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PEDRO ORTMAN CAVALIN

ESTRUTURA DE COMUNIDADES DE ESPÉCIES LENHOSAS AO LONGO DE UM GRADIENTE DE ALTITUDE NA FLORESTA OMBRÓFILA DENSA ATLÂNTICA DO SUDESTE BRASILEIRO: UMA ABORDAGEM FILOGENÉTICA E FUNCIONAL

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e aprovada pela Comissão Julgadora.

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

Orientador: Prof. Dr. Carlos Alfredo Joly

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“*We think in generalities, but we live in detail*”

Alfred North Whitehead (1926).

“*I perceive that, when an acorn and a chestnut fall side by side, the one does not remain inert to make way for the other, but both obey their own laws, and spring and grow and flourish as best they can, till one, perchance, overshadows and destroys the other. If a plant cannot live according to its nature, it dies; and so a man.*”

Henry David Thoreau (1854), “Walden”.

Resumo

Um grande número de espécies co-ocorre em florestas tropicais. Diferenciação de nicho e processos estocásticos são invocados como mecanismos que possibilitam essa coexistência de espécies. Recentemente, métodos filogeneticamente explícitos ou com base em atributos funcionais (considerados bons indicadores de nicho de regeneração, história de vida e tolerância ambiental) vem sendo usados para analisar tais mecanismos. No presente trabalho, estudei comunidades de espécies lenhosas no sub-bosque ao longo de um gradiente de altitude na Floresta Ombrófila Densa (FOD) Atlântica no Parque Estadual da Serra do Mar, SP, tentando relacionar a estrutura de comunidades com variáveis ambientais, e se tais relações variam de acordo com a altitude. Analisamos a estrutura filogenética em três sítios localizados em diferentes cotas altitudinais (FOD de Terras Baixas, 70 m; FOD Submontana, 370 m; FOD Montana, 1070 m). Em nenhum dos sítios foi observada estruturação filogenética, tampouco relações da estrutura filogenética com variáveis ambientais. Em seguida, analisamos a estrutura de comunidade baseada em atributos funcionais. Apesar de haver correlações entre atributos funcionais e variáveis ambientais no nível das espécies, as comunidades não apresentaram estrutura significativamente diferente do esperado pelo acaso, embora o conjunto de espécies comuns tenha apresentado boa correlação entre atributos funcionais e variáveis ambientais. Por fim, analisamos como a estrutura de comunidades, baseada em atributos funcionais, em um sítio (FOD Submontana) varia entre coortes de plantas de diferentes tamanhos. Em geral, plantas de menor tamanho são mais similares entre si do que o esperado pelo acaso, enquanto que plantas de maior tamanho não diferem do esperado pelo acaso. Quando árvores de dossel são analisadas em separado, nenhuma das classes de tamanho difere do esperado pelo acaso. Mortalidade causada pela abundância de vizinhos, e independente de suas identidades, pode ser responsável pela ausência de mudança na estrutura da comunidade baseada em atributos ao longo das coortes. Discutimos a ausência de variação na estruturação das comunidades ao longo do gradiente de altitude na FOD Atlântica, levando em consideração as características do mesmo, e propomos estratégias para o melhor entendimento da dinâmica dessas comunidades.

Abstract

A large number of species co-occur in tropical forests. Niche differentiation and stochastic processes are commonly invoked to explain species co-occurrence. Recently, phylogenetically explicit or trait-based (functional traits are considered to be good proxies for regeneration niche, life history, and environmental tolerance) methods have been used to assess these mechanisms. In the present study, We have surveyed understory woody species communities along an altitudinal gradient on the Atlantic Dense Ombrophilous Forest at the Serra do Mar State Park, São Paulo State, Brazil, analyzing the relationships between community structure and environmental variables, and how these relationships vary along the gradient. Community phylogenetic structure was assessed in three sites differing in altitude (Lowland, 70 m; Lower Montane, 370 m; Montane, 1070 m). No phylogenetic structure was found in any site, nor correlations between phylogenetic structure and environmental variables. We then analyzed trait-based community structure. We observed no community structure, even though there were significant correlations between functional traits and environmental variables at species-level on a set of frequent species. Finally, we assessed how trait-based community structure varied between plant cohorts of differing sizes. In general, smaller plants were functionally more similar to each other than expected by chance, while larger plants showed no significant structuring. When only canopy trees are separately analyzed, no size-class cohort differs from the random expectation. This lack of change in structuring among cohorts may be due to mortality caused by neighboring stem density, irrespective of species identity. We then discuss the absence of community phylogenetic and functional structuring of understory woody plants communities along the altitudinal gradient on the Atlantic Forest, taking into account its peculiarities, and propose strategies that could advance the understanding of these communities' dynamics.

Sumário

Introdução Geral

As florestas tropicais ocorrem desde o nível do mar até mais de 2000 m de altitude. Ao longo dessa variação de altitude há formação de diversos gradientes abióticos, principalmente relacionados a temperatura, radiação, precipitação, e fatores edáficos. De maneira geral tais gradientes são não-lineares e dependem de fatores como latitude e posição da vertente, dificultando generalizações globais sobre a relação entre vegetação e altitude (Körner 2007). No entanto, em latitudes intertropicais, há um aumento de pluviosidade e da nebulosidade, e diminuição da radiação líquida total, quando se sobe do nível do mar até aproximadamente 1000 m de altitude (Körner 2007, Leuschner 2000). Além disso, as disponibilidades de nitrogênio, fósforo e potássio no solo em geral diminuem, e o teor de matéria orgânica no solo aumenta, com o aumento de altitude (Tanner *et al.* 1998).

Associadas à variação altitudinal, e aos gradientes que se formam ao longo dela, ocorrem variações florísticas e fisionômicas. De maneira geral, florestas tropicais montanas apresentam menor riqueza de espécies, dossel mais baixo e aumento na densidade de árvores, do que florestas tropicais de terras baixas (Grubb 1977, Lieberman *et al.* 1996, Vazquez-G. e Givnish 1998). Além disso, há variações na morfologia e anatomia foliar ao longo de gradientes altitudinais. Com o aumento de altitude, diminui a frequência de espécies com folhas grandes, a espessura média da lâmina foliar aumenta (Grubb *et al*. 1963, Velázquez-Rosa *et al*. 2002), e há uma tendência à diminuição da área foliar específica (AFE; Bruijnzeel *et al*. 1993, Turner 1994). Além da morfologia foliar, com o aumento de altitude há diminuição da concentração de nitrogênio foliar (Vitousek e Sanford 1986), e uma diminuição de amplitude nos valores de densidade da madeira (Williamson 1984). Tais variações morfológicas e fisiológicas se devem em parte à substituição de espécies ao longo do gradiente altitudinal, e em parte à variação ecotípica e/ou plástica de espécies que ocorrem ao longo do gradiente (Velazquez-Rosa *et al.* 2002). Por exemplo, *Metrosideros polymorpha*, uma espécie dominante nas florestas tropicais do Havaí, apresenta diminuição da área foliar e AFE, e aumento na eficiência de carboxilação e conteúdo de nitrogênio foliar por unidade de área, com o aumento da altitude (Cordell *et al.* 1999).

Todos os trabalhos que evidenciam a variação de atributos funcionais de árvores ao longo de gradientes de altitude foram realizados com indivíduos adultos. No entanto, na floresta tropical ombrófila de La Chonta, Bolívia, os atributos funcionais de 58 espécies arbóreas foram mais correlacionados ao nicho regenerativo (indivíduos jovens) do que ao nicho de indivíduos adultos (Poorter 2007). Isso indica que a composição local de espécies se deve mais às condições ambientais encontradas pelos indivíduos no início de seu ciclo de vida. Em uma revisão sobre a coexistência de espécies vegetais, Silvertown (2004) argumenta que a separação de nicho entre espécies, incluindo aí gradientes luminosos, umidade do solo e partição de recursos nutricionais, tem papel importante na manutenção da diversidade local, ainda que outros processos como dinâmica de clareiras, mortalidade denso-dependente e limitação de recrutamento sejam também importantes (Wright 2002). Wright (2002) ainda argumenta que a baixa densidade de indivíduos jovens no sobosque reduz as oportunidades de competição entre indivíduos, e que todas as espécies aptas a tolerar o denso sombreamento oferecido pelo dossel podem potencialmente coexistir. Assim, a composição local de espécies em florestas tropicais seria controlada, em parte, pela capacidade de sobrevivência e crescimento sob as condições locais de disponibilidade de recursos, e em parte por processos estocásticos de dispersão, com a competição por recursos tendo provavelmente uma importância limitada. Em outras palavras, a composição de espécies em um dado local é determinada por filtros históricos (incluindo processos atuais de dispersão e padrões históricos de surgimento e migração de linhagens), abióticos (crescimento e sobrevivência sob diferentes condições ambientais), e bióticos (interações entre espécies, com competição, inibição e facilitação; Grime 1998, Lortie *et al.* 2004).

Os efeitos dos filtros histórico, abiótico e biótico podem ser vistos como regras de montagem de comunidades: tais regras determinam a composição local de espécies a partir de um pool regional de espécies (Diamond 1975). Apesar do conceito ter sido inicialmente proposto com a finalidade de detectar padrões de presença ou abundância de espécies ou grupos funcionais determinados *a priori*, Weiher e Keddy (1995) argumentam que regras de montagem de comunidade formuladas com base em atributos funcionais são mais claras e mais generalizáveis. Isso ocorre porque atributos funcionais podem ser relacionados ao uso de recursos e à tolerância a condições específicas dando, portanto, indicações sobre os nichos ocupados pelas espécies (Fonseca *et al.* 2000, Keddy 2001, Wright *et al.* 2004), e porque as regras potencialmente observadas não dependem da composição florística local, permitindo comparações entre comunidades floristicamente muito distintas. Além disso, pode-se supor que espécies funcionalmente similares apresentarão maior competição por recursos, levando eventualmente à exclusão competitiva ou ao deslocamento de caracteres.

Diversos atributos funcionais estão relacionados a processos que influenciam a sobrevivência e o crescimento de plantas lenhosas em florestas tropicais: a AFE se relaciona à economia de carbono da folhas (Reich *et al.* 2003, Wright *et al.* 2004), a área foliar relaciona-se à captura de luz e ao balanço térmico foliar (Cornelissen *et al.* 2003, Poorter e Rozendaal 2008), a densidade da madeira está relacionada à resistência à cavitação em ambientes secos (Ackerly 2004) e à tolerância ao sombreamento e ao dano mecânico no sub-bosque de florestas (van Gelder *et al.* 2006, Alvarez-Clare e Kitajima 2007), e a altura potencial está relacionada à captura de luz e à longevidade (Falster e Westoby 2005). Esse conjunto de atributos está, portanto, relacionado ao crescimento e sobrevivência de indivíduos jovens em florestas tropicais. Além disso, estes atributos são relativamente ortogonais entre si em espécies arbóreas de sete florestas neotropicais dando, portanto, informações independentes sobre as estratégias de crescimento e sobrevivência das espécies (Wright *et al*. 2007). No entanto, outros atributos são importantes no contexto da estruturação de florestas tropicais, como atributos relacionados à dispersão e polinização, resistência à herbivoria, capacidade de rebrota, e características fisiológicas.

Frequentemente se assume, conceitual ou estatisticamente, que as espécies são entidades independentes, quando na verdade elas compartilham diferentes graus de história evolutiva. Para contornar esse problema, foram propostos diversos métodos filogeneticamente explícitos para lidar não apenas com variações fenotípicas de um conjunto de espécies, mas para quantificar a estrutura filogenética de comunidades (Webb 2000). Várias métricas foram desenvolvidas nesse sentido, mas de maneira geral a questão a ser respondida é se as espécies que co-ocorrem tendem a ser filogeneticamente mais agregadas ou segregadas do que o esperado pelo acaso (Webb *et al.* 2002).

De maneira geral, espera-se que a filtragem de habitat seja exercida em ambientes restritivos ao crescimento ou à sobrevivência dos indivíduos. É o que deve ocorrer com indivíduos jovens no sub-bosque de florestas tropicais, segundo a proposta de Wright (2002): a competição é pouco frequente entre os indivíduos jovens, e todas as espécies com características que permitam a sobrevivência sob baixa disponibilidade de radiação estarão presentes. Assim, pode-se supor que as espécies presentes em locais com densa cobertura de dossel sejam similares entre si. Por outro lado, a diferenciação de nicho deve ocorrer em locais com alta heterogeneidade na disponibilidade de recursos, ou locais em que a competição por recursos seja mais intensa. Em florestas tropicais, espera-se que essas condições ocorram em sítios com maior disponibilidade de luz e nutrientes: em geral, terrenos muito inclinados e clareiras. Por outro lado, a diferenciação de nicho pode indicar que dois processos estão ocorrendo: aumento do espaço de nicho ocupado meramente por um aumento na heterogeneidade na disponibilidade de recursos, ou pelo deslocamento de caracteres como resultado da competição por recursos entre indivíduos. A diferença fundamental entre ambos os processos é que a competição imprime um padrão claro no deslocamento de caracteres, relacionado à similaridade limitante: o espaçamento dos valores dos atributos entre indivíduos tende a ser mais regular do que o esperado pelo acaso (Ricklefs e Travis 1980).

Por outro lado, Wright (2002) também argumenta que árvores adultas podem apresentar uma forte competição por recursos, especialmente através da sobreposição de suas copas e consequente interferência na captura e luz, e pelo denso emaranhado de raízes finas no solo. Por isso, é razoável supor que a competição ganhe importância à medida que os indivíduos jovens crescem, ou que ela seja mais importante em indivíduos adultos. De fato, Kraft e colaboradores (2008), trabalhando com modelos nulos baseados em atributos funcionais de espécies lenhosas em uma floresta tropical no Equador, encontraram uma maior estruturação da comunidade de árvores adultas do que nos indivíduos jovens.

Trabalhos recentes têm mostrado padrões de filtragem de habitat e diferenciação de nicho em comunidades vegetais lenhosas (Cornwell *et al.* 2006, Kraft *et al.* 2008, Cornwell e Ackerly 2009, Silva e Batalha 2009). Cornwell e Ackerly (2009) verificaram relações entre filtragem de habitat de atributos funcionais e umidade do solo em um mosaico de vegetações na costa da California. No caso do cerrado brasileiro, Silva e Batalha (2009) observaram filtragem de habitat para alguns atributos foliares em cerrado *sensu strictu*. Kraft *et al.* (2008) observaram padrões de filtragem de habitat e diferenciação de nicho em atributos funcionais de árvores em uma floresta tropical no Equador.

Objetivos e estrutura da tese

A presente tese teve como objetivos investigar os fatores que estruturam a Floresta Ombrófila Densa (FOD) Atlântica ao longo de um gradiente de altitude, concentrando-se na vegetação de sub-bosque, incluindo o componente arbóreo regenerante e o componente arbustivo residente.

No primeiro capítulo, foi investigada a estrutura filogenética das comunidades de espécies arbustivas e arbóreas presentes no sub-bosque da FOD, e de que maneira variáveis ambientais relacionadas à disponibilidade de luz, nutrientes e água a afetam.

No segundo capítulo foi explorada a estrutura das comunidades de espécies arbustivas e arbóreas presentes no sub-bosque da FOD com base em atributos funcionais. Avaliamos como os atributos funcionais variam ao longo de um gradiente de altitude, como as variáveis ambientais se relacionam aos atributos funcionais, e que papel desempenham as espécies abundantes e raras na estruturação da comunidade.

No terceiro capítulo testamos se a estrutura da comunidade de árvores de um trecho de FOD Submontana, avaliada através de atributos funcionais, difere entre estratos de diferentes tamanhos e se os atributos mensurados diretamente em indivíduos jovens podem informar sobre a estrutura da comunidade de árvores adultas.

Área de estudo

Esse trabalho foi desenvolvido no Parque Estadual da Serra do Mar (PESM), Estado de São Paulo, Brasil (23º17'-23º34'S, 45º02'-45º11'W). O PESM representa a maior porção contínua preservada de Mata Atlântica do Brasil , com cerca de 315 mil hectares, compreendendo um mosaico vegetacional que inclui Formações Pioneiras com Influência Marinha (Dunas), Formações Pioneiras com Influência Fluvial (Caxetal), Formações Pioneiras com Influência Flúvio-Marinha (Mangues), Floresta de Restinga, e Floresta Ombrófila Densa de Terras Baixas, Submontana e Montana (Velloso *et al.* 1991, Assis 1999).

Em 2006, foi iniciado um projeto de grande porte, visando compreender a estrutura e o funcionamento da FOD ao longo de grande parte da variação altitudinal encontrada no PESM - "*Composição florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar*" (Joly e Martinelli 2006). Dentro do âmbito do projeto foram instaladas 14 parcelas de 1-ha em dois Núcleos do PESM – Núcleos Picinguaba e Santa Virgínia –, sendo alocadas uma parcela em Floresta de Restinga (5-15 m de altitude), 5 parcelas em FOD de Terras Baixas (50-100 m), 4 parcelas em FOD Submontana (200-400 m), e 4 parcelas em FOD Montana (900-1100 m). Em todas as parcelas foram realizados inventórios de todas as árvores, palmeiras e fetos arborescentes com diâmetro à altura do peito acima de 4,8 cm. Estes levantamentos forneceram subsídios para a escolha dos sítios estudados nesta tese: uma parcela na FOD de Terras Baixas (~70 m de altitude), uma parcela na FOD Submontana (~370 m), e uma parcela na FOD Montana (~1070 m; fig. 1). Além dos levantamentos do estrato arbóreo, a disponibilidade de informações sobre características físico-química dos solo, especialmente conteúdo total de nitrogênio, foi decisiva para a escolha das áreas.

O clima da região é tropical, variando de tropical úmido nas porções mais baixas a tropical temperado nas porções mais elevadas do PESM, com temperaturas médias variando entre *ca.* 22 °C no município de Ubatuba, próximo do Núcleo Picinguaba e dos sítios de FOD de Terras Baixas e Submontana, até *ca.* 18 °C no município de São Luís do Paraitinga, próximo do sítio de FOD Montana (Setzer 1966). A precipitação anual média supera os 2000 mm, bem distribuídos ao longo do ano. Mesmo nos meses menos chuvosos, de maio a agosto, a precipitação mensal nunca é inferior a 60 mm (Sentelhas et al. 1999). Além disso, há frequente formação de neblina, especialmente nas porções mais altas do Parque (Silva-Dias 1995).

A parcela instalada na FOD de Terras Baixas encontra-se no sopé da serra, com relevo pouco íngreme, grande quantidade de matacões, e apresentou 142 espécies distribuídas em 41 famílias, sendo as famílias mais ricas em espécies Myrtaceae, Rubiaceae e Fabaceae (Cruz Campos 2008). A parcela instalada na FOD Submontana encontra-se à meia encosta, apresentando terreno altamente declivoso. Nela foram encontradas 206 espécies pertencentes a 48 famílias, sendo as famílias mais ricas novamente Myrtaceae, Rubiaceae e Fabaceae (Rochelle 2008). A parcela instalada na FOD Montana se localiza no alto da serra, sobre terreno altamente acidentado, e apresentou 189 espécies distribuídas em 43 famílias, sendo as famílias mais ricas Myrtaceae, Lauraceae e Monimiaceae (Padgurschi et al. 2011). É notável a presença, nesta parcela, a presença de bambus nativos em alta densidade (Padgurschi et al. 2011), que produzem serrapilheira copiosa e, aparentemente, bastante refratária.

Os solos sobre os quais cresce a Floresta Ombrófila Densa do PESM são em geral arenosos, bastante rasos em alguns trechos da Serra, ácidos e pobres em nutrientes (Martins 2010). Há uma

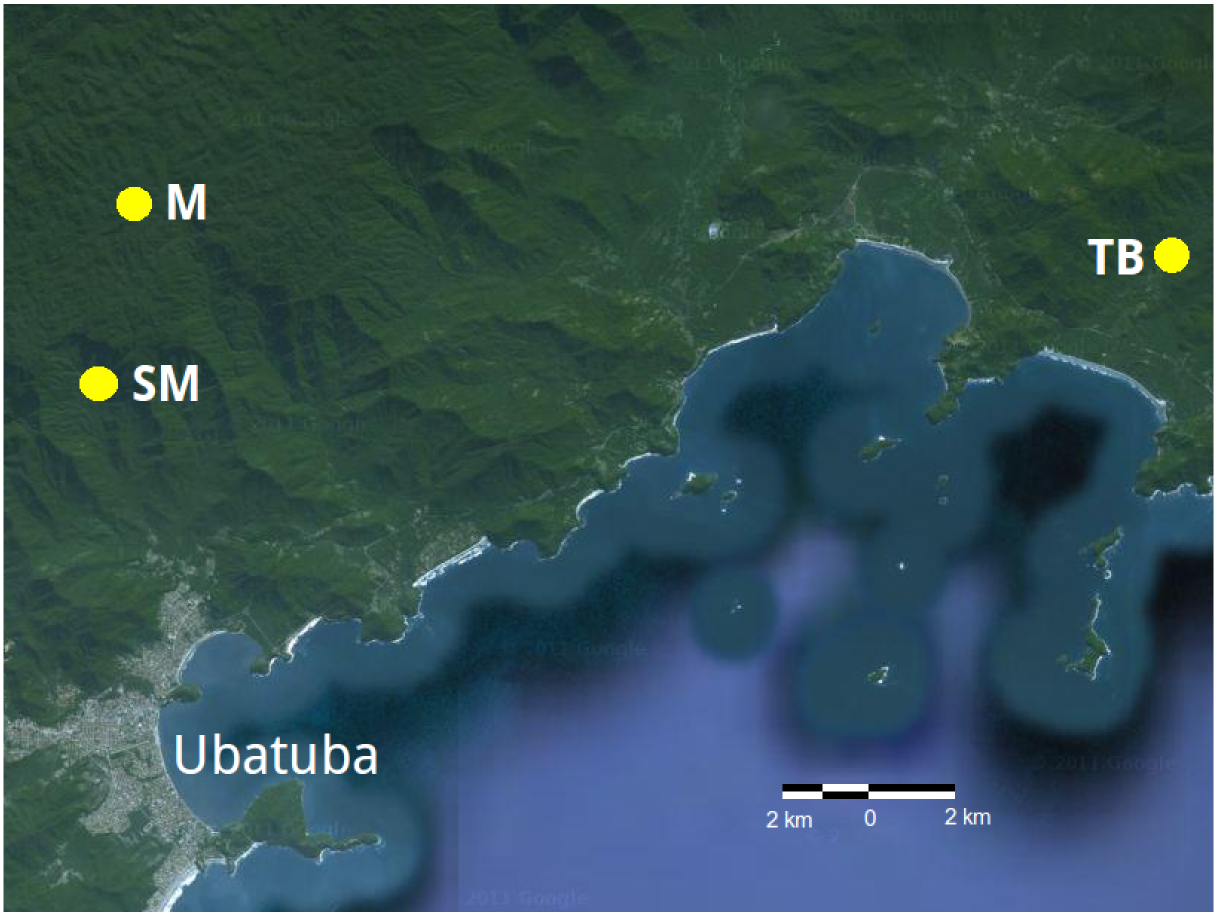

Figura 1: Localização das parcelas estudadas na Floresta Ombrófila densa de Terras Baixas (TB, 70 m de altitude), Submontana (SM, 370 m) e Montana (M, 1070 m), no litoral norte do Estado de São Paulo. A cidade de Ubatuba localiza-se a aproximadamente 23°26' S, 45°04' W.

tendência de aumento dos teores de nitrogênio total e matéria orgânica com o aumento da altitude, possivelmente decorrente da combinação de um aumento na produção de serrapilheira com a altitude (Martins 2010) aliada à diminuição das taxas de decomposição (Sousa Neto 2008). Além disso, a biomassa total dos estandes aumenta com a altitude, apesar da grande variabilidade encontrada dentro de cada formação (Alves et al. 2010).

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Capítulo 1

Phylogenetic community structure of understory woody plants in relation to microhabitat along an elevation gradient of tropical Atlantic rain forest in SE Brazil

Phylogenetic community structure of understory woody plants in relation to microhabitat along an elevation gradient of tropical Atlantic rain forest in SE Brazil

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Abstract

Two niche-based processes are considered important in the structuring of ecological communities: competitive exclusion, which prevents the coexistence of similar species, and habitat filtering, which promotes the coexistence of similar species. We aimed to test the assumption that functional traits are conserved along the phylogeny, and to examine the correlations between phylogenetic community structure and small-scale environmental variables. We studied communities of understory shrubs and tree juveniles in three sites with differing elevations within a tropical rain forest, surveying a total of 47 quadrats with 100-m^2 each. Data on wood density, specific leaf area, leaf area, and specific maximum height, were combined with a phylogenetic tree based on APG III to assess the phylogenetic signal of these traits. Net relatedness index (NRI) and nearest taxon index (NTI) were used as indexes of community phylogenetic structure. We found that functional traits were generally conserved along the phylogeny, but that there is no significant phylogenetic community structure within each site, neither significant correlations between NRI or NTI and micro-environmental variables. Thus, although evolutionary distance between species seemed to be an appropriate proxy for niche requirements, the understory communities of the Atlantic rain forest displayed no evidence for an habitat filtering occurring at local level.

Keywords: Micro-habitat, nearest taxon index, net relatedness index, phylogenetic signal, tropical rain forest, understory.

Introduction

One of the goals of ecology is to identify the mechanisms of plant community assembly and species coexistence (Tilman and Pacala 1993, Hubbell 2001, Webb *et al.* 2002). Two different niche-based processes are generally considered important in community assembly. The first is competitive exclusion, which should prevent the coexistence of species whose niches overlap by a great degree (Tilman 1982, Coomes and Grubb 2000); the second is environmental filtering, which leads to an increase in the niche overlap of coexisting species (Weiher and Keddy 1995, Chase 2003). As niches tend to be conserved within evolutionary lineages (Brooks and McLennan 1991, Harvey and Pagel 1991, Blomberg *et al.* 2003), the analysis of the phylogenetic structure of a community should helps us to identify the processes that organize the community. Competitive exclusion, as well as negative indirect interactions between relatives (*e.g.* herbivores, pathogens), will tend to give rise to a pattern of phylogenetic overdispersion, while environmental filtering will restrict coexistence to species that share some ecological traits, leading to a pattern of phylogenetic clustering (Webb *et al*. 2002).

These processes are not mutually exclusive, and may occur simultaneously and with differing intensities, depending on several factors, including spatial scale (Cavender-Bares *et al*. 2006, Swenson *et al*. 2006), organism size scale (Swenson *et al.* 2007), and environmental factors (Kembel and Hubbell 2006). In general, habitats where resources are abundant should have a predominance of competitive interactions, while stressful or resource-depleted habitats should have a stronger filter on species (Grime 1977, Goldberg and Novoplansky 1997). More specifically, in the case of plants in the understory of tropical forests, Wright (2002) argues that their density is so low that they generally lack the opportunity to engage in competition among themselves, even though they are being suppressed by canopy trees, concluding that "*[e]very species able to tolerate the understory environment could* *potentially coexist*". If this is the case, and if species' life-history and niche requirements are phylogenetically conserved, then a set of coexisting species would be increasingly phylogenetically clustered with decreasing resource availability.

The Brazilian Atlantic rain forest is mainly a coastal forest, occurring from northeastern to southern Brazil. Only *ca.* 8% of its original area remains (Morellato and Haddad 2000), and most of it in small and disconnected fragments under great anthropic pressure, being considered a biodiversity hotspot (Myers et al. 2000). Besides occupying a vast latitudinal range, the Atlantic rain forest also occupies an altitudinal range that, even while not being particularly extensive (sea level to *ca.* 2000 m a.s.l.), is remarkable by its steepness, especially at the seaward face of the Serra do Mar mountain range. A better understanding of the phylogenetic structure of the Atlantic forest may be helpful to better understand the effects of climate change on its dynamics, and to plan restoration efforts.

Thus, the objectives of the present work are: 1) to test the assumption that functional traits, as proxies of niche and life-history, are conserved along the phylogeny; 2) to describe the phylogenetic structure of the understory tree saplings and shrubs at three sites of Brazilian Atlantic rain forest along an elevation range; and 3) to examine the correlations between small-scale environmental variables and phylogenetic community structure within each site. Regarding the environment-phylogenetic structure question, we hypothesize that communities located at increasingly resource-poor or stressful micro-habitats (deeper shade, lower nutrient availability, lower water availability) within each site will be increasingly phylogenetically clustered.

Material and Methods

Field site and sampling

We assessed the effect of environmental variables on phylogenetic community structure of understory woody vegetation at three sites along an elevation gradient of a tropical rain forest. Field work was carried out at the Serra do Mar State Park (PESM), São Paulo State, Brazil (23º17’-23º34’S, 45º02’-

45º11'W; 0-1300 m a.s.l.), where a network of fourteen 1-ha permanent plots have been previously established to study the structure and dynamics of the Brazilian Atlantic rain forest (see Alves *et al.* 2010 for more details on sampling design and site characterization). The Park comprises mainly of typical tropical Rain Forest, with a continuous canopy *ca*. 20 m high and a high diversity of tree species (100-200 spp. ha^{-1}), with a general predominance of Myrtaceae, Fabaceae, Rubiaceae, and Lauraceae species (Rizzini 1997, Tabarelli and Mantovani 1999,). Regional climate ranges from humid tropical to subtropical with hot summers (Af and Cfa types in Köppen, respectively), with mean annual temperatures around 18-22 ºC, annual precipitation ranging from 2000 to 2500 mm, and typically only one month per year with precipitation lower than 60 mm (Sentelhas *et al.* 1999). Ocean winds cause frequent cloud cover and fog, especially at higher elevations (Silva-Dias 1995). Soil moisture content, total nitrogen and carbon, and ammonium and nitrate soil concentrations increase with elevation (Susian Martins *pers. comm.*, Sousa Neto 2008), but even at the highest elevation the soils are very poor.

Three sites were chosen, based on the availability of plots already established at the PESM and in order to cover a large portion of the elevation gradient: one plot at a lowland forest site (LL; mean elevation 70 m a.s.l.), one at lower montane forest site (*LM*; 370 m a.s.l.), and one at montane forest site (*M*; 1070 m a.s.l.). At each site, sampling was performed at sixteen 100 m^2 plots at each site. The plots were arranged in 4 x 4 grids, with each plot 30 m apart from the next. Every dicotyledonous, self-supporting woody individuals with height between one and two meters was tagged and identified, up to species level whenever possible, following the APG III classification (Angiosperm Phylogeny Group 2009). Multiple stem were considered as single individuals, and stems resprouted from large trees were excluded. Relative frequency of each species at each site was calculated as the number of plots in which it was present, divided by the total number of plots sampled. One plot at the LL site had only two species and was excluded from analyses.

Leaf samples were taken from every individual, and stem samples were taken from *ca*. 95% of all individuals (we avoided sampling both very small, unbranched, tree juveniles, and individuals being monitored by other researchers) . We sampled only healthy, fully expanded leaves, numbering from 2 to 20 depending on leaf size. Leaves were digitalized on a flatbed scanner (at 150 dpi) then dried at 55 ºC for at least 72 hours. Leaf area was estimated by analysis of scanned leaf images by *ImageJ* 1.38 (Abramoff et al. 2004), and specific leaf area (SLA) was calculated as leaf sample dry mass divided by leaf sample area. Stem samples for estimation of wood density (WD) were taken either from lateral branches or, when the individual was unbranched, from the main stem. After removing pith, phloem and bark, fresh volume of stems were measured by water displacement, then dry mass was obtained after samples were oven-dried at 55 ºC for at least one week. WD was then calculated as sample dry mass divided by sample fresh volume. Given the high variability of stem morphology, it was impossible to standardize stem width of samples. Nevertheless, we found no significant correlation between WD and fresh stem width (*data not shown*). Maximum height (H_{MAX}) of each species was determined by consulting local flora monographs (Wanderley *et al.* 2003 and subsequent volumes), the database of the PESM plot network (C.A. Joly, *unpublished results*), and *in situ* observations.

Phylogenetic tree and phylogenetic community structure

We built a phylogenetic tree including all species sampled in the three sites, using Phylomatic, a phylogenetic database and toolkit for the assembly of phylogenetic trees (Webb and Donoghue 2005) . We used Phylomatic reference tree R20091110, based on APG III (2009), and manually resolved relationships between genera inside a few families for which such information was available (Fabaceae: Doyle *et al.* 2000; Melastomataceae: Michelangeli *et al.* 2004; Myrtaceae: Lucas *et al.* 2007; Rubiaceae: Bremer and Mannen 2000, Robbrecth and Mannen 2006). Branch lengths were calculated by setting fixed the estimated minimum ages of some nodes, according to Wilkström et al. (2001), then evenly spacing the remaining nodes in-between. This was made using the BLADJ module of Phylocom 4.1 (Webb et al. 2008a).

We measured the phylogenetic signal (*K*) of functional traits and species relative frequency, separately for each site. A significant phylogenetic signal indicates that the trait is conserved tree-wide, implying that closely related species are more similar to each other than expected by chance (Blomberg et al. 2003). For each site the phylogenetic tree described above was pruned to include only the species present at the site, then the variance of phylogenetic independent contrasts (PIC s^2) was calculated for each trait. To determine if the phylogenetic signal is higher than expected by chance, a distribution of expected PIC s^2 in the absence of phylogenetic signal was obtained by randomly swapping traits values among the tips of the phylogenetic tree. This procedure was repeated 999 times, and if the observed PIC s^2 was lower than 95% of these values of expected PIC s^2, then the phylogenetic signal was considered stronger than expected by chance (Blomberg et al. 2003).

To assess community phylogenetic structure, we first computed two different phylogenetic distances among the species at each plot, mean phylogenetic distance (MPD) and mean nearest neighbor distance (MNND); each of these variables captures a different aspect of species phylogenetic relatedness. MPD is the mean phylogenetic distance among all pairs of species in a given plot, and MNND is the mean phylogenetic distance of each species to its nearest relative, both expressed in millions of years (Webb 2000, Webb *et al.* 2002). To test whether species within a given plot were phylogenetically clustered or overdispersed, we compared observed values of MPD and MNND to expected values under a null model in which species frequency and plot richness were kept constant (using the independent swap algorithm described in Gotelli 2000). This null model keeps adequate Type I error rates (Hardy 2008). We generated 999 null plots and computed means and standard deviations for MPD and MNND, then used these to generate measures of standardized effect size (Gotelli and Rohde 2002). Net relatedness index (NRI) is defined as the negative of the difference between observed and mean expected MPD, divided by the standard deviation of MPD of a given plot (Webb 2000). Positive NRI scores indicate that species in a community are more closely related than expected by chance, due to tree-wide phylogenetically clustering of co-ocurring species, while negative scores indicate that species are less closely related than expected by chance. Nearest taxon index (NTI) is defined as the negative of the difference between observed and mean expected MNND, divided by the standard deviation of MND of a given plot (Webb 2000). Positive NTI indicates that species tend to co-occur more than expected by chance with its nearest relatives, while negative NTI indicates that species tend to co-occur less than expected by chance with its nearest relatives. Thus, NTI shows phylogenetic clustering or repulsion at terminal branches of a phylogeny (Webb et al. 2002). NRI and NTI were then compared between sites of differing elevations with a one-way ANOVA, and each site was separately compared to $\mu=0$ with a *t* test. These analyses were performed with the package Picante 1.2 (Kembel *et al.* 2010) in R 2.12 (R Development Core Team 2006).

Correlations with environmental variables

One sample of the upper 30 cm of soil were taken at each plot and analyzed for total N with a Carlo-Erba elemental analyzer (CE Elantech, NJ, USA). Canopy openness (*CO*), a proxy for light availability at the understory, was estimated by analyzing hemispherical photographs taken at the center of each plot (at 1.3 m high), aimed at the zenith, with software Gap Light Analyzer (Frazer *et al.* 1999). Microtopography was represented by two variables: plot maximum slope and terrain convexity index (*CI*). Plot maximum slope was considered as the slope of an imaginary line connecting the lowest and highest vertices of a given plot, measured with a high-precision electronic theodolite. *CI* was defined as the mean altitude of the focal plot vertices in relation to the mean altitude of the external vertices of the adjacent plots (thus, the 12 vertices of a 30 x 30 m quadrat centered at the focal plot; Yamakura *et al.* 1995). Positive *CI* indicates a convex plot, and negative *CI* indicates a concave plot. Soil water retention is negatively correlated with *CI* (Pachepsky *et al.* 2001). We made correlations between these environmental variables and phylogenetic community structure indexes, NRI and NTI, separately for each site. We applied Bonferroni correction on the statistical significance of p-values.

According to our hypothesis, we expected NRI/NTI to present positive correlations with *CI* and terrain slope, and negative correlations with *CO* ans soil N.

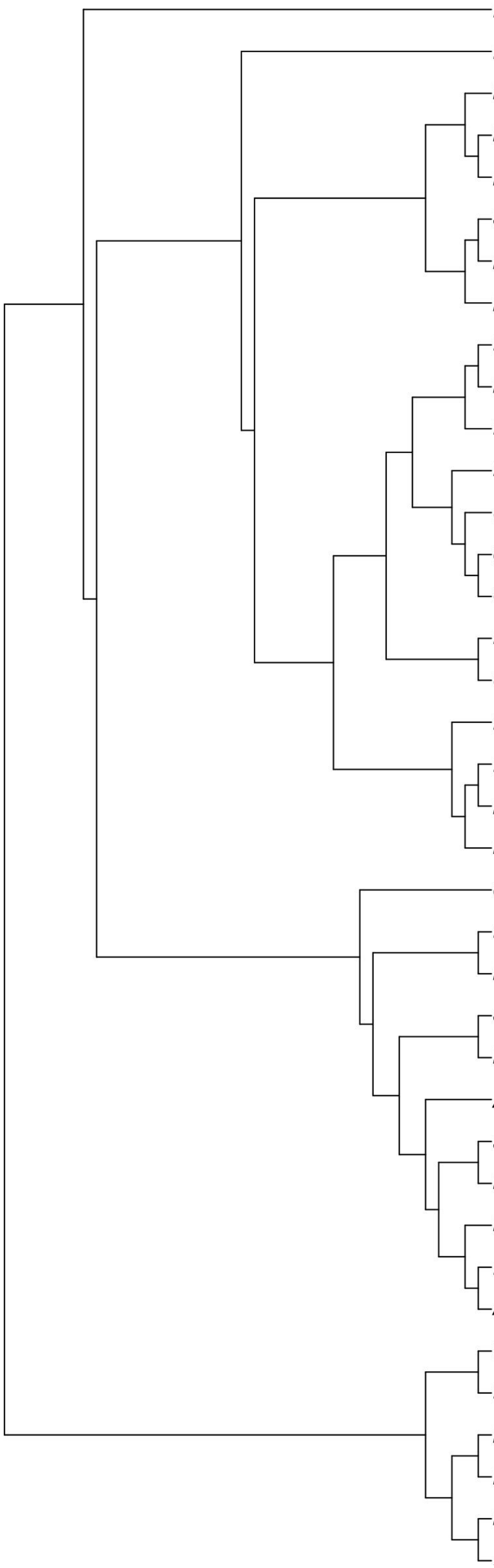
Results

Taking the three sites together, we sampled a total of 199 species, distributed into 87 genera and 38 families. The richest families were Myrtaceae (47 spp.), Rubiaceae (24 spp.), Lauraceae (13 spp.), Melastomataceae (12 spp.) and Fabaceae (10 spp.; fig. 1). The LM site was the richest, with 99 species, while the M site had 83, and the LL had 68 species. Individual plots ranged from 5 to 18 species at the LL site, from 8 to 26 species at the LM site, and from 6 to 23 species at the M site.

H_{MAX} and WD displayed a stronger phylogenetic signal than expected by chance at all sites, while SLA presented a significant phylogenetic signal only at LM and M sites (table 1), indicating tree-wide trait conservatism. Leaf area and species relative frequency displayed no phylogenetic signal (table 1).

Median NRI and NTI were close to zero in all three sites (fig. 2), and mean NRI and NTI were statistically indistinguishable from zero (*t* test, $p > 0.05$ in every case), indicating that there is no significant overall phylogenetic clustering or overdispersion, either tree-wide or near the tips of the phylogeny. When individual plots are compared to the null models, only 1 out of 15 plots at the LL site and 1 out of 16 plots at the M site had significantly lower than expected NRI and, on the other hand, only 1 out of 16 plots at the LM site had a significantly higher than expected NTI while 3 out of 16 plots at the M site had a lower than expected NTI.

Correlations between environmental variables and indexes of community phylogenetic structure were weak to moderate, with correlation coefficients ranging from -0.56 to 0.29, and none of them statistically significant after Bonferroni correction of p-values (table 2).



	LL	LM	M	Total
Prote	--	1	1	1
Picramni	--	1	--	1
Myrt	14	23	23	47
Memecyl	--	1	1	1
Melastomat	2	6	6	12
Sapind	--	3	1	3
Meli	2	1	1	3
Malv	1	2	--	2
Phyllant	1	--	--	1
Malpighi	--	1	--	1
Euphorbi	2	--	3	4
Erythroxyl	1	2	--	2
Clusi	1	1	1	1
Ochn	3	1	1	3
Chrysobalan	--	3	1	4
Elaeocarp	1	1	--	1
Celastr	2	--	1	3
Fab	4	4	3	10
Ros	--	--	1	1
Mor	2	2	--	3
Begoni	1	1	1	2
Olac	1	1	--	2
Polygon	--	--	1	1
Nyctagin	1	1	2	2
Sapot	2	7	3	7
Myrsin	--	2	2	3
Arali	1	--	1	1
Solan	--	--	1	1
Boragin	--	1	1	2
Bignoni	1	1	--	2
Rubi	13	15	10	24
Apocyn	1	2	--	2
Winter	--	--	1	1
Piper	2	4	3	9
Monimi	2	3	7	9
Laur	3	5	5	13
Myristic	2	2	--	2
Annon	1	1	1	2

Figure 1: Simplified phylogenetic tree (collapsed to family-level, branch lengths out of scale) of understory tree juveniles and shrubs at three Rain Forest sites along an elevation gradient (LL, lowland, 70 m; LM, lower montane, 370 m; M, montane, 1070 m) at the Serra do Mar State Park, São Paulo state, Brazil. Under each site label is listed the number of species of each family found at each site, and the total number of species occurring at all sites taken together.

Table 1: Phylogenetic signal, K, of functional traits (maximum height, wood density, SLA and individual leaf area) and relative frequency of occurrence of understory tree juveniles and shrubs at three Rain Forest sites along an elevation gradient (LL, lowland, 70 m; LM, lower montane, 370 m; M, montane, 1070 m) at the Serra do Mar State Park, São Paulo state, Brazil. Values in bold indicate stronger phylogenetic signal than expected by random tip swap. Also shown are the variances of expected (PIC s^2_{EXP}) and observed (PIC s^2_{OBS}) phylogenetic independent contrasts, and p-values.

Site	**Trait**	**K**	**PIC s^2_{OBS}**	**PIC s^2_{EXP}**	**p**
LL	H_{MAX}	0.508	0.579	1.120	**<0.001**
	WD	0.696	3.17E−04	6.38E−04	**<0.001**
	SLA	0.368	132	178	0.112
	Leaf area	0.303	1.41E−02	1.67E−02	0.146
	Freq	0.368	0.124	0.176	0.078
LM	H_{MAX}	0.391	0.733	1.250	**<0.001**
	WD	0.646	3.24E−04	8.28E−04	**<0.001**
	SLA	0.449	56	111	**<0.001**
	Leaf area	0.244	2.70E−02	2.85E−02	0.375
	Freq	0.180	0.226	0.176	0.908
M	H_{MAX}	0.486	0.583	1.110	**<0.001**
	WD	0.599	3.01E−04	7.22E−04	**<0.001**
	SLA	0.439	54	106	**<0.001**
	Leaf area	0.223	2.42E−02	2.43E−02	0.508
	Freq	0.17	0.193	0.141	0.899

Figure 2: Indexes of community phylogenetic structure, Net Relatedness Index (NRI; panel a) and Nearest Taxon Index (NTI, panel b), at three Rain Forest sites along an elevation gradient (LL, lowland, 70 m; LM, lower montane, 370 m; M, montane, 1070 m) at the Serra do Mar State Park, São Paulo state, Brazil. Positive values indicate phylogenetic overdispersion, while negative values indicate phylogenetic clustering. Neither index indicated significant phylogenetic structure in any of the sites, and the sites did not differed significantly from each other. Box plots showing maximum and minimum values (whiskers), interquartile range (box limits), and median.

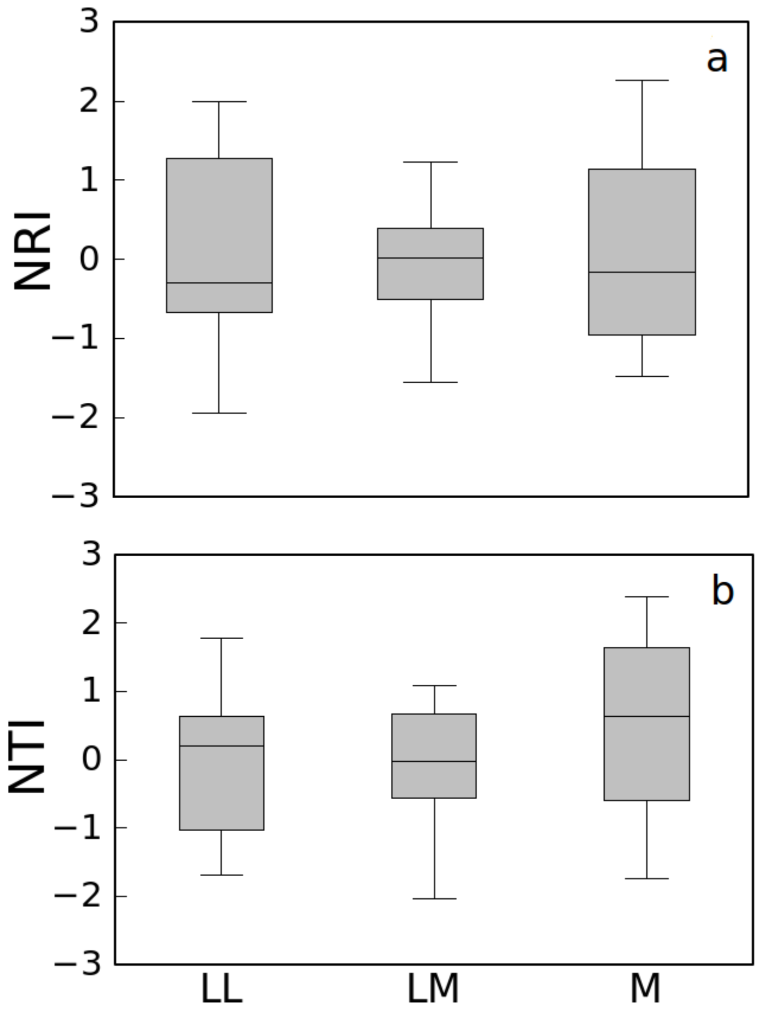


Table 2: Correlation coefficients and p-values of the relationship between environmental variables (CO, canopy openness; total soil nitrogen; CI, topographic convexity index; and mean terrain slope) and phylogenetic community structure indexes (NRI, net relatedness index, and NRI, nearest taxon index) of understory tree juveniles and shrubs at three Rain Forest sites along an elevation gradient (LL, lowland, 70 m; LM, lower montane, 370 m; M, montane, 1070 m) at the Serra do Mar State Park, São Paulo state, Brazil. No correlations were significant at the Bonferroni-corrected p-value of 0.017.

		NRI		**NTI**	
Variable	**Site**	*R*	*p*	*R*	*p*
CO	LL	0.10	0.73	0.21	0.45
	LM	−0.16	0.56	−0.08	0.77
	M	−0.01	0.98	−0.01	0.98
Soil N	LL	0.07	0.80	0.13	0.64
	LM	0.29	0.28	−0.56	0.03
	M	−0.11	0.67	−0.35	0.18
CI	LL	−0.33	0.23	−0.11	0.69
	LM	−0.26	0.33	0.14	0.61
	M	0.01	0.96	0.09	0.75
Slope	LL	−0.37	0.17	−0.19	0.50
	LM	0.10	0.70	−0.44	0.08
	M	0.10	0.72	−0.01	0.96

Discussion

Wood density is a trait indicative of a species' place along the succession continuum (ter Steege and Hammond 2001), as well as related to individual survival in tropical forests (Kraft et al. 2010); H_{MAX} is related to the species' light capture strategy (Falster and Westoby 2005, Poorter et al. 2005), while SLA is linked to growth rates and leaf carbon economy (Reich et al. 1992, Reich *et al.* 2003, Wright *et al.* 2004). Taken together, these traits capture an important part of the life-history strategy of forest plants, and were found to be phylogenetically conserved across the phylogeny. In principle, this means that the degree of phylogenetic relatedness between co-occurring species may be used to infer niche-based community assembly processes (Webb 2000, Webb et al. 2002). On the other hand, species frequency presented no phylogenetic signal, which helps to keep adequate type I error rates when testing phylogenetic structure hypothesis using null models (Hardy 2008, Kembel 2009).

Phylogenetic community structure

Phylogenetic clustering is expected when niches are conserved in the evolution of lineages and environmental filtering is the dominant ecological process structuring a community (Weiher and Keddy 1995, Webb 2000). We have, however, found no overall signal of phylogenetic clustering or overdispersion, either with NRI or NTI. This may have occurred for several reasons, including 1) environmental filtering, which would lead to phylogenetic clustering, may be counterbalanced by other factors, such as sampling scale (Cavender-Bares et al. 2006, Swenson and Enquist 2009); and 2) other, unmeasured traits may play an antagonistic role in the community assembly process (Swenson and Enquist 2009).

First, the detection of habitat filtering signal may be influenced by the spatial scale of sampling. The phylogenetic structure of tree communities in a tropical forest in Panama, assessed at spatial scales from 10 x 10 m to 100 x 100 m, were close to random, with a slight tendency of greater clustering at the smaller spatial scale (Kembel and Hubbell 2006). Swenson *et al.* (2007) have found significant phylogenetic overdispersion at 5 x 5 m spatial scale in three out of five sites of tropical forest, while larger spatial scales (10 x 10 m and 15 x 15 m) were close to random in most sites. Moreover, Swenson *et al.* (2007) also found an increase in phylogenetic overdispersion with plant stem size. The rationale behind these finds is that, when sampling large organisms over small spatial scales, competition for resources will be the most important factor in community assembly, leading to phylogenetic overdispersion (Weiher and Keddy 1995, Swenson et al. 2007). At the same time, when small organisms are sampled over large spatial scales, a higher environmental variation between sampling units would lead to habitat filtering, which in turn would lead to phylogenetic clustering. It remains a possibility, then, that the quadrats sampled in the present study were too large in relation to the plant size sampled, preventing us from detecting a phylogenetic signal. On the other hand, there was also a large internal heterogeneity in terms of light conditions and microtopography in at least some of the quadrats (P.O. Cavalin, *pers. obs.*); this could potentially lead to an inclusion of several microhabitats within quadrats. If these “co-occurring” microhabitats were subjecting plants to disparate filtering effects, then analyzing them as if they pertained to a single, homogeneous quadrat would probably prevent us from detecting a phylogenetic clustering.

Secondly, other traits may be important for between-species niches differentiation. Swenson and Enquist (2009), studying phylogenetic and functional community assembly in a tropical rain forest in Costa Rica, have found that maximum height and seed mass are overdispersed, while LA, SLA and WD are clustered, suggesting that these antagonistic patterns led to the random phylogenetic dispersion they have found at a previous work (Swenson and Enquist 2007). In the present study, LA displayed no phylogenetic signal, and may thus contribute to the random phylogenetic structure we have found. Poorter and Rozendaal (2008) argue that large leaves enable a plant to forage efficiently for light and to put a greater investment in vertical growth, and may thus be important in the forest understory. Other traits, especially those related to defense against herbivory (Lucas et al. 2000, Eichhorn et al. 2007) crown architecture (Poorter and Werger 1999, Sterck et al. 2003, Sterck et al. 2006), and physiology (Baltzer and Thomas 2007) may be important to promote species persistence and coexistence in the understory of the Brazilian Atlantic rain forest.

Microhabitats and phylogenetic community structure

We have found no clear correlations between quadrat environmental variables and degree of phylogenetic clustering or overdispersion. Kembel and Hubbell (2006) have found phylogenetic clustered tree communities occurring in plateaus and young forests at the Barro Colorado Island (BCI) permanent plot, suggesting that a relatively stressful dry-season soil moisture could filter conserved functional traits. Even though the studied Atlantic rain forest sites are located in a very humid region, with generally one dry month per year, two-week long dry spells are not uncommon (P.O. Cavalin, *pers. obs.*), and even longer dry spells may occur every few years; such rare and extreme events may have a great impact on the survival of seedlings and saplings (Gutschick and BassiriRad 2003, Bunker and Carson 2005) and, hence, on phylogenetic community structure.

In conclusion, we have found no evidence of community phylogenetic structure in the understory of the Atlantic Rain Forest, nor differences associated with an elevation gradient. Nevertheless, it is possible that the tree community becomes more structured as the growing trees increasingly interact with each other as they reach the canopy. Studies of community structure based on functional traits, and along the ontogenetic trajectories of individuals, could cast some light on the deterministic factors influencing the assembly of Rain Forest tree communities.

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Capítulo 2

Trait based community structure of understory tree saplings and shrubs along an elevation gradient on a tropical rain forest, SE Brazil

Trait based community structure of understory tree saplings and shrubs along an elevation gradient on a tropical rain forest, SE Brazil

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Abstract

There are two categories of theories of species coexistence: those that rely on species ecological strategies and niches to explain coexistence, and those that disregard such informations and instead invoke dispersal and stochastic demographic processes. Within the niche theories framework, competition and habitat filtering are two processes leading to recognizable patterns in functional traits distribution of co-occurring species. We searched for evidence of trait-based habitat filtering on understory woody plants at three sites along an altitudinal gradient (70 m, 370 m, 1070 m) at the tropical rain forest in SE Brazil. We measured wood density, specific leaf area, leaf area and maximum height of 1091 individuals belonging to 199 species in 47 quadrats with 100 m^2 each, and compared observed trait-related metrics, such as average values and ranges, to expected values under different null models, using either species means or individual values. Functional traits of frequent species at each altitude were similar, except for smaller leaves at the montane site (1070 m). Comparisons to null models based on species means showed no evidence of habitat filtering; on the other hand, co-occuring individuals displayed significantly lower ranges than expected by chance for most functional traits. Species tended to occur spatially aggregated according to standardized Morisita index, but partial Mantel tests showed significant relations between quadrat-level mean traits and micro-habitat variables. Specific mean trait values were only correlated with topographic micro-habitat variables when frequent species were considered. We conclude that the dynamics of locally frequent and rare species may be determined by different processes operating at different spatial scales, and suggest that within-species variation in functional traits may be an important component in the community assembly process.

Keywords: Altitudinal gradient, community assembly, micro-habitat, specific leaf area, tropical rain forest, understory, wood density, woody plants.

Introduction

One of the goals of ecology is to explain patterns of species co-occurrence, especially in highly diverse sites. There are basically two broad categories of theories of species coexistence: those that rely on species ecological strategies and niches to explain coexistence, and those that disregard such informations and instead invoke dispersal and stochastic demographic processes. Niche theories had an important role on the historical development of ecological research (Chase and Leibold 2003). Neutral theory was developed to explain woody species coexistence in diverse tropical forests (Hubbell 2001), a traditionally problematic situation from the niche theory perspective. Neutral theory follows the basic assumption that species are functionally equivalent, being demographically identical, on a per capita basis, in terms of birth, death and dispersal (Hubbell 2005).

Under the framework of niche theories, two mechanisms are thought to influence the community assembly process. First, competition tends to prevent coexistence of species too similar to each other (limiting similarity; Chase and Leibold 2003, Silvertown 2004). Second, abiotic environment may impose barriers to establishment or survival, leading to a pattern of coexistence of similar species (environmental filtering; Weiher and Keddy 1999, Cornwell et al. 2006). In recent years, several studies have tested whether tropical tree forest communities are structured, either from a phylogenetic (Webb 2000, Kembel and Hubbell 2006, Swenson et al. 2007) or from a trait-based perspectives (Kraft et al. 2008, Kraft and Ackerly 2010, Swenson and Enquist 2009). From a trait-based perspective, environmental filtering would result in coexisting species having trait values more similar among them than expected by chance. Additionally, if environmental filtering occur along an environmental gradient, different groups of species will tend to occupy different points along the gradient, with a resulting shift of community-averaged trait value (Ackerly 2003).

Most studies on trait-based community assembly are made using species mean trait values along with presence/absence information of each species at each sampling unit (Weiher and Keddy 1995, Kraft et al. 2008, Swenson and Enquist 2009) or, in a few cases, mean trait values of each species at each sampling unit (Cornwell et al. 2006, Ackerly and Cornwell 2007, Cornwell and Ackerly 2009). Nevertheless, intraspecific variability – both phenotypic and genetic differences among individuals – may be a significant part of the total variability found at a given site (Baraloto 2010), and thus its contemplation should give additional insights on community assembly.

In the present study, we aim to: (1) assess the trait-based community structure in the understory of tropical rain forest along an elevation gradient in the Atlantic coast of southeastern Brazil. We expect to find evidence for environmental filtering, that is, to find coexisting species (or individuals) more similar among themselves than expected by chance; (2) examine the relationships between species-based and community-based functional traits and environmental variables, comparing frequent and rare species.

Material and Methods

Field site and sampling

Field work was carried out at the Serra do Mar State Park (PESM), São Paulo State, Brazil (23º17’-23º34’S, 45º02’-45º11’W; 0-1300 m a.s.l.), where a network of 13 1-ha permanent plots have been previously established to study the structure and dynamics of the Brazilian Atlantic rain forest (see Alves *et al.* 2010 for more details on sampling design and site characterization). The Park comprises mainly of typical tropical Rain Forest, with a continuous canopy *ca*. 20 m high and a high diversity of tree species (100-200 spp. ha^{-1}), with a general predominance of Myrtaceae, Fabaceae, Rubiaceae, and Lauraceae species (Rizzini 1997, Tabarelli and Mantovani 1999). Regional climate ranges from humid tropical to subtropical with hot summers (Af and Cfa types in Köppen, respectively), with mean annual temperatures around 18-22 °C, annual precipitation ranging from 2000 to 2500 mm, and typically only one month per year with precipitation lower than 60 mm (Sentelhas *et al.* 1999). Ocean winds cause frequent cloud cover and fog, especially at higher elevations (Silva-Dias 1995). Soil moisture content, total nitrogen and carbon, and ammonium and nitrate soil concentrations increase with elevation (Susian Martins *pers. comm.*, Sousa Neto 2008), but even at the highest elevation the soils are very poor.

Three sites were chosen, based on the availability of plots already established at the PESM and in order to cover a large portion of the elevation gradient: one plot at a lowland forest site (LL; mean elevation 70 m a.s.l.), one at lower montane forest site (LM; 370 m a.s.l.), and one at montane forest site (M; 1070 m a.s.l.). At each site, sampling was performed at 16 100 m^2 plots at each site. The plots were arranged in 4 x 4 grids, with each plot 30 m apart from the next. Every dicotyledonous, self-supporting woody individuals with height between one and two meters was tagged and identified, up to species level whenever possible, following the APG III classification (Angiosperm Phylogeny Group 2009). Multiple stem were considered as single individuals, and stems obviously resprouted from large trees were excluded. Relative frequency of each species at each site was calculated as the number of plots in which it was present, divided by the total number of plots sampled. One plot at the LL site had only two species and was excluded from analyses.

Leaf samples were taken from every individual, and stem samples were taken from *ca*. 95% of all individuals (we avoided sampling both very small tree juveniles and individuals being monitored by other researchers). We sampled only healthy, fully expanded leaves, numbering from 2 to 20 per individual, depending on leaf size. Leaves were digitalized on a flatbed scanner (at 150 dpi) then dried at 55 ºC for at least 72 hours. Leaf area was estimated by analysis of scanned leaf images by *ImageJ* 1.38 (Abramoff *et al.* 2004), and specific leaf area (SLA) was calculated as leaf sample dry mass divided by leaf sample area. Stem samples for estimation of wood density (WD) were taken either from lateral branches or, when the individual was unbranched, from the main stem. After removing pith, phloem and bark, fresh volume of stems were measured by water displacement, then dry mass was obtained after samples were oven-dried at 55 ºC for at least one week. WD was then calculated as sample dry mass divided by sample fresh volume. Given the high variability of stem morphology between species, it was impossible to standardize stem width of samples. Nevertheless, we found no significant correlation between WD and fresh stem width (*data not shown*). Maximum height (H_{MAX}) of each species was determined by consulting local flora monographs (Wanderley *et al.* 2003 and subsequent volumes), the database of the plot network at PESM (C.A. Joly, *unpublished results*), and *in situ* observations.

One sample of the upper 30 cm of soil were taken at each plot and analyzed for total N with a Carlo-Erba elemental analyzer (CE Elantech, NJ, USA). Canopy openness (*CO*), a proxy for light availability at the understory, was estimated by analyzing hemispherical photographs taken at the center of each plot (at 1.3 m high), aimed at the zenith, with software Gap Light Analyzer (Frazer *et al.* 1999). Microtopography was represented by two variables: plot maximum slope and terrain convexity index (*CI*). Plot maximum slope was considered as the slope of an imaginary line connecting the lowest and highest vertices of a given plot, measured with a high-precision electronic theodolite. *CI* was defined as the mean altitude of the focal plot vertices in relation to the mean altitude of the external vertices of the adjacent plots (thus, the 12 vertices of a 30 x 30 m quadrat centered at the focal plot; Yakamura *et al.* 1995). Positive *CI* indicates a convex plot, and negative *CI* indicates a concave plot. Soil water retention is negatively correlated with *CI* (Pachepsky *et al.* 2001).

Data analysis

To characterize general differences between sites, we performed an ANOVA, followed by HSD Tukey post-hoc test, to compare functional traits between sites, considering species as our sampling units. Relatively rare species (less than four individuals) were excluded from the analysis.

For each trait in each plot we computed trait mean, variance, kurtosis, range, and the standard deviation of neighbor distance (SDND). Range and variance are sensitive to habitat filtering effects (Cornwell *et al.* 2006, Kraft *et al.* 2008), while SDND and kurtosis are thought to be influenced by limiting similarity (Ricklefs & Travis 1980, Kraft *et al.* 2008, Cornwell and Ackerly 2009). Trait range was computed as the difference between minimum and maximum values found at a given plot, whether species or individuals were being considered. Species (or individuals) within a given plot were put in order according to a given trait, then SDND was computed as the standard deviation of the distances between every pair of consecutive values. Thus, SDND=0 means an even spacing between species or individuals. As SDND is correlated with range, we divided SDND by range to obtain SDND*r* (Ingram and Shurin 2009, Kraft and Ackerly 2010). To test whether these metrics indicate any degree of non-random community structuring, observed values of trait metrics were compared to null models.

First, we used the RA3 algorithm (Gotelli and Graves 1996), in which plot richness and species frequencies are held fixed, and species are drawn without replacement, to build null communities. This procedure was repeated 999 times to generate expected distributions of each metric explained above, separately for each site. Each combination of trait/metric of the observed plots was then compared to the mean expected values of the null communities with paired two-tailed Wilcoxon tests, for each site separately and pooling plots from all sites. Secondly, we included intra-specific variation into the analysis, by building a null model in which we simply shuffled individuals between plots. While the number of individuals at each plot is kept constant, this approach makes it impossible to keep plot species richness (S) constant; in this case, S was also compared between observed and expected communities. In this case, observed and expected plots were paired by number of individuals; to compare observed and expected values also as paired by S, we derived site-specific equations, with the form *y*=a+b*ln(S+c), giving the relationship between expected S and trait metrics (all equations described very accurately the relationship, with R>0.99); then extracted from the equations the expected trait metric values correspondent to each observed S. The comparison between observed and mean expected values (paired by both number of individuals and S) was as described above. We have also built null models in which species could be drawn from all sites, *i.e.* we assumed that species could disperse freely between sites, but the results were essentially identical and are thus not presented.

To further assess the strength of habitat filtering, we tested whether species occur at a narrower range of micro-habitats than expected by chance. We assigned to each species values of environmental ranges, defined as the difference between the extreme values of each environmental variables in the plots where they were actually sampled. Species occurring in a single plot were excluded from the analyses. Environmental range is expected to increase with absolute frequency (F_{ABS}), thus at each value of F_{ABS} we made 999 random draws, and compared observed values to mean expected values with a paired one-tailed Wilcoxon test, separately for each site.

We assessed spatial aggregation within each species by computing the standardized Morisita index (Morisita 1962) for each species at each site. Species with values below -0.5 are considered to have their individuals distributed more evenly across plots than expected, while species with values above 0.5 are considered to have their individuals more aggregated than expected by chance (Smith-Gill 1975). As aggregation patterns may arise due to either limited dispersal or habitat filtering, we used simple Mantel tests (Mantel 1967, Manly 1986) to assess the spatial autocorrelation of traits mean plot values and environmental variables, and spatially explicit correlation between traits and environment, and partial Mantel tests (Smouse *et al.* 1986) to assess correlations between traits and environmental variables while controlling for the effects of distance. If Mantel *r* decreases after controlling for the effects of distance, then distance between plots is more important than environmental variables for determining trait values (Legendre and Legendre 1998), implying that limited dispersal is more important than habitat filtering.

To assess whether frequent and rare species differed in their contribution to our ability to discern environmental filtering at the plot level (*i.e.* how well traits were correlated to environmental variables), we performed regression between species mean trait values and species mean environmental values. Species mean environmental values were calculated as the mean environmental values of all plots where a given species was sampled at each site. A species was considered frequent if it occurred in at least four plots at each site. We performed regressions only considering frequent species, and regressions with all species. All analyses were performed in R 2.12 (R Development Core Team 2006).

Results

We have sampled a total of 199 species across all three sites. The LM site presented 461 individuals distributed among 99 species, while the M site had 338 individuals distributed among 83 species, and the LL had 292 individuals distributed among 68 species. Most species occurred at a single site, but 47 species were found at two sites and 7 species were found at the three sites (see Apendix). Individual plots presented 5-18 species and 7-31 individuals at the LL site, 8-26 species and 17-51 individuals at the LM site, and 6-23 species and 8-43 individuals at the M site. Species abundance curves had the characteristic inverse-J shape, with several singleton species at each site: 28 at the LL, 48 at the LM, and 24 at the M sites. Species with at least four individuals numbered 23 at the LL, 25 at the LM, and 28 at the M site. Functional traits of the most abundant species were similar between sites, with the exception of Leaf Area, which was significantly smaller in the M site than at LL and LM sites (H_{MAX}: $F_{2,63}=0.82$, $p>0.05$; SLA: $F_{2,75}=0.14$, $p>0.05$; WD: $F_{2,75}=0.18$, $p>0.05$; Leaf Area: $F_{2,75}=3.44$, $p<0.05$; Fig. 1a-d).

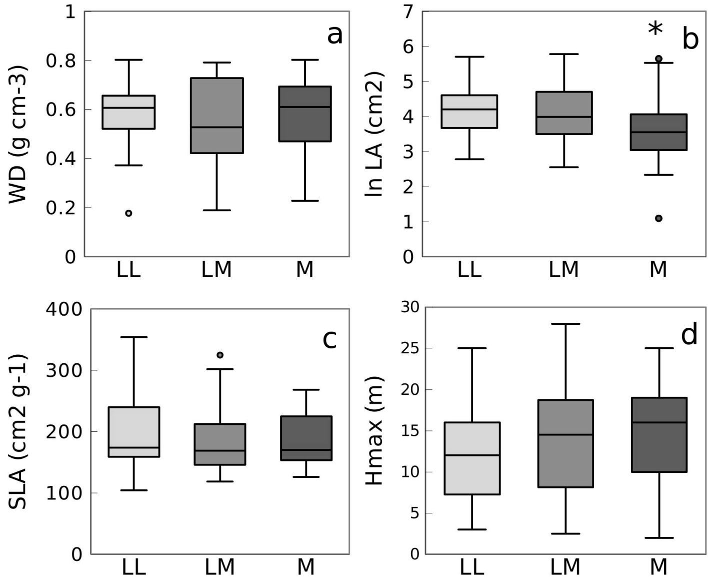


Figure 1: Comparison of functional traits of understory tree saplings and shrubs at three sites of tropical rain forest along an elevation gradient in southeastern Brazil (Lowland, 70 m; Lower Montane, 370 m; Montane, 1070 m a.s.l.): (a) wood density; (b) leaf area; (c) specific leaf area; and (d) maximum height. Sites were compared with one-way ANOVAS, and only in the case of leaf area species at the Montane site were significantly different from the other sites (indicated by an asterisk). Box plot indicates non-outlier range (whiskers), interquartile range (IQR, box limits), median (central line), and outliers (dots, > 1.5 IQR; asterisks, >3.0 IQR).

When community traits structure was analyzed using species means, the observed communities displayed few differences to the null model, when sites were either pooled or analyzed separately (Table 1). When intra-specific variability was taken into account, on the other hand, ranges and variances of all traits were lower than expected by chance when sites where pooled, with the exception of WD range (Table 2), indicating a potential habitat filtering effect. When sites were analyzed separately, again there were few differences from the null model (Table 2). Nevertheless, the observed species richness was significantly lower than expected by the null model, either when sites were pooled or analyzed separately (Fig. 2). When the expected values from the individual-based model were compared to observed values as paired by S instead of number of individuals, the results were very similar to those of the species-based model (*data not shown*).

In general, species at all three sites occupied a narrower range of micro-habitats than expected by chance. Species tended to occupy plots with a narrower range of soil N than expected by

Table 1: Comparison between species-based observed and expected metrics of functional traits of understory tree saplings and shrubs communities at three sites of tropical rain forest along an elevation gradient in southeastern Brazil (Lowland, 70 m; Lower Montane, 370 m; Montane, 1070 m a.s.l.), shown as p-values of paired bicaudal Wilcoxon tests. Significant values in bold, and an indication of whether observed values (O) were higher or lower than expected values (E). Also shown are p-values of test performed with plots from all sites pooled.

Trait	*Metric*	**Pooled**	**Lowland**	**Lower Montane**	**Montane**
H_{MAX}	mean	0.663	**0.004** O > E	0.348	0.159
	range	0.440	0.421	**0.044** O > E	**0.034** O < E
	variance	0.358	0.639	0.669	0.083
	kurtosis	0.446	0.359	0.117	0.231
	SDNDr	0.525	0.934	0.074	0.231
WD	mean	0.702	0.600	0.433	0.495
	range	0.060	0.600	**0.013** O > E	0.495
	variance	0.305	0.151	**0.008** O > E	0.632
	kurtosis	0.109	0.083	0.495	0.348
	SDNDr	0.404	0.151	0.211	0.404
SLA	mean	0.286	0.252	0.130	0.298
	range	0.604	0.600	0.528	0.562
	variance	0.838	0.720	0.860	0.782
	kurtosis	0.596	0.847	**0.034** O < E	0.323
	SDNDr	0.765	0.934	0.274	0.404
LA	mean	0.912	0.107	0.348	0.323
	range	0.880	0.169	1.000	0.298
	variance	0.830	**0.026** O > E	0.744	0.298
	kurtosis	0.525	0.600	0.093	0.980
	SDNDr	**0.012** O > E	0.188	0.193	1.000

chance at the M site only, and did not differed from the null model in regard to canopy openness (Fig. 3a-f). Regarding micro-topography, species tended to occur at a narrower range of CI at both LL and LM sites, and at a narrower range of terrain slope at the M site (Fig. 4a-f). Also, at all sites species tended to occur either randomly or clustered, according to the standardized Morisita Index. No species presented a significantly regular distribution, while at least some species (15-20% at each site) were significantly clustered (Fig. 5a-c).

Table 2: Comparison between individual-based observed and expected species richness and metrics of functional traits of understory tree saplings and shrubs communities at three sites of tropical rain forest along an elevation gradient in southeastern Brazil (see legend to Table 1 for details).

Trait	*Metric*	**Pooled**	**Lowland**	**Lower Montane**	**Montane**
S		**0.000** O<E	**0.000** O<E	**0.009** O<E	**0.001** O<E
H_{MAX}	mean	0.525	0.890	0.632	0.464
	range	**0.015** O<E	0.208	0.323	0.083
	variance	**0.048** O<E	0.639	0.252	0.175
	kurtosis	0.589	0.454	0.821	0.860
	SDNDr	**0.000** O>E	**0.018** O>E	0.058	**0.003** O>E
WD	mean	0.887	0.847	0.821	0.464
	range	0.098	0.208	0.669	0.404
	variance	**0.015** O<E	0.169	0.274	0.117
	kurtosis	0.281	0.934	0.528	0.298
	SDNDr	0.078	**0.048** O>E	0.562	0.632
SLA	mean	0.305	0.720	0.632	0.375
	range	**0.040** O<E	0.151	0.175	0.860
	variance	**0.047** O<E	0.073	0.464	0.495
	kurtosis	0.124	0.359	0.058	0.980
	SDNDr	0.398	0.639	0.274	0.669
LA	mean	0.472	0.890	0.940	0.231
	range	**0.048** O<E	0.524	0.298	0.175
	variance	**0.012** O<E	0.600	0.211	**0.025** O<E
	kurtosis	0.929	0.978	0.252	0.252
	SDNDr	0.846	0.934	0.528	0.495

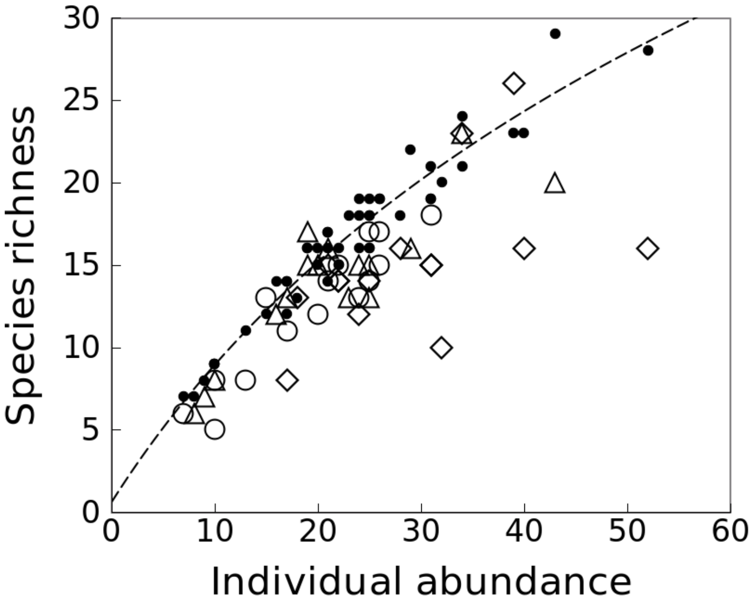


Figure 2: Comparison between observed and expected species richness per plot at three sites of tropical rain forest along an elevation gradient in southeastern Brazil (Lowland, ○; Lower Montane, ◊; Montane, Δ). Black dots are mean expected values extracted from 999 runs of the null model. The broken line, fitted to the expected values of all sites pooled, is included as a heuristic guide. All sites had significantly less species than the null model expectations according to two-tailed paired Wilcoxon test.

To assess whether the tendency of occupying a narrow range of micro-habitats was a mere reflection of individuals within species being clustered, we examined spatial autocorrelations of traits and environmental variables and spatially explicit correlations between traits and environment. According to simple Mantel tests, soil N, CI and terrain slope presented significant spatial autocorrelation at the LL site, while CO and terrain slope presented spatial autocorrelation at the LM site (Table 3). WD was significantly spatially autocorrelated at the LL site only (Table 3). Simple Mantel tests also have shown that H_{MAX} was positively correlated with CO at the LL site, while SLA and WD were positively correlated with CI at sites LL and LM, and Leaf Area was positively correlated with terrain slope at the M site (Table 4). These results did not change when analyzed with a partial Mantel test, which sorts out the effects of distance between plots (*data not shown*), suggesting that these correlations are primarily driven by the environment and not by distance itself.

Relationships between species-mean environmental variables and functional traits were performed both using only frequent species and all species at each site. In general, environment-trait relationships were stronger when only frequent species were considered (Table 5, Fig. 6a-c). Frequent species had a positive relationship between CI and WD and a negative relationship between SLA and both CI and soil N at LL and LM sites, a negative relationship between LA and slope at LM and M sites, and a negative relationship between LA and CI at the M site only (Table 5). The inclusion of rare species (occurring at three or less plots) decreased regression coefficient in almost every case, with the exception of Slope-SLA relationship at the M site (table 5).

Figure 3: Comparison between observed and expected ranges of habitat occupied by understory tree saplings and shrubs at three sites of tropical rain forest along an elevational gradient in southeastern Brazil: a-b, Montane site (1070 m); c-d, Lower Montane site (370 m); e-f, Lowland site (70 m). Left panels, range of canopy openness; right panels, range of total soil Nitrogen content. Open circles are observed ranges of each species occupying at least two plots, and black dots are mean expected values obtained from 999 runs of the null model. Broken lines fitting expected values are only included as a heuristic guide. Cases in which species occupied a significantly narrower range of habitats than expected by chance, according to a paired Wilcoxon test, are indicated.

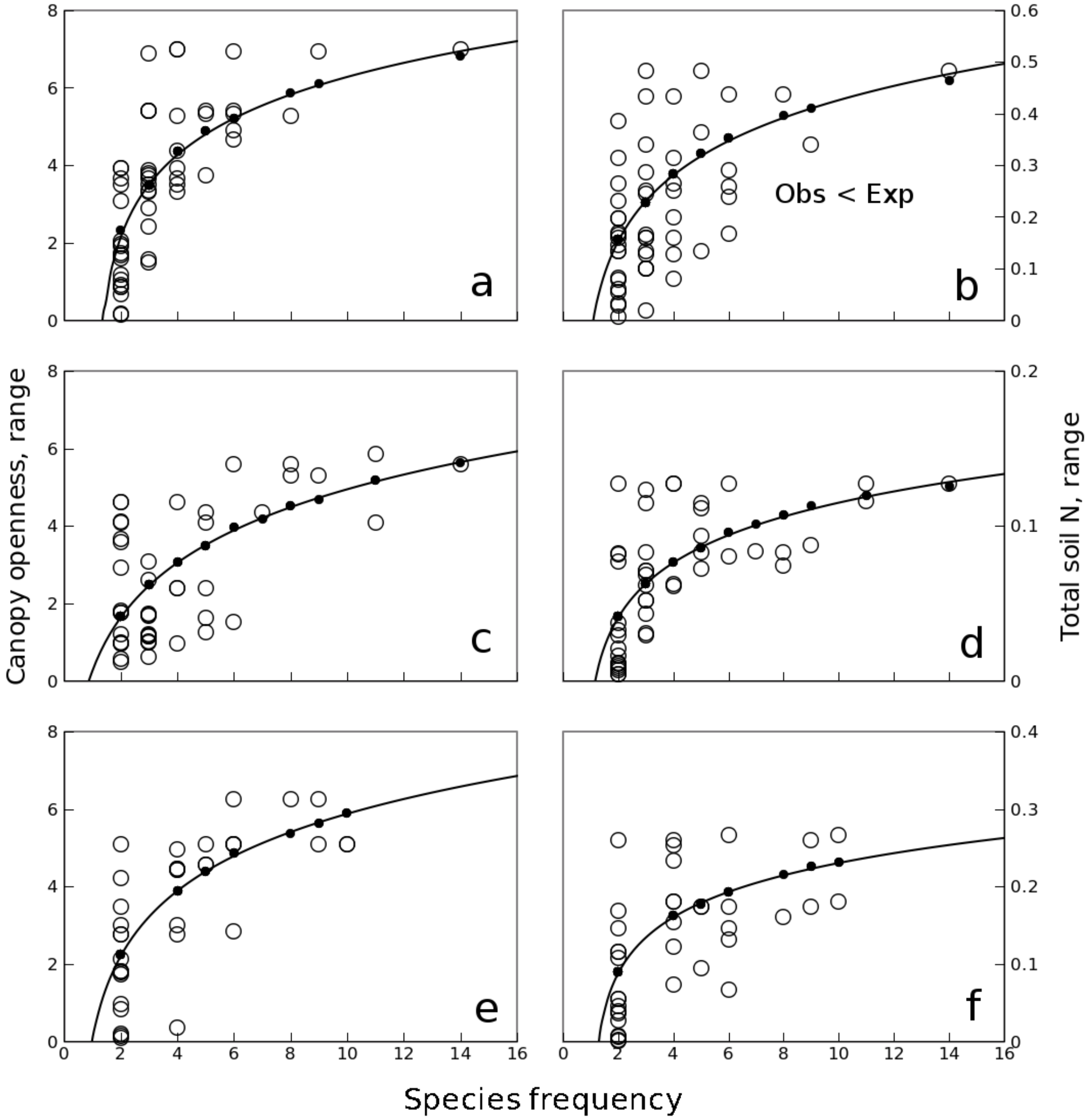
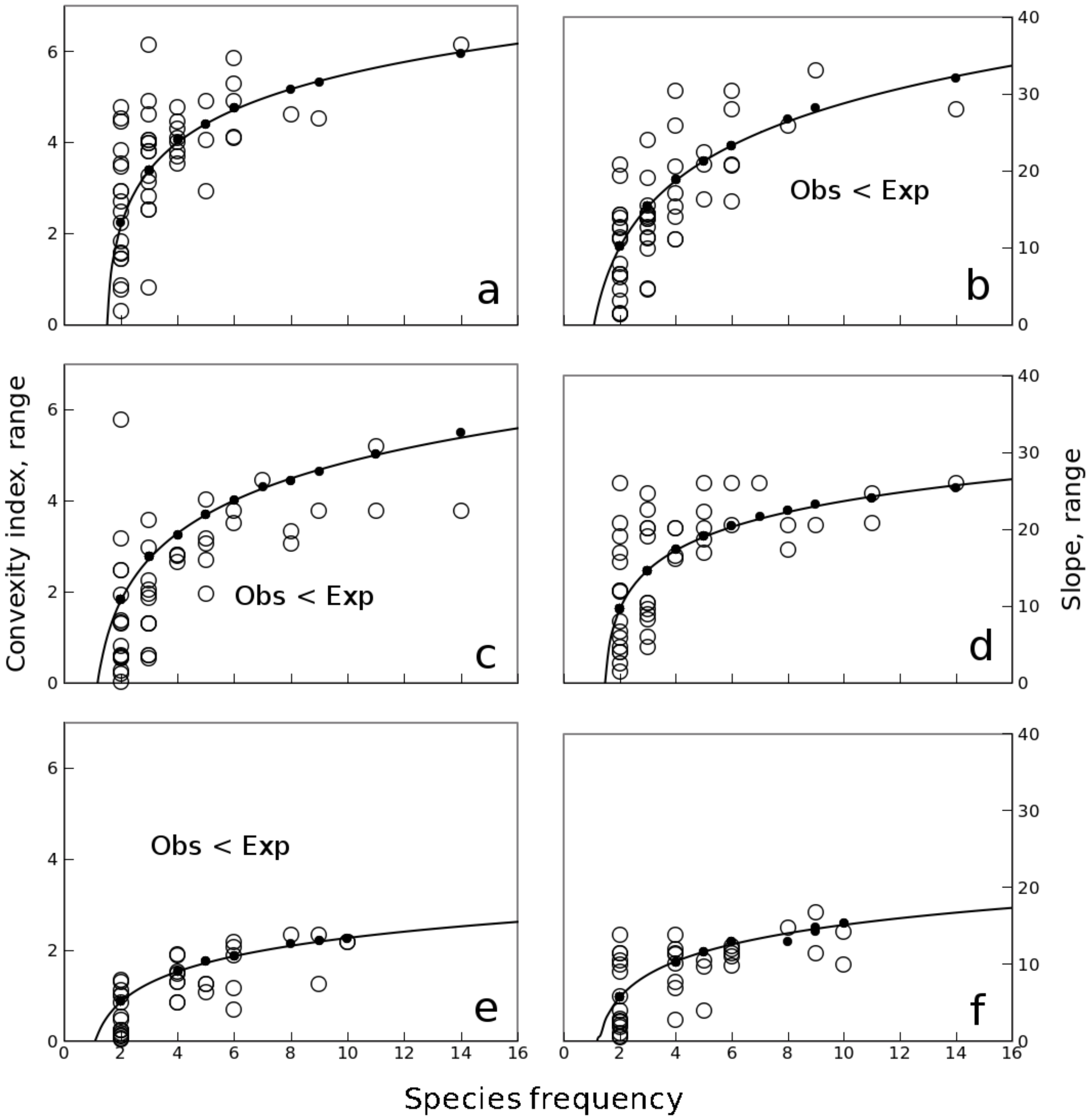


Figure 4: Comparison between observed and expected ranges of habitat occupied by understory tree saplings and shrubs at three sites of tropical rain forest along an elevational gradient in southeastern Brazil: a-b, Montane site (1070 m); c-d, Lower Montane site (370 m); e-f, Lowland site (70 m). Left panels, Index of topographical convexity; right panels, range of terrain slope. See legend of Figure 3 for details.



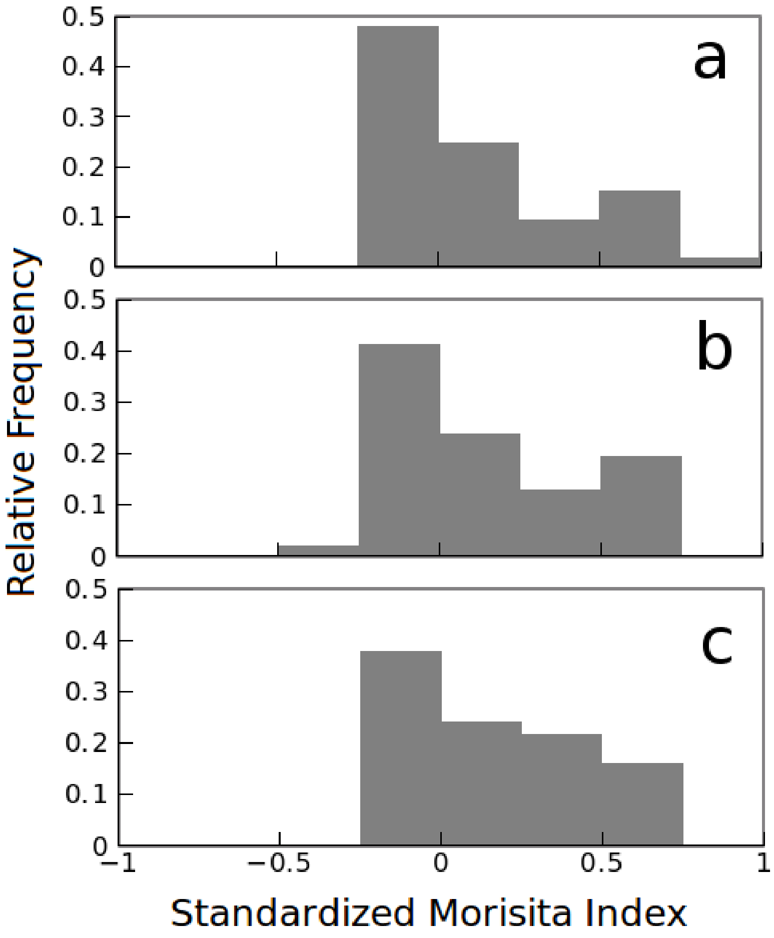


Figure 5: Distributions of standardized Morisita Index of aggregation observed at three sites of tropical rain forest along an elevational gradient in south-eastern Brazil: (a), Montane site (1070 m); (b), Lower Montane site (370 m); and (c), Lowland site (70 m). Species with Morisita Index higher than 0.5 have its indivi-duals occurring significantly ag-gregated. Species occurring in at least two plots at each site were included in the analysis.

Table 3: Spatial autocorrelations of environmental variables and plot-mean functional traits of understory tree saplings and shrubs at three sites of tropical rain forest along an elevation gradient in southeastern Brazil (Lowland, 70 m; Lower Montane, 370 m; Montane, 1070 m a.s.l.). Positive Mantel *r* coefficients indicate positive autocorrelation.

	Lowland		**Lower montane**		**Montane**	
Variable	Mantel r	p-value	Mantel r	p-value	Mantel r	p-value
CO	−0.073	0.540	**0.302**	**0.005**	0.156	0.160
N	**0.334**	**0.004**	0.148	0.190	−0.073	0.510
CI	**0.39**	**0.003**	0.121	0.270	−0.016	0.880
Slope	**0.45**	**0.001**	**0.218**	**0.035**	0.087	0.440
H_{MAX}	0.21	0.110	−0.187	0.100	0.042	0.700
WD	**0.31**	**0.010**	0.129	0.290	−0.097	0.440
SLA	0.211	0.083	0.010	0.920	0.164	0.170
LA	0.024	0.840	0.136	0.240	0.074	0.550

Table 4: Spatial correlations between environmental variables and plot-mean functional traits of understory tree saplings and shrubs at three sites of tropical rain forest along an elevation gradient in southeastern Brazil (Lowland, 70 m; Lower Montane, 370 m; Montane, 1070 m a.s.l.). Positive Mantel *r* coefficients indicate a positive spatial correlation between environmental variable and functional trait.

		Lowland		**Lower montane**		**Montane**	
Variable	**Trait**	Mantel r	p-value	Mantel r	p-value	Mantel r	p-value
CO	H_{MAX}	**0.323**	**0.040**	−0.103	0.540	0.081	0.540
	WD	0.158	0.270	−0.013	0.940	0.046	0.760
	SLA	0.086	0.570	0.068	0.780	−0.034	0.820
	LA	0.214	0.100	−0.091	0.550	0.082	0.590
N	H_{MAX}	−0.263	0.100	−0.02	0.900	−0.129	0.330
	WD	0.035	0.830	*0.238*	*0.065*	−0.027	0.870
	SLA	−0.054	0.770	0.264	0.110	0.008	0.960
	LA	−0.214	0.140	−0.08	0.620	−0.100	0.530
CI	H_{MAX}	0.170	0.210	0.186	0.190	0.067	0.520
	WD	**0.283**	**0.032**	**0.286**	**0.036**	−0.083	0.510
	SLA	**0.232**	**0.043**	**0.512**	**0.029**	−0.024	0.840
	LA	−0.026	0.830	0.031	0.820	**0.243**	**0.039**
Slope	H_{MAX}	0.065	0.700	−0.047	0.710	0.142	0.330
	WD	0.086	0.550	0.042	0.740	−0.063	0.710
	SLA	−0.035	0.800	−0.068	0.720	0.108	0.510
	LA	0.073	0.570	−0.057	0.670	0.165	0.310

Table 5: Relationships between species-means environmental variables and functional traits of understory tree saplings and shrubs at three sites of tropical rain forest along an elevation gradient in southeastern Brazil. Regression coefficients (R^2) and p-values of simple regressions performed only with frequent species (occurring in at least four plots) or with all species. Significant regressions in bold.

		Lowland (70 m)				**Lower Montane (370 m)**				**Montane (1070 m)**			
		Frequent		*All*		*Frequent*		*All*		*Frequent*		*All*	
Trait	**Envir**	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
H_{MAX}	CO	0.01	0.71	0.00	0.99	0.07	0.28	0.01	0.50	0.00	0.91	0.01	0.33
	Soil N	0.05	0.34	0.00	0.72	0.18	0.08	0.03	0.12	0.11	0.22	0.00	0.75
	CI	0.00	0.67	0.00	0.62	**0.29**	**0.021**	0.00	0.84	0.01	0.67	0.01	0.44
	Slope	0.02	0.51	0.00	0.80	0.07	0.29	0.00	0.86	0.00	0.99	0.00	0.98
WD	CO	0.00	0.92	0.00	0.94	0.15	0.11	0.01	0.35	0.00	0.97	0.01	0.30
	Soil N	0.18	0.052	0.00	0.63	0.14	0.12	**0.07**	**0.011**	0.14	0.12	0.00	0.37
	CI	**0.37**	**0.003**	0.00	0.68	**0.28**	**0.023**	0.02	0.13	0.05	0.34	0.04	0.064
	Slope	0.02	0.54	0.05	0.072	**0.38**	**0.007**	0.02	0.15	0.11	0.16	0.01	0.49
SLA	CO	0.04	0.41	0.00	0.42	0.21	0.057	0.01	0.37	0.00	0.83	0.02	0.16
	Soil N	**0.22**	**0.033**	0.00	0.89	**0.28**	**0.024**	**0.06**	**0.011**	0.03	0.50	0.00	0.91
	CI	**0.24**	**0.024**	0.02	0.25	**0.53**	**0.001**	**0.05**	**0.022**	0.00	0.78	0.01	0.43
	Slope	0.01	0.71	0.03	0.19	0.11	0.19	0.02	0.20	0.00	0.95	**0.15**	**0.001**
LA	CO	0.00	0.79	0.01	0.57	0.08	0.26	0.01	0.45	0.01	0.69	0.00	0.85
	Soil N	0.04	0.41	0.01	0.59	0.07	0.30	0.00	0.97	0.01	0.67	0.01	0.44
	CI	0.11	0.14	0.03	0.16	0.09	0.23	0.01	0.50	**0.29**	**0.016**	**0.10**	**0.004**
	Slope	0.08	0.22	0.04	0.09	**0.33**	**0.013**	0.00	0.70	**0.35**	**0.008**	0.02	0.17

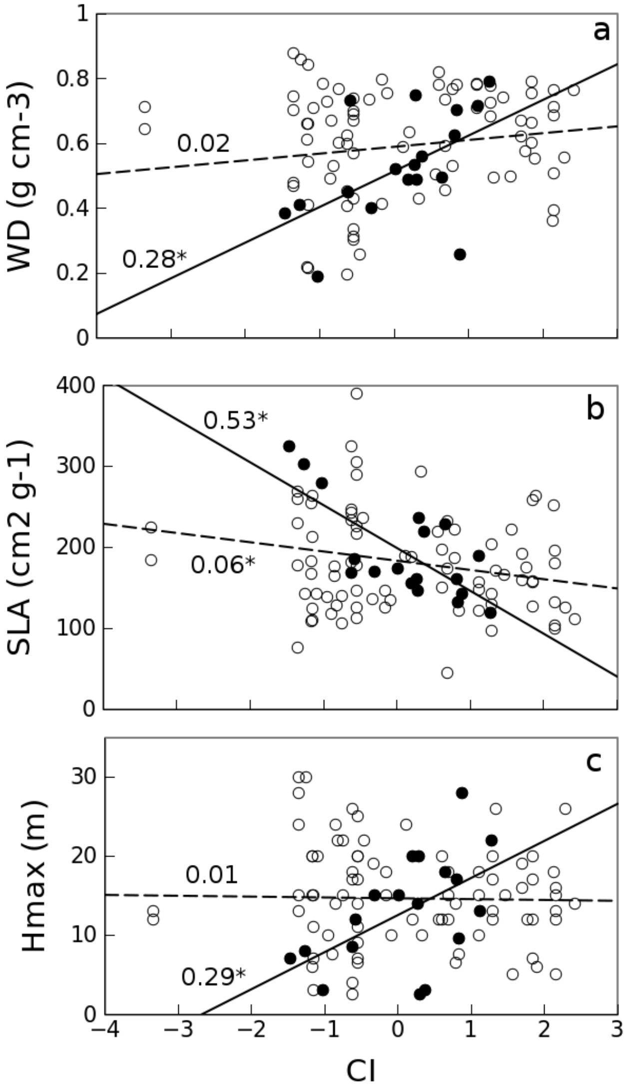


Figure 6: An example of differences of trait-environment relationships, when considering either only frequent species (occurring in at least four plots) or all species at the site: (a) wood density; (b) specific leaf area; and (c) maximum height, all regressed against topographic convexity index at the lower montane site (370 m a.s.l.). Black dots are frequent species, open dots are rare species (occurring at three or less plots). Continuous lines are fitted regression using frequent species only, dotted lines are fitted regression using all species, including frequent ones. Regression coefficients (R^2) are shown next to each fitted regression. Significant regressions ($p<0.05$) are marked with asterisks.

Discussion

The goals of this study were to assess how functional traits varied along an elevation gradient, to test whether a community of tree saplings and shrubs at the understory of a tropical rain forest exhibited a non-random structure of functional traits, and how frequent and rare species differed in their associations with microhabitats. Comparing the most abundant species at each site, we found that LA was the only trait that differed between sites, being significantly smaller at the M site. This result is in accordance to studies where adult trees leaf area was measured along elevation ranges (Dolph and

Dilcher 1980, Velázquez-Rosa et al. 2002). Nevertheless, the functional significance of this variation of leaf size along with altitude is not clear, and the variation of leaf size within a given site or "climate belt" has been emphasized (Dolph and Dilcher 1980, Turner 1994). A slight tendency of an increase in H_{MAX} with altitude was also observed (Fig. 1d), reflecting the relative rarity of shrubs at the M site, in contrast to LL and LM sites where *Psychotria* spp. (Rubiaceae) dominates the understory. It is not clear, however, why shrubs are less abundant at the montane forest site, especially when there even more species of *Psychotria* in this site than in either the lowland or lower montane sites (six species on M, against three in LL and 5 in LM).

Trait-based community structure

We hypothesized that coexisting species would be more similar to each other than expected by chance, due to local habitat filtering. We have found no evidence of habitat filtering when species means were used to build null models. Several studies in tropical forests have found evidences of trait overdispersion or aggregation and, in general, saplings have lower signal of trait community structure than adult plants (Cavender-Bares *et al.* 2006, Kraft *et al.* 2008, Swenson and Enquist 2009). On the other hand, we have found that co-occurring individuals were more similar to each other than expected by chance: for all traits, both trait range and variances of were smaller than expected (with the exception of WD range, which was no different from the null model expectation). In this case, however, species richness was also significantly lower than expected by chance, implying that individuals of a given species tended to occur in aggregation, as was indeed confirmed by the Morisita aggregation index. Thus, the apparent signal of habitat filtering was the reflection of the fact that interspecific trait variation was higher than interspecific variation, and that individuals tended to co-occur with co-specifics.

Condit *et al.* (1992) have assessed sapling recruitment distance in relation to adult individuals in 80 species of trees and shrubs on a tropical forest in Barro Colorado Island, and found that, even though most species showed a random pattern of recruitment, 27 species recruited preferentially near co-specific adults. Other studies have found strong dispersal (Hubbell et al. 1999) or recruitment limitation (Harms et al. 2000). Thus, the apparent signal of habitat filtering we observed at the individual-level analysis could, in principle, be a consequence of dispersal and/or recruitment limitation alone. Nevertheless, we have also found significant relationships between environmental variables and functional traits, either at plot level (analyzed with spatial correlations) or at species level (analyzed with simple regressions). Such relationships are often viewed as consistent with habitat filtering, defined as "*an exclusion of species outside of the viable range of trait values in each sampled habitat*" (Cornwell and Ackerly 2009).

Topographic CI presented a positive relationship with WD, and negative relationships with SLA and LA. Assuming that CI is negatively correlated with soil water retention (Pachepsky *et al.* 2001), this means that, in general, drier plots were occupied by plants with denser wood, smaller leaves and smaller SLA. Similar patterns were found in a California vegetation (Cornwell and Ackerly 2009) and across precipitation gradients in southeastern Australia (Wright *et al.* 2002), as well as on a tropical forest in Ecuador, where species occurring at ridgetops had lower than expected SLA and those occupying valleys had higher than expected SLA (Kraft and Ackerly 2008). Plants with high WD are able to resist embolism when submitted to low soil water potential (Hacke *et al.* 2001), and low SLA values are associated with long leaf life span (Reich *et al.* 1997) and, more generally, to a retentive biomass strategy. Additionally, leaves developed under low water availability have lower expansion rates, with smaller and more packed cells and a lower fraction of air spaces, all of which may reduce water requirements during dry periods (Poorter *et al.* 2009), although whether these features are important for plants in a shaded understory is still unclear.

Plants occupying steeper slopes at the LM and M sites tended to have smaller leaves, as well as those occupying convex plots in the M site. While plants with smaller leaves are reported to occupy drier sites (Fonseca *et al.* 2000), the functional significance of leaf area appears to shift depending on both water availability and irradiation (Givnish and Vermeij 1976). At the LM site only, convex sites are occupied by taller species, which is in line with Aranha (2008) who observed that, at the same site, herbs and shrubs tend to dominate (in terms of richness and abundance) the understory at concave plots, while trees and lianas tend to dominate the understory at convex plots.

While frequent species show clear habitat associations, any given plot have at least many rare species (*data not shown*). It is probable that these rare species act as a source of noise when communities are compared to null models in search of habitat filtering signal, especially when sample size is relatively small.

Frequent and rare species

The species-abundance curves for all three sites had the characteristic inverse-J shape, with a few abundant and many rare species. As it became evident from species-level environment-trait relationships, frequent species as a group present a good fit between their phenotypes and the environment they occupy, while rare species seems to haphazardly occupy the available understory habitats (see Fig. 6). A good fit between phenotype and environment may arise due to habitat selection (Bazzaz 1991; *e.g.* some shrubs like *Begonia* sp., *Psychotria* sp. and *Piper* sp. seems to display some degree of clonal growth, and may actively spread into specific habitats), differential mortality driven by environmental factors (Condit *et al.* 1995), or phenotypic plasticity (Sultan 2000). Species that rely primarily on the two first processes may be considered habitat specialists; species that rely primarily on phenotypic plasticity may be considered habitat generalists. It is noteworthy that intraspecific variation of traits in function of environmental variation displayed a wide variation, with some species displaying positive, others negative, relationships between traits and environmental variables, while most of them showed little or no variation (*data not shown*). Thus, it is possible that frequent species present a wide range of strategies to cope with environmental variability in order to ensure population persistence.

A poor fit between environment and trait may be a result of sampling error (of either environmental variable or trait), or an indication that the species is either a habitat generalist or a survivor of a germination event in an inadequate habitat (which may decrease the odds of survival to a mature stage). It is probable that our set of rare species is a mix of these possibilities. Nevertheless, Pandit *et al.* (2009), studying marine invertebrates in rock pools, shows that habitat specialists respond more to local, environmental processes, while generalists respond to regional, dispersal processes. In fact, Magurran and Henderson (2003) show that the arrival of rare species at an estuarine fish community can be modeled as stochastic events, while persistent species are often biologically associated with estuarine habitats. Thus, it is possible that community assembly of tropical forest understory is a result of mostly deterministic processes acting on specialist species at local scale, and mostly stochastic processes acting on generalist species on a regional scale. Studies on how to concatenate these processes acting on different spatial scales could help to clarify forest community assembly.

We conclude that, even though we have found no evidence of habitat filtering using the null model approach (possibly due to a small sample size within each site), we could provide evidence for a deterministic pattern of micro-habitat association thanks to the inclusion of within-species functional traits variation coupled with micro-environment measurements. We suggest that within-species spatial patterns and dynamics may be an important component of the community assembly process, and thus should be more frequently contemplated in order to advance our knowledge of community structure.

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Capítulo 3

The influence of plant size on trait-based community structure in a stand of Atlantic lower montane tropical rain forest, SE Brazil

The influence of plant size on trait-based community structure in a stand of Atlantic lower montane tropical rain forest, SE Brazil

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Abstract

Tropical rain forest tree communities have been shown to be locally structured by niche-based processes, with functional traits often serving as proxies for niche requirements. Different processes imprint characteristic patterns on the distribution of traits of co-occuring species: habitat filtering makes co-occurring species more similar to each other than expected by chance, and competition leads to the exclusion of similar species, making them less similar than expected by chance. We tested the hypothesis that, when woody individuals plants are grouped by size, traits of co-occuring species would shift, from clustered at the smaller size due to a strong filtering effect imposed by the canopy, to overdispersed at the largest (canopy tree) size due to increased competition for resources. We surveyed 0.5 ha of a lower montane tropical rain forest in SE Brazil, grouping shrub and tree individuals in four size classes based on DBH, and assigned to them functional trait values – wood density (WD), specific leaf area (SLA), leaf area (LA) and maximum height (H_{MAX})– obtained from a previous survey of saplings and shrubs. A comparison between saplings and adults functional traits of 26 common tree species showed a good correlation (R between 0.50 and 0.89) between these stages. Null models were used to compare observed and expected ranges of traits among co-occuring species. When all species were analyzed together, species richness, WD, SLA, and LA showed lower than expected ranges at the two smaller size classes. The same pattern was found when only shrubs and treelets (H_{MAX} < 10 m) were considered, while no departure from random expectations was found when only canopy trees were considered. Thus, while understory shrubs and treelets seems to be functionally aggregated, in part due to spatial aggregation of con-specifics, canopy trees apparently does not shift from functional aggregation to overdispersion as they grow towards the canopy, refuting our hypothesis. We further discuss the possible effects of sampling scale on the observation of patterns of community functional structure.

Keywords: Functional traits, tropical rain forest, shrubs, size, species coexistence, trees.

Introduction

Tropical rain forest tree communities have, in the last few years, been shown to be locally structured by niche-based processes (Webb 2000, Kembel and Hubbell 2006, Swanson and Enquist 2007, Kraft et al. 2008). Such processes are thought to be mediated by functional traits; such traits are related to resource acquisition, life history, environmental tolerance, regeneration niche (Westoby et al. 2002, Ackerly 2003, Poorter 2007), and have often a non-random distribution along environmental gradients (Fonseca 2000, Wright et al. 2005, Cornwell and Ackerly 2009). Co-occurring species may be either more similar to each other or more different from each other than expected by chance, depending on the prevailing mechanism structuring a community: in the first case, environmental filtering is supposed to restrict the range of successful strategies, while in the second case competition for resources forbid species too similar to coexist indefinitely (Weiher and Keddy 1995, 1999). The relative importance of each of these processes may vary with several factors, including resource availability, spatial scale, and environmental stress.

Tropical forests are patches of tree stands in different stages of regeneration, being the result of a complex process called gap-phase dynamics (Hartshorne 1978, Whitmore 1978, Brokaw 1982). In addition to treefall gaps, smaller openings in the canopy – branch gaps and brief sunflecks – let a small portion of the sun (*ca.* 0.5-5%) radiation reach the forest floor. The growth of seedlings and saplings is light-limited in the understory under a mature canopy, and their density is generally so low that competition is arguably unimportant in the forest floor (Wright 2002, Paine et al. 2008). At this stage, survival is a matter of avoiding herbivory (Coley and Barone 1996), resisting pathogen infections and mechanical damage (Alvarez-Clare and Kitajima 2007), keeping low metabolic rates in general, and responding efficiently to brief bursts of light that eventually pass through the canopy. As trees gain greater access to light as they grow vertically, though, they begin to interact more intensely with each other, and competition for both light and soil resources may start to build up, especially between canopy trees.

Functional traits are related to the regeneration niche and environmental tolerance in tropical forests. Wood density is positively correlated with survival (Kraft et al. 2010); a high SLA may increase light acquisition and thus growth rates, but a low SLA may increase resistance to herbivory (Eichhorn et al. 2007) and leaf lifespan (Reich et al. 1997). Having large leaves may enable efficient light foraging and increased investment in vertical growth (Poorter and Rozendaal 2008). Maximum height may facilitate species coexistence by allowing different light-capture strategies (Falster and Westoby 2003, Poorter et al. 2005). Thus, the goal of this study is to test the following hypothesis: functional traits of coexisting seedlings and saplings at the understory will tend to converge due to environmental filtering, while in adult trees they will tend to diverge as a result of continuing competition – and eventual competitive exclusion – during the sapling-to-adult transition. For this, we assessed the trait-based community structure of trees and shrubs in a tropical rain forest in southeastern Brazil, from seedlings to adult trees.

Material and Methods

Field site and sampling

We assessed the effect of environmental variables on phylogenetic community structure of understory woody vegetation at three sites along an elevation gradient of a tropical rain forest. Field work was carried out at the Serra do Mar State Park (PESM), São Paulo State, Brazil (23º17’-23º34’S, 45º02’-45º11’W; 0-1300 m a.s.l.), where fourteen 1-ha permanent plots have been previously established to study the structure and dynamics of the Brazilian Atlantic rain forest (see Alves *et al.* 2010 for more details on sampling design and site characterization). The Park comprises mainly of typical tropical Rain Forest, with a continuous canopy *ca*. 20 m high and a high diversity of tree species (100-200 spp. ha^{-1}), with a general predominance of Myrtaceae, Fabaceae, Rubiaceae, and Lauraceae species (Rizzini 1997, Tabarelli and Mantovani 1999). Regional climate is humid tropical (Af type according to Köppen), with mean annual temperatures around 22 °C, annual precipitation ranging from 2000 to 2500 mm, and typically only one month per year with precipitation lower than 60 mm (Sentelhas *et al.* 1999). Soils are sandy and very poor in nutrients (Martins 2010).

On a 1-ha plot, located at a well preserved primary forest at *ca.* 370 m a.s.l., 50 quadrats with 100 m^2 were haphazardly chosen for sampling. All trees with at least 4.8 cm diameter at breast height (DBH) were tagged, and had their height visually estimated. A smaller quadrat (9 m^2) at the center of each 100 m^2 quadrat was used to sample tree seedlings and saplings, shrubs and treelets with at least 30 cm high and less than 4.8 cm DBH. In this case, diameter at base height was recorded, and height was measured with a graduated pole. Plants were identified, up to species level when possible, by comparing samples to herbaria vouchers, and by specialists. Each sampled individual was then assigned to one of four size class bins, according to DBH (diameter at base height for the smaller classes, and at breast height for the larger classes): DBH <1 cm, from 1 cm up to 5 cm, 5 cm up to 10 cm, and >10 cm. Species richness was calculated separately for each size class bin at every quadrat. These size classes are somewhat arbitrary, but we suggest they represent, broadly speaking, ontogenetic stages of trees that have been used for years to study and describe ecological processes in tropical forests. In order, from smaller to larger, these size bins represent seedlings, saplings, pole-sized trees, and canopy trees. Small shrubs could be grouped with saplings, and large shrubs and treelets could be grouped with pole-sized trees. Even though this nomenclature is not exact in relation to our size class divisions, we will use it throughout the text for clarity sake.

Functional traits

Functional traits – maximum height (H_{MAX}), wood density (WD), specific leaf area (SLA) and leaf area (LA) – of 114 tree and shrub species were obtained from a previous study (*the present thesis, chapter 2*). These traits (with the exception of H_{MAX}) have been measured in 1-2 m high individuals (*ca*. 0.5-2.5 cm DBH), sampled at the same 1-ha plot referred to in the previous section. As we are interested in applying these values to a whole woody plant community, including adult trees, we compared a subset of it to values of functional traits measured in adult trees. A dataset of 26 tree species, with traits measured in 3-6 individuals per species, was used (part of the FAPESP Brazil Rain Forest Database in Kattge et al. 2011). These mature tree individuals were sampled in another 1-ha plot, *ca*. 1 km distant from the plot where the present study was conducted. The methods used to measure traits in these two datasets were identical. Pearson's product-moment correlation coefficients between sapling and adult measurements were calculated for WD, SLA and LA. A strong correlation would imply that species ranks along trait axes are consistent along plant ontogeny, and thus across plant size classes. This would allow us to treat static size classes as analogues of stages of ontogenetic trajectories.

Data analysis

For each trait and size class at each quadrat, we calculated the observed range as the difference between maximum and minimum values. In general, co-existing species are considered more similar to each other, regarding a given trait, as range decreases. To test whether a given trait presented a smaller or larger range than expected by chance at a given plot, we built null models in which plot individual abundances at each size class were kept constant, and individuals were shuffled across plots, but within size class. Species richness and traits ranges were recorded for every size class at each random-generated plot, and this process was repeated 999 times. Means and standard deviations were then calculated for the null distributions of each variable at each size class. Standardized size effects (*z* scores) were then calculated for each variable at each observed plot, as the difference between the observed and the mean expected values of the variable, divided by the standard deviation of expected values (see Gotelli and Rohde 2002). Positive *z* scores indicate a broader range of functional trait values (or higher S) than expected by chance, while negative *z* scores indicate a narrower range of functional trait values (or lower S) than expected by chance, and *z* scores of individual samples that fall outside the range of 2 to -2 are considered significantly different from zero (Gotelli and Rohde 2002). We then tested whether the median z scores for all samples within a given size class was different from a null expectation of zero using the non-parametric two-tailed Wilcoxon test.

When considering all species, differences between size classes may arise simply due to differences in species composition; *e.g.*, tall trees occur in all size classes, but shrubs are restricted to the smaller size classes. Hence, we divided species in two groups, based on maximum height: canopy tree species that grow at least to a height of 10 m, sufficient to reach the bottom of the canopy, and a group composed of treelets and shrubs, species that complete their life cycle in the understory, never reaching 10 m high. We then repeated the null model analysis, using only species from each group. In the case of treelets and shrubs, the largest size class was not used in the analysis. All analyses were made in R 2.12 (R Development Core Team 2006).

Results

We recorded a total of 381-525 individuals at each size class, of which 71-88% were assigned values of functional traits based on our trait database, distributed among 92-117 species, of which 58-67% were included in our database (table 1). Out of a total of 278 species, 46 were classified as treelets or shrubs (H_{MAX} < 10 m; 490 individuals), while the remaining 231 species were considered as canopy trees (965 individuals). Most species absent from our trait database were rare species, or species undetermined at species level. Individual heights showed a very small overlap between size classes (*data not shown*). WD tended to increase, while SLA and LA tended to decrease, with size class, but the differences were small (table 1), in part due to a considerable degree of overlap in species composition between size classes (*data not shown*).

Table 1: Ecological and morphological characterization of a community of trees and shrubs in a tropical rain forest in Southeastern Brazil, stratified in size classes according to stem DBH. Assigned species and individuals refers to the percentage of the total samples at each size class for which trait values were assigned. DBH was measured at base height in plants of the two smaller size classes, and at breast height (1.3 m) at the larger size classes. DBH and height (H) are medians of all individual sampled at each size class at 50 plots; maximum height (H_{MAX}), wood density (WD), specific leaf area (SLA) and leaf area (LA) are means of all species recorded at a given size class.

	Size class (cm DBH)			
	<1	*1-5*	*5-10*	*>10*
Number of species	92	117	115	116
assigned	67%	64%	64%	58%
Individuals	445	525	409	381
assigned	88%	85%	84%	71%
DBH (cm)	0.65	1.77	6.68	17.51
H (m)	0.5	1.4	7.0	12.9
H_{MAX} (m)	14.8	15.0	16.1	17.2
WD (g cm^{-3})	0.580	0.592	0.595	0.615
SLA (cm^2 g^{-1})	186.8	184.3	181.1	175.9
LA (cm^2)	80.8	84.0	86.7	86.5

Correlations between sapling and adult values of functional traits were all positive and statistically significant. Saplings and adult trees had highly correlated WD (R=0.89; Fig. 1a) and SLA (R=0.76; Fig. 1b), and moderately correlated LA (R=0.50; Fig. 1c). Saplings tended to have larger leaves with higher SLA when compared to adult individuals, although WD was fairly similar between them. Moreover, the relationships have an approximate 1:1 scaling, which means that a given set of coexisting species should display similar trait ranges both as saplings and adults.

When all species were pooled, size classes displayed some differences regarding *z* scores of species richness and functional traits; in general, z scores were significantly more negative than expected by chance at seedling and sapling size classes, according to Wilcoxon tests (Fig. 2, left column), meaning that trait ranges were smaller than expected by chance. Nevertheless, H_{MAX} range did not differed from zero in any size class (Fig. 2d). When canopy trees were analyzed separately, z

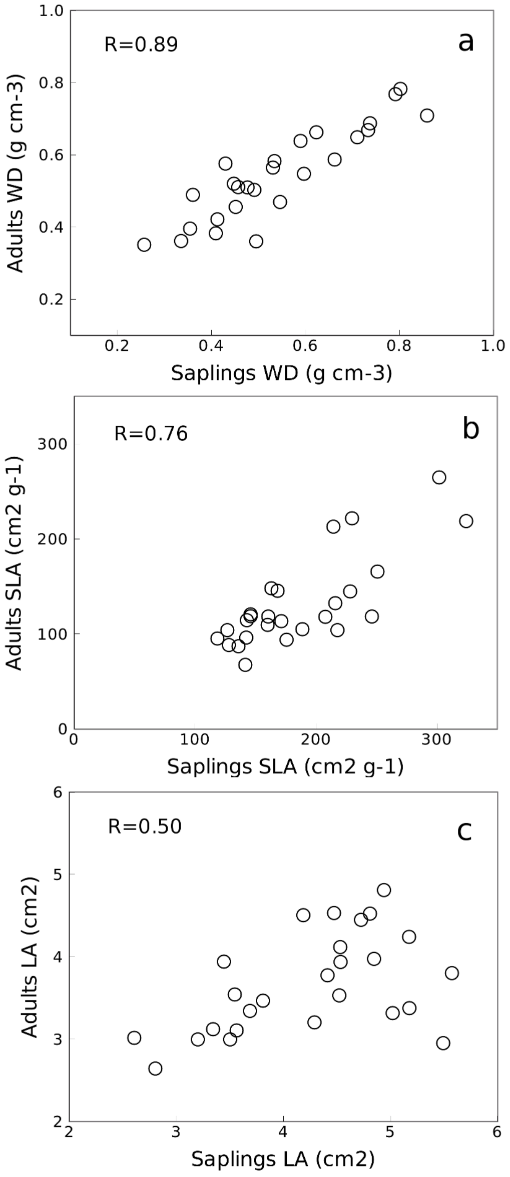
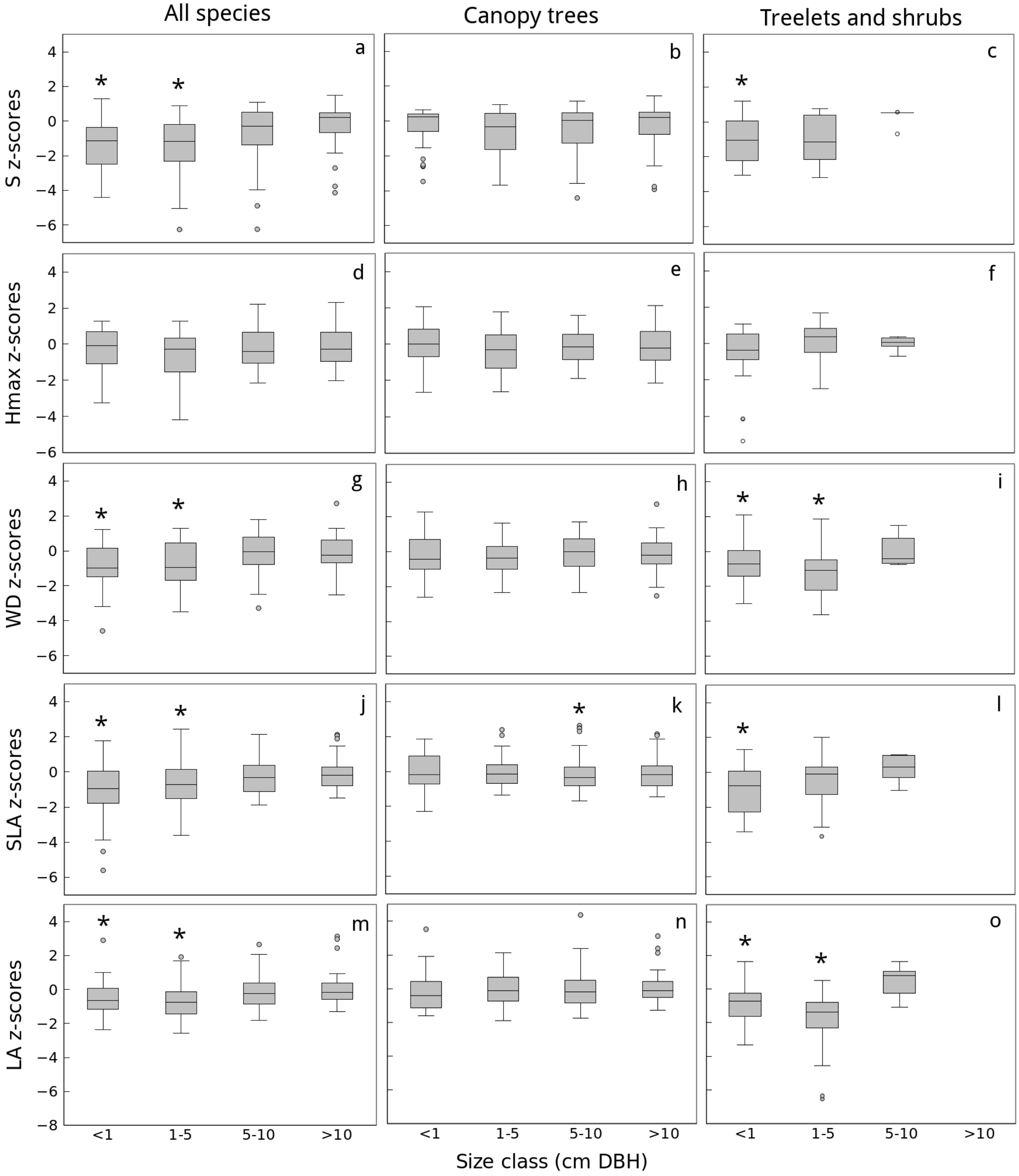


Figure 1: Correlations between sapling and adult values of functional traits in 26 rain forest tree species in southeastern Brazil: (a) wood density (p<0.001); (b) specific leaf area (P<0.001); (c) leaf area (P<0.05). Pearson correlation coefficient are given for each trait.

scores of species richness and all functional traits ranges were statistically indistinguishable from random at all size classes (Fig. 2, middle column). When only treelets and shrubs were analyzed, species richness and SLA range were lower than expected by chance only at the seedling size class (Fig. 2c,l), WD and LA ranges were lower than expected by chance at the seedling and sapling size classes. (Fig. 2i,o), and H_{MAX} range did not depart from random expectations (Fig. 2f).


All species
Canopy trees
Treelets and shrubs
S z-scores
Hmax z-scores
WD z-scores
SLA z-scores
LA z-scores
a
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g
h
i
j
k
l
m
n
o
*
4
2
0
−2
−4
−6
−8
<1
1-5
5-10
>10
Size class (cm DBH)

Figure 2: Standardized effect sizes (z scores) of functional traits ranges and species richness of woody plant communities separated into four size classes in a tropical rain forest in Southeastern Brazil: *a-c*, species richness (S); *d-f*, maximum height (H_{MAX}); *g-i*, wood density (WD); *j-l*, specific leaf area (SLA); and *m-o*, leaf area (LA). Left column, all species; central column, only canopy tree species ($H_{MAX} \geq 10$ m); right column, treelets and shrubs ($H_{MAX} < 10$ m). Boxes indicate median and interquartile range, whiskers indicate non-outlier range, and circles are outliers. Positive values of effect sizes indicate a broader range of functional trait values (or higher S) than expected by chance, while negative values of effect sizes indicate a narrower range of functional trait values (or lower S) than expected by chance. Box plot indicates non-outlier range (whiskers), interquartile range (IQR, box limits), median (central line), and outliers (>1.5 IQR). Boxes marked with asterisks have medians significantly different from zero according to two-tailed Wilcoxon tests ($p<0.05$).

Discussion

We have found that seedling and sapling communities tend to present individuals with functional traits more similar among them than expected by chance, while pole-sized and canopy trees did not depart significantly from the null expectations. This pattern was seemingly imprinted on the community by shrubs and treelets, included in the smaller size bins; when canopy trees were analyzed separately, no trait departed from the null expectation in any size class. This refuted our hypothesis that, as co-occurring tree grows towards the canopy, they would tend to become morphologically more dissimilar due to competitive exclusion. Shrubs and treelets, on the other hand, seem to diverge from the smaller to the larger size classes, although this result must be viewed with caution since the largest size class had a small sample size (six plots), possibly making the Wilcoxon analysis lack statistical power.

A number of recent studies have examined the degree of departure from a random assemblage in saplings and adult trees. Kraft et al. (2008), studying a rain forest plot in Ecuador, have compared trait spacing evenness (standard deviation of nearest neighbor distance; competition is thought to lead to even spacing; Cornwell and Ackerly 2009) of functional traits between adult and sapling cohorts, and found that adult cohorts presented a significantly stronger signal of spacing evenness in leaf nitrogen concentration and seed mass. Swenson et al. (2007) found that adult trees tend to be less phylogenetically related than expected by chance, while saplings are randomly distributed, at the 10 x 10 m spatial scale but, on a subsequent study, they have found a general trend of trait clustering among coexisting species (Swenson and Enquist 2009). Gonzalez et al. (2010) observed a higher species evenness in adult trees when compared to saplings at two sites of tropical forest in French Guyana, suggesting it is a result of negative density-dependence during the sapling-to-adult transition. In contrast, we found no significant differences in the species richness z-scores between size classes of canopy trees; a negative z-score may be considered equivalent to a low species evenness. With such contrasting results, the question of whether communities of tree species in tropical forests become more functionally clustered or overdispersed as individuals grow larger seems to be still unsettled.

Species richness of treelets and shrubs at the smaller size class, and all species at the two smaller size classes, was lower than expected by chance. This means that the observed quadrats had its individuals distributed among less species than expected. As intraspecific differences were null in our analysis, the significant habitat filtering we observed could be a numerical artifact. Nevertheless, intraspecific variation is typically much lower than interspecific variation in the traits we measured (Ackerly et al. 2002, Shipley and Almeida-Cortez 2003, Swenson and Enquist 2007a), so we suggest that at least a part of the habitat filtering effect is due to a combination of species-habitat association (*this thesis, chapter 2)* and low intraspecific trait variation. Some of the most abundant shrubs present at the site seems to be capable of spreading by clonal growth (*Psychotria* spp., *Begonia hookeriana*, *Piper* spp.; C. Corrêa, *personal communication*; Kinsman 1990), which potentially render these species capable of active habitat selection (Bazzaz 1991), facilitating spatial aggregation.

While canopy trees displayed no apparent change in the pattern of traits co-occurrence, shrubs and treelets showed an apparent significant filtering at the two smaller size bins which disappeared at the largest size bin. Maximum height of a species is related to crown and trunk allometries: shrubs and understory treelets have thicker trunks and wider, deeper crowns, than canopy trees of similar height (King 1990, Nicola and Pickett 1983, Poorter et al. 2003). Thus, the disappearance of a filtering effect in treelets and shrubs may be related to an increase in competitive interactions between individuals with wide crowns as they grow, which could lead to character displacement by phenotypic plasticity.

Uriarte et al. (2004), studying neighborhood effects on sapling growth for 60 species at Barro Colorado Island, Panama, have shown that more than half of the species respond to crowding, independently of neighbor identity. Additionally, survival of saplings and trees are strongly affected by crowding (Hubbell et al. 2001). This could be an explanation for the general lack of change in functional clustering along size classes, given that most species would be excluded (or, alternatively, blocked from entering the next size class) irrespective of the functional traits of neighbors. Aditionally, individual tree and shrub survival are affected by stem density up to a distance of 50 m (Hubbell et al. 2001), a much greater distance than the quadrat size of 10 x 10 m that we sampled. Thus, we suggest that a temporal analysis of growth and survival over a large spatial scale, coupled with information on functional traits, is needed to further our understanding of the dynamics of community assembly on the Atlantic rain forest.

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Discussão Geral

Discussão Geral

O presente estudo foi realizado dentro do âmbito de um Projeto Temático (Joly e Martinelli 2006), que teve como objetivo estudar a estrutura e o funcionamento da Foresta Ombrófila Densa Atlântica ao longo de um gradiente de altitude na Serra do Mar. O desenho amostral geral do Projeto Temático contava com quatro parcelas de 1 ha em cada cota altimétrica. Por questões logísticas, entretanto, durante a realização do presente estudo foi amostrada apenas uma parcela por cota (*capítulos 1 e 2 desta tese*) e, portanto, não há réplicas verdadeiras nas comparações entre elas. Por esse motivo, é difícil chegar a conclusões fortes acerca da variação de atributos funcionais ou estrutura da comunidade ao longo do gradiente altimétrico. Entretanto, os resultados dos capítulos 1 e 2 nos levam a crer que não há grande variação, em termos tanto de estrutura filogenética quanto de estrutura baseada em atributos, entre comunidades de plantas lenhosas de sub-bosque ao longo do trecho de gradiente altitudinal amostrado. Por outro lado, os resultados do capítulo 3 no permitem sugerir que esse mesmo padrão é mantido na estruturação das árvores de dossel. Entretanto, seria proveitoso analisar a estrutura filogenética de todas as parcelas levantadas pelo Projeto Temático para responder a essa questão.

A variação altitudinal total contemplada por esse estudo foi de cerca de 1000 m, o que pode ser considerada uma variação pequena (Körner 2007), especialmente considerando-se que há montanhas tropicais com mais de 2500 m de altitude (Leuschner 2000). Florestas Montanas, em geral, têm árvores de menor porte e folhas esclerófilas (Grubb 1977, Lieberman *et al.* 1996, Vazquez-G. e Givnish 1998), características atribuídas à menor disponibilidade de nutrientes ou maior déficit de pressão de vapor do ar (Leuschner 2000). No entanto, no curto gradiente da Serra do Mar, Alves et al. (2010) encontraram justamente o padrão oposto: árvores de tamanho comparável, e um aumento de biomassa com a altitude. De maneira geral, a composição de espécies não muda drasticamente ao longo do gradiente; no sub-bosque, há uma substituição de Rubiaceae por Melastomataceae, e um aumento da abundância e riqueza de Monimiaceae e Lauraceae. No entanto, Myrtaceae foi a família mais importante ao longo de todo o gradiente, e poucas famílias ocorreram exclusivamente em um único sítio (ver Fig. 1, Capítulo 1). Além disso, dentre os atributos funcionais apenas a área foliar diferiu entre sítios, sendo significativamente menor na Floresta Montana. Com tais similaridades em termos de estrutura florestal, composição filogenética e atributos funcionais, não surpreende que não tenham sido encontradas diferenças na estrutura de comunidade entre os sítios em diferentes cotas altimétricas, tanto na abordagem filogenética quanto na baseada em atributos funcionais.

No segundo capítulo da tese, discutimos os diferentes papéis de espécies localmente comuns e raras na estruturação da comunidade. Espécies localmente comuns apresentam uma aparente especialização ambiental, especialmente em relação a aspectos da microtopografia; em outras palavras, espécies comuns parecem se segregar espacialmente, de maneira determinada por diferenças entre seus atributos funcionais. Por outro lado, espécies localmente raras, quando tomadas em conjunto, não apresentaram uma segregação de microhabitat relacionada a diferenças funcionais. É provável que pelo menos parte dessa ausência de correlação entre atributos e ambiente encontrada em espécies raras se dê em função de problemas de amostragem (por exemplo, na determinação de valores médios das espécies). Infelizmente, dado que a maior parte das comunidades ecológicas amostradas (em especial nos trópicos) apresenta o mesmo padrão de poucas espécies comuns e muitas espécies raras, esse é um problema com o qual será necessário lidar. Por um lado, a amostragem de apenas um indivíduo por espécie pode ser adequada, dependendo do objetivo do estudo (e.g. determinação da relação entre atributos funcionais e funcionamento de ecossistemas; Baraloto et al. 2010). Por outro, Magurran e Henderson (2003) demonstraram que as chegadas de espécies raras em uma comunidade estuarina de peixes pode ser modeladas como eventos estocásticos, enquanto que a flutuação de espécies comuns se dá em função de processos determinísticos relacionados ao habitat. Portanto, é possível que uma comunidade local seja formada por um grupo de espécies *core*, localmente abundantes e especialistas, cujas dinâmicas são dirigidas por processos determinísticos, e um grupo de espécies acessórias, generalistas, cujas dinâmicas são dirigidas por processos estocásticos e de dispersão em escala regional.

Scudeller et al. (2001) analisaram padrões de variação florística da Floresta Ombrófila Densa do sudeste do Brasil, e observaram que 77% das espécies (de um total de 771) apresentaram baixa constância, ocorrendo em poucos levantamentos, e distribuição restrita. Algumas espécies, no entanto, apresentaram ampla distribuição, embora geralmente com baixa abundância local (Scudeller et al. 2001); estas seriam boas candidatas a serem consideradas espécies generalistas, regidas por processos estocásticos de dispersão em escala regional.

No terceiro capítulo da tese, analisamos a variação do efeito da filtragem ambiental e da competição entre espécies sobre a estrutura da comunidade baseada em atributos funcionais em coortes de espécies de diferentes tamanho, levando em consideração ora todas as espécies presentes na comunidade, ora apenas as árvores de dossel. Para isso, utilizamos dados de atributos funcionais de indivíduos jovens para suprir a ausência de dados referentes a indivíduos adultos; para um subconjunto de espécies arbóreas, observamos uma boa correlação entre os dados de indivíduos jovens e adultos. No entanto, a obtenção de um conjunto extenso de dados de indivíduos adultos, especialmente se a variação intraespecífica fosse contemplada, seria preciosa para chegarmos a conclusões mais precisas acerca do processo de estruturação da comunidade. De qualquer maneira, observamos um efeito significativo da filtragem ambiental nas coortes de menor tamanho (diâmetro à altura do peito, DAP, < 5 cm), e a dissipação desse efeito nas coortes com DAP > 5 cm, indicando que talvez o efeito inicial da filtragem ambiental seja contrabalançada por um posterior deslocamento competitivo e/ou mortalidade denso-dependente (*e.g.* causada por herbivoria ou patógenos). No entanto, observações de coortes estáticas podem não se traduzir perfeitamente na dinâmica temporal da comunidade.

Portanto, sugerimos que o processo de montagem de comunidades pode ser melhor compreendido com a inclusão simultânea de diversas escalas espaciais, afim de determinar componentes determinísticos locais e e estocásticos regionais, e a observação direta da dinâmica temporal de crescimento e mortalidade de indivíduos.

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Anexo: Lista de espécies amostradas em três parcelas ao longo de um gradiente altitudinal em Floresta Ombrófila Densa Atlântica no Parque Estadual da Serra do Mar, São Paulo, Brasil. Os números sob os cabeçalhos **TB** (Terras Baixas, 70 m de altitude), **SM** (Submontana, 370 m) e **M** (Montana, 1070 m) indicam o número de indivíduos observados para cada espécie. Valores em negrito indicam as espécies mais abundantes em cada sítio. A altura máxima, H_{MAX}, de cada espécie, é dada, assim como a fonte de onde foi extraída essa informação (1, base de dados do projeto Biota Gradiente Funcional; 2, a série "Flora Fanerogâmica do estado de São Paulo"; 3, observações diretas em campo.

Família	**Espécie**	**TB**	**SM**	**M**	**H_{MAX}**	**fonte**
Annonaceae	*Guatteria australis* A. St.-Hil.	2	1		13	1
	Guatteria gomeziana A. St.-Hil.			2	18	1
Apocynaceae	*Malouetia arborea* (Vell.) Miers		1		18	1
	Tabernaemontana laeta Mart.	1	2		10	1
Araliaceae	*Schefflera calva* (Cham.) Frodin & Fiaschi	1		2	14	1
Begoniaceae	*Begonia hookeriana* Gardner	**8**	**16**		3.4	1
	Begonia sp.			4	1.5	3
Bignoniaceae	*Tabebuia serratifolia* (Vahl) G. Nicholson	1	1		20	1
Boraginaceae	*Cordia taguahyensis* Vell.		2		15	2
	Cordia trichoclada A. DC.			1	6.5	2
Celastraceae	*Maytenus robusta* Reissek	1			15	1
	Salacia grandifolia (Mart.) G. Don	4			8	1
	Salacia sp.			2		
Chrysobalanaceae	*Couepia venosa* Prance		1		13	2
	Hirtella hebeclada Moric. ex DC.		1		16	1
	Licania hoehnei Pilg.		2		30	1
	Licania kunthiana Hook.			**8**	25	2
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi	**13**	**14**	2	17	1
Elaeocarpaceae	*Sloanea guianensis* (Aubl.) Benth.	3	3		24	1
Erythroxylaceae	*Erythroxylum* cf. *speciosum* O.E. Schulz		1		17	1
	Erythroxylum sp.	2	1		14	1
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.			1	23	1
	Pausandra morisiana (Casar.) Radlk.	2			12	1
	Sapium glandulosum (L.) Morong			3	16	1
	Tetrorchidium rubrivenum Poepp.	1		1	15	2
Fabaceae	*Copaifera trapezifolia* Hayne		1		19	1
	Dahlstedtia pinnata (Benth.) Malme	2		7	12	1

	Inga capitata Desv.		3		14	1
	Inga lanceifolia Benth.			1		
	Inga marginata Willd.		1		14	1
	Inga striata Benth.			2	15	1
	Myrocarpus frondosus Allemão	1			16	1
	Swartzia simplex var. grandifolia (Raddi) R.S. Cowan	6			14	1
	Tachigali denudata (Vogel) Oliveira-Filho	1			14	2
	Zollernia ilicifolia (Brongn.) Vogel	2	1		11	1
Lauraceae	*Aniba viridis* Mez		1		15	1
	Cryptocarya mandioccana Meisn.			4	25	1
	Cryptocarya moschata Nees. & Mart.		3		24	2
	Cryptocarya saligna Mez	1			16	1
	Licaria armeniaca (Nees) Kosterm.	1			13	1
	Nectandra membranaceae (Sw.) Griseb.			3	18	1
	Ocotea catharinensis Mez			2		
	Ocotea dispersa (Nees) Mez		1		18	1
	Ocotea elegans Mez			6	19	2
	Ocotea glaziovii Mez	2			20	2
	Ocotea paranapiacabensis Coe-Teixeira		1		15	1
	Ocotea venulosa (Nees) Baitello		2		12	2
	Ocotea sp.			6		
Malpighiaceae	*Byrsonima ligustrifolia* Saint-Hilaire		3		12	1
Malvaceae	*Eriotheca pentaphylla* (Vell.) A. Robyns	3	**27**		23	1
	Quararibea turbinata (Sw.) Poir.		7		15	2
Melastomataceae	*Henrietella glabra* (Vell.) Cogn.		1	1	6	3
	Leandra acutiflora (Naudin) Cogn.		3		6	1
	Leandra cf. dasytricha (A. Gray) Cogn.		1			
	Leandra purpurascens (DC.) Cogn.			**9**		
	Leandra sp. 1	1				
	Leandra sp. 2			2		
	Meriania calyptrata (Naudin) Triana		**16**		7	1
	Miconia cabucu Hoehne			4	12	2
	Miconia dodecandra (Desr.) Cogn.		1		11	1
	Miconia rigidiuscula Cogn.			**13**	10	2
	Miconia sp. 1	1				
	Miconia sp. 2			**10**		
	Ossaea sanguinea Cogn.		1		2	2
Meliaceae	*Cabralea canjerana* (Vell.) Mart.	1		2	20	1

	Cedrela fissilis Vell.		1		25	2
	Trichilia sylvatica C. DC.	2			20	1
Memecylaceae	*Mouriri chamissoana* Cogn.		1	3	12	2
Monimiaceae	*Mollinedia argyrogyna* Perkins		1	**19**	16	2
	Mollinedia blumenaviana Perkins			3		
	Mollinedia engleriana Perkins		3	1	10	1
	Mollinedia gilgiana Perkins		1		28	
	Mollinedia glabra (Spreng.) Perkins			1	10	
	Mollinedia lamprophyla Perkins	1			17	1
	Mollinedia salicifolia Perkins			2	15	
	Mollinedia schottiana (Spreng.) Perkins	7		4	12	1
	Mollinedia uleana Perkins			1	10	1
Moraceae	*Brosimum guianense* (Aubl.) Huber		1		12	1
	Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Wess. Boer	**9**			16	1
	Sorocea hilarii Gaudich.	1	6		17	1
Myristicaceae	*Virola bicuhyba* (Schott ex Spreng.) Warb.	2	4		26	1
	Virola gardneri (A. DC.) Warb.	2	3		25	2
Myrsinaceae	*Ardisia martiana* Miq.	1	7	3	9	1
	Myrsine gardneriana A. DC.			1	17	2
	Myrsine hermogenesii (Jung. Mend. & Bernacci) Freitas & Kinoshita		1		12	1
Myrtaceae	*Calyptranthes grandifolia* O. Berg	1	1		22	1
	Calyptranthes lucida Mart. ex DC.			2	18	1
	Calyptranthes pileata D. Legrand		2		13	
	Calyptranthes strigipes O. Berg	1	3	4	16	1
	Calyptranthes ubatubana Sobral & Rochelle	1	6		10	1
	Calyptranthes sp. K1			4		
	Calyptranthes sp. K2			1		
	Campomanesia sp. 1			1		
	Blepharocalyx sp.1			**14**		
	Eugenia batingabranca Sobral		2		20	1
	Eugenia cf. *cereja* D. Legrand	**8**			14	1
	Eugenia cf. *neoaustralis* Sobral		3		12	1
	Eugenia cuprea (O. Berg) Mattos		2		12	1
	Eugenia excelsa O. Berg	1			13	1
	Eugenia cf. fusca O. Berg	**9**			16	1
	Eugenia linguaeformis O. Berg	1	1		15	1

	Eugenia melanogyna (D. Legrand) Sobral		1		11	1
	Eugenia multicostata D. Legrand		2		7.5	2
	Eugenia oblongata O. Berg.	6	1	2	17	1
	Eugenia plicata Nied.		4		6.5	1
	Eugenia prasina O. Berg	1	4	1	15	1
	Eugenia subavenia O. Berg	1	5	**8**	12	1
	Eugenia sp. 1	5	1		10	1
	Eugenia sp. 2			2		
	Eugenia sp. 3			2		
	Eugenia sp. 4			5		
	Eugenia sp. J1		4			
	Eugenia sp. J2		1			
	Gomidesia blanchetiana O. Berg	**13**		1	9	1
	Gomidesia sp. J1		**11**			
	Gomidesia sp. J2		1			
	Marlierea cf. *obscura* O. Berg			4	14	1
	Marlierea glazioviana Kiareskou		1		15	1
	Marlierea suaveolens Cambess.		1		10	1
	Marlierea silvatica (Gardner) Kiaersk.	1			18	1
	Marlierea tomentosa Cambess.	1	4		19	1
	Marlierea sp. K1			1		
	Myrceugenia glaucescens (Cambess.) D. Legrand & Kausel			1		
	Myrcia cf. *anacardiifolia* Gardner			1		
	Myrcia cf. *splendens* (Sw.) DC.			3	19	
	Myrcia guianensis (Aubl.) DC.			5		
	Myrcia spectabilis DC.	1			16	1
	Myrcia tijucensis Kiaersk			**18**		
	Myrciaria floribunda (H. West ex Willd.) O. Berg	2		1	15	1
	Neomitranthes glomerata (D. Legrand) D. Legrand		2	1	18	2
	Myrtaceae sp.			2		
Nyctaginaceae	*Guapira areolata* (Heimerl) Lundell			**28**	10	1
	Guapira opposita (Vell.) Reitz	**13**	4	**14**	18	2
Ochnaceae	*Ouratea multiflora* (Pohl.) Engl.	1	5	3	15	
	Ouratea parviflora Baill.	7			9	1
	Ouratea verticillata (Vell.) Engl.	**15**			4	3
Olacaceae	*Heisteria silvianii* Schwacke		2		16	1
	Tetrastylidium engleri Schwacke	6			21	1

Phyllanthaceae	*Phyllanthus* sp.	**25**			3	3
Picramniaceae	*Picramnia ciliata* Mart.		1		7	1
Piperaceae	*Piper malacophyllum* (C. Presl) C.DC.	1			1.5	1
	Piper scutifolium Yunck.		3		1.5	
	Piper setebarraense E.F.Guim. & L.H.P.Costa		4		2	1
	Piper xylosteoides (Kunth.) Steudel		2		5	1
	Piper sp. J1		2			
	Piper sp. E1	3				
	Piper sp. K1			1		
	Piper sp. K2			3		
	Piper sp. K3			**8**		
Polygonaceae	*Coccoloba glaziovii* Lindau			2	8	1
Proteaceae	*Roupala brasiliensis* Klotzsch		9	3	20	2
Rosaceae	*Prunus myrtifolia* (L.) Urb.			1	15	2
Rubiaceae	*Bathysa australis* (A. St.-Hil.) Benth. & Hook. f.	4		2	16	1
	Bathysa mendoncaei K. Schum.	3	**12**		18	1
	Coussarea accedens Müll. Arg.	5	1		13	1
	Coussarea meridionalis var. porophylla (Vell.) Müll. Arg.	2	**18**		15	1
	Faramea picinguabae M. Gomes	**8**			8	2
	Faramea pachyanta Müll. Arg.		8		20	1
	Posoqueria latifolia (Rudge) Roem. & Schult		1	1	14	2
	Psychotria birotula L.B.Sm. & Downs	7	1		6.5	1
	Psychotria nemorosa Gardner			**8**	4	2
	Psychotria hastisepala Müll. Arg.		**34**		3.3	1
	Psychotria leitana C.M.Taylor	**23**	**106**		3.7	1
	Psychotria nuda (Cham. & Schltdl.) Wawra	**17**	**10**		8	1
	Psychotria patentinervia Müll. Arg.		1		5	2
	Psychotria suterella Müll. Arg.			2	4	2
	Psychotria vellosiana Benth.			5		
	Psychotria sp. 2			2		
	Psychotria sp. 3			4		
	Psychotria sp. 4			4		
	Randia armata (Sw.) DC.	1	1		12	2
	Rudgea vellerea Müll. Arg.	7	1		9	1
	Rudgea coriacea (Spreng.) K.Schum.		1		7	2
	Rudgea coronata ssp. leiocarpoides (Müll. Arg.) Zappi	1		2	8	1
	Rudgea jasminoides (Cham.) Müell. Arg.		5	2	10	1

	Rustia formosa (Cham. & Schltdl. ex DC.) Klotzsch	2	2		18	1
	Sabicea grisea Cham. & Schltdl.	3			3	2
Sapindaceae	*Cupania oblongifolia* Mart.		1		20	1
	Cupania vernalis Cambess.		1	3	14	1
	Matayba guianensis Aubl.		1		14	1
Sapotaceae	*Chrysophyllum flexuosum* Mart.		1		15	1
	Chrysophyllum viride Mart. & Eichler	1	1	**11**	15	1
	Ecclinusa ramiflora Mart.	2	3		20	1
	Micropholis compta Pierre		1		12	1
	Pouteria caimito (Ruiz & Pav.) Radlk.		1	1	24	2
	Pouteria psammophylla (Mart.) Radlk.		2		20	1
	Pouteria venosa (Mart.) Baehni		1	1	14	1
Solanaceae	*Solanum* sp.			6		
Winteraceae	*Drymis brasiliensis* Miers			1	8	2