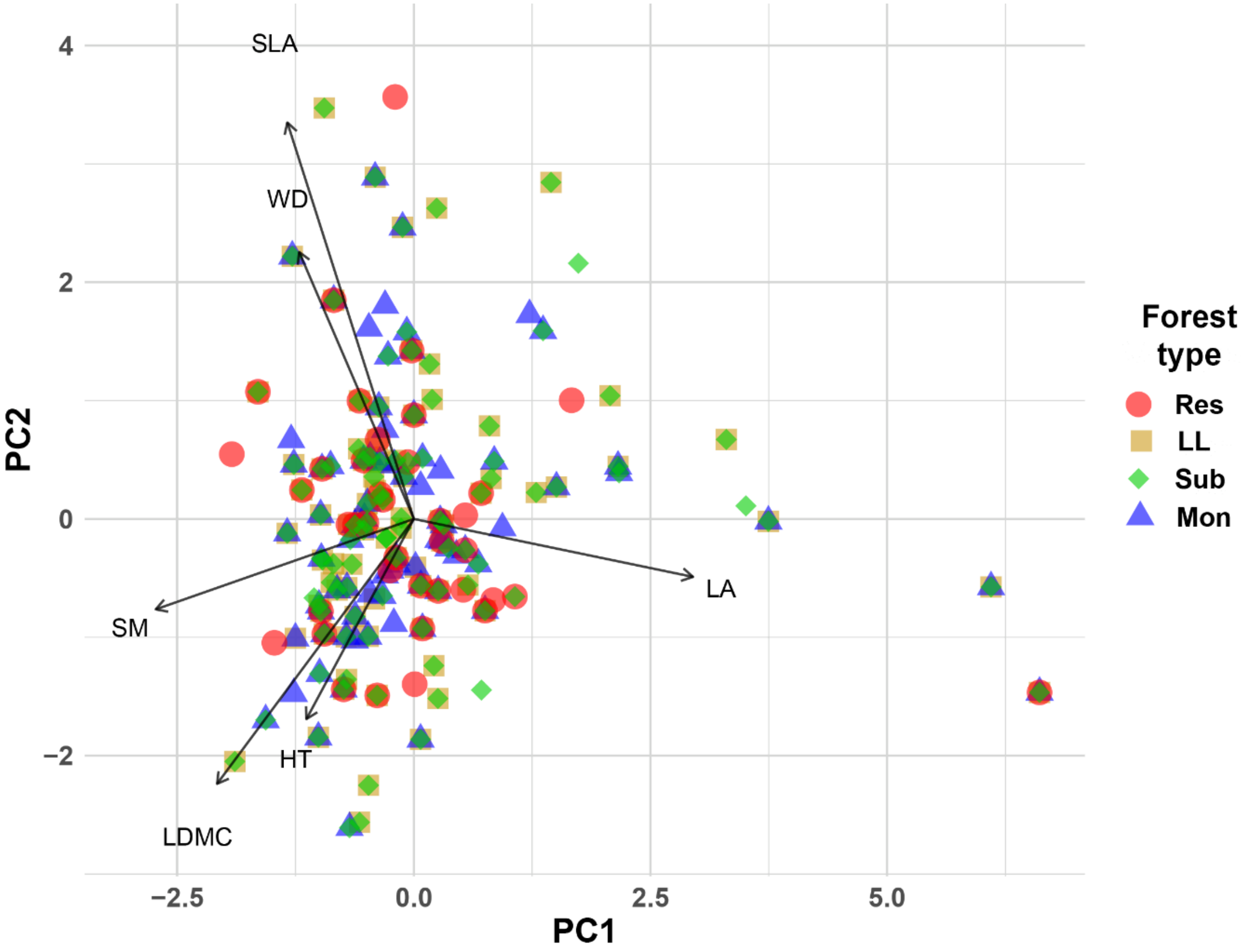
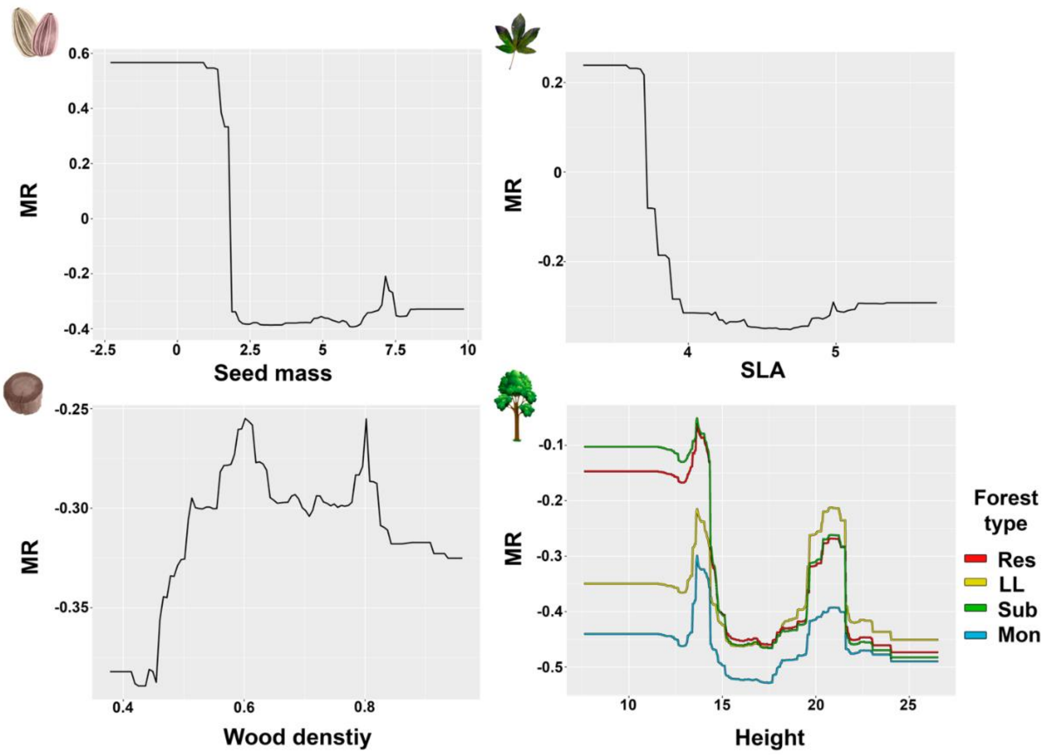


Figure S3. Results of the Principal Component Analyses applied to functional traits of 133 tree species from Atlantic forest, southeastern Brazil. Traits measured: HT: height; LA: leaf area; LDMC: leaf dry matter content; SM: seed mass; SLA: specific leaf area; WD: wood density; Res: *Restinga* forest; LL: Lowland forest; Sub: Submontane forest; Mon: Montane forest.

Whole time-interval



Time-interval 3 (drought)

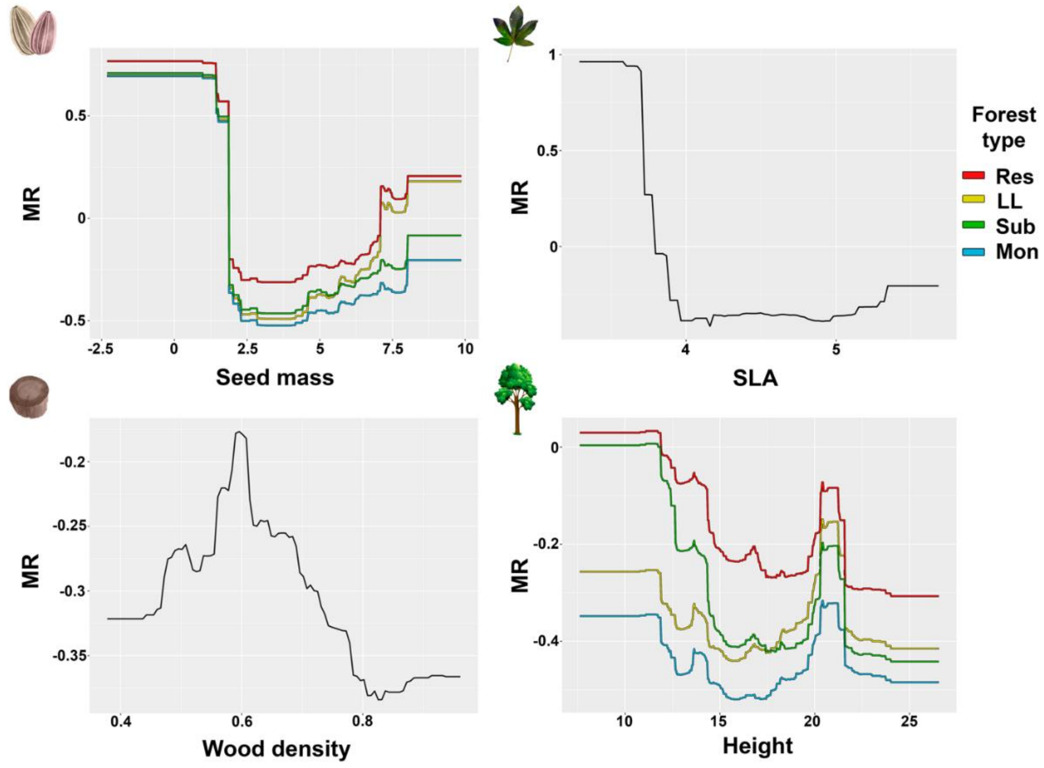


Figure S4. Trait-mortality relationships outcomes of tree species from Brazilian Atlantic forest. Mortality rates (MR) are presented as predicted values from boosted regression trees analysis (see the methods). SLA: specific leaf area. Res: *Restinga* forest; LL: Lowland forest; Sub: Submontane forest; Mon: Montane forest.

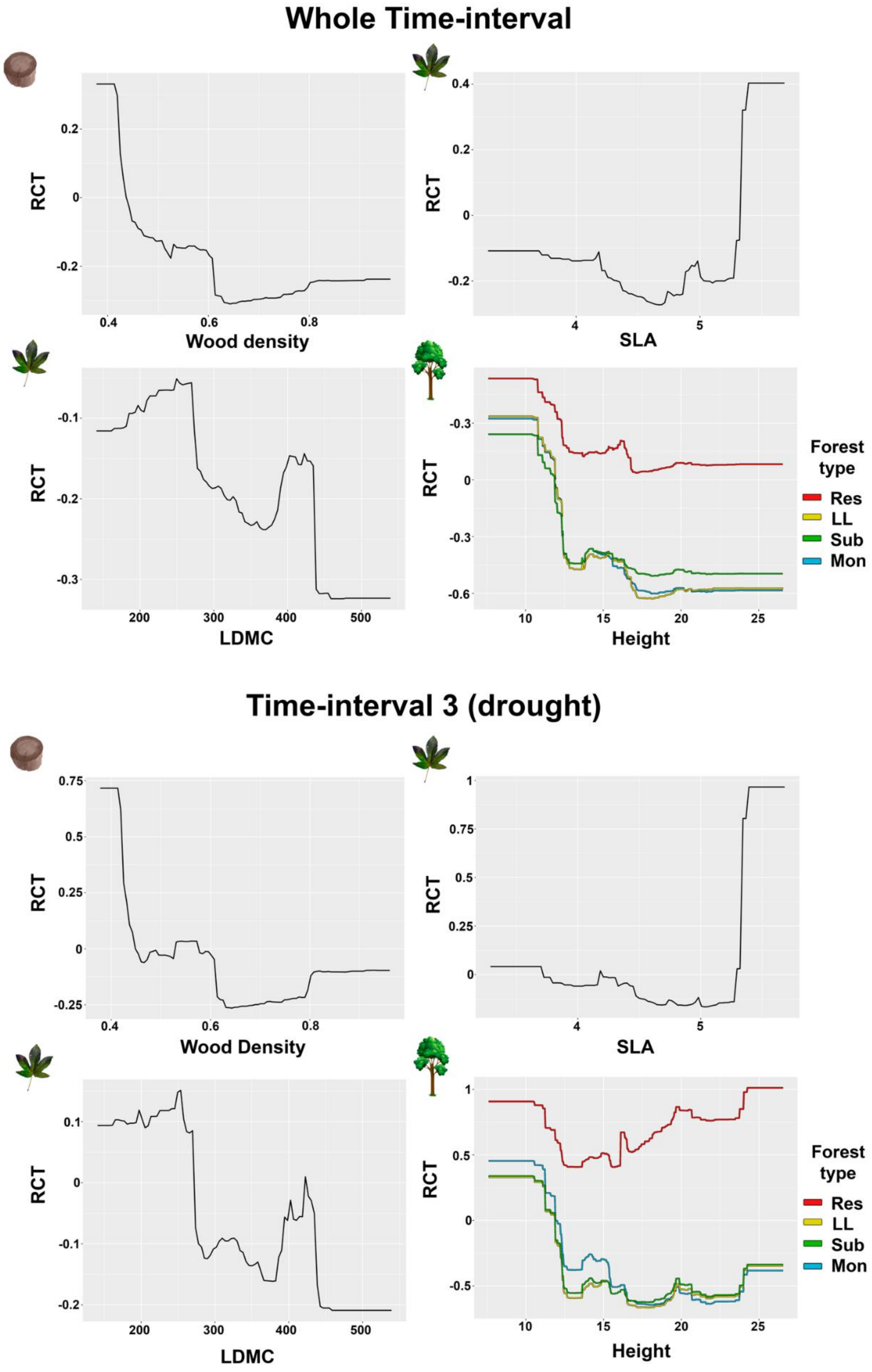


Figure S5. Trait-recruitment relationships outcomes of tree species from Brazilian Atlantic forest. Recruitment rates (RCT) are presented as predicted values from boosted regression trees analysis (see the methods). LDMC: leaf dry matter content; SLA: specific leaf area. Res: *Restinga* forest; LL: Lowland forest; Sub: Submontane forest; Mon: Montane forest.

CONSIDERAÇÕES FINAIS

Neste trabalho, realizamos três estudos sobre temas centrais na ecologia de comunidades, usando um grande conjunto de dados de indivíduos arbóreos em um sistema montanhoso da Floresta Atlântica. Apesar de independentes, os estudos seguem uma ampliação de complexidade em suas abordagens, que refletem um breve alvorecer do meu conhecimento ecológico e as mudanças no meu pensamento científico.

Nossos resultados revelam a importância de que estudos em ecologia de comunidades usem uma abordagem taxonômica, evolutiva e funcional integrada para compreender, não apenas as relações de variação da diversidade ao longo de gradiente ambientais, mas também os processos e mecanismos ecológicos que conduzem ao padrão e funcionamento ecossistêmico. Salientamos haver melhor compreensão dos padrões de diversidade das comunidades vegetais ao longo de gradientes ambientais que foi observada por meio de análises em diferentes arranjos de espécies, ou seja, confrontando o padrão da comunidade com os padrões apresentados por suas famílias com maior abundância e das espécies raras.

Integramos análises de diversidade local (*alpha*) e regional (*beta*) sob ambas as abordagens, diversidade de espécies e filogenética, e apuramos os múltiplos processos ecológicos que conduzem os mecanismos de montagem de comunidades. Ao longo do gradiente de elevação na Floresta Atlântica, verificamos um padrão de variação monotônica e um decréscimo da diversidade de espécies e filogenética, respectivamente. A diferença nos resultados nos levou a compreender o papel da elevação na diversidade local, promovendo maior número de espécies em áreas de média elevação, apesar de conter maior diversidade de espécies da mesma família. Os resultados da diversidade regional abriram caminho para compreender que a limitação de dispersão não é um processo determinante na distribuição de espécies nesse ambiente, mas condições abióticas locais mais restritivas, como o solo sazonalmente alagadiço e temperaturas baixas em maiores elevações, são filtros ambientais que levam a uma composição distinta. A partição de nicho parece ser um processo fundamental para manutenção da mega-diversidade de áreas intermediárias.

Diferentemente do que esperávamos, o corte seletivo de madeira e o filtro ambiental de elevação promoveram um aumento na diversidade filogenética. Além disso, esse padrão foi modificado? pelos clados usados na análise. A inclusão ou exclusão de um clado basal, as samambaias arbóreas (Cyatheaceae), nas análises filogenéticas, alterou os resultados encontrados. Com isso, pudemos compreender os efeitos de perda de diversidade em locais antropizados e como este distúrbio pode gerar diferentes consequências em comunidades sob diferentes condições climáticas. O filtro ambiental de elevação levou a uma estrutura filogenética agrupada de comunidades e ofuscou os efeitos da extração seletiva de madeira. Porém, quando o filtro de elevação foi excluído, encontramos que a abertura de nichos criados por perturbações na exploração madeireira, levando a maior co-ocorrência de espécies distantemente aparentadas, porém com menor diversidade de espécies. Além disso, os efeitos da elevação e da exploração madeireira foram melhor elucidados em larga escala nestas comunidades arbóreas tropicais. Assim, destacamos a relevância do desenho experimental para compreender o papel dos filtros ambientais e distúrbios nos processos que atuam na estruturação de comunidades.

Após explorar os padrões de diversidade sob uma perspectiva taxonômica e evolutiva, integramos a ecologia funcional com novas técnicas de análise de dados para compreender como os atributos das espécies moldam as suas taxas demográficas. Por meio da utilização do aprendizado de máquinas, muito aplicado em estudos com conjuntos de dados gigantescos e manipulações eleitorais, como a ocorrida em 2016 nos Estados Unidos da América e 2018 no Brasil, conseguimos melhorar os modelos de predição das relações entre atributos e taxas demográficas, utilizando o conceito de fenótipos multifuncionais com respostas demográficas semelhantes e os efeitos do contexto ambiental. As possibilidades de distintos fenótipos multifuncionais apresentarem taxas demográficas próximas foram considerados a partir das interações entre os atributos das espécies, ou seja, verificamos a possibilidade de duas espécies diferentes em suas características, apresentarem taxas demográficas semelhantes por combinarem de forma diferente estes atributos. Essa premissa foi testada considerando, também, diferentes contextos ambientais, em que consideramos os tipos florestais e o período de amostragem dos dados (incluindo ou não um evento de seca) como fatores de influência na relação atributo-demografia. Concluímos que os estudos baseados em características devem considerar o contexto ambiental (espaço e tempo) e as interações de características para entender as mudanças na demografia das comunidades de árvores tropicais. Para avaliar quais, onde e quando os traços são funcionais, é necessário incorporar o conceito de fenótipos multifuncionais, resultante das interações dos atributos em diferentes habitats e período de avaliação.

No meu entendimento, esta tese demonstra a importância de considerar os estudos em ecologia de comunidade com uma grande visão integrada, principalmente, em sistemas ecológicos complexos e mega-diversos, como a Floresta Atlântica, para trazer novas formas de análises e auxiliar na compreensão questões ainda sem respostas, como os processos ecológicos e mecanismos que atuam na manutenção da co-ocorrência de um enorme número de espécies e indivíduos em floresta tropicais e o funcionamento de suas comunidades. Além disso, mostramos como técnicas de análises utilizadas em outras áreas, como o ‘aprendizado de máquina’ nos subcampos da Engenharia e da Ciência da Computação, podem ser uma grande contribuição para as nossas pesquisas em ecologia.